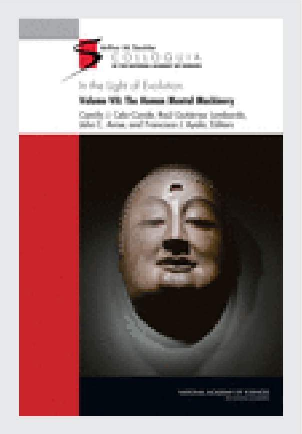


In the Light of Evolution: Volume VII: The Human Mental Machinery

DETAILS

394 pages | 6 x 9 | HARDBACK
ISBN 978-0-309-29640-3 | DOI 10.17226/18573

AUTHORS

Camilo J. Cela-Conde, Raul Gutierrez Lombardo, John C. Avise, and Framcosco J. Ayala, Editors; Arthur M. Sackler Colloquia of the National Academy of Sciences; National Academy of Sciences

In the Light of Evolution

Volume VII: The Human Mental Machinery

In the Light of Evolution

Volume VII: The Human Mental Machinery

CAMILO J. CELA-CONDE, RAÚL GUTIÉRREZ LOMBARDO,
JOHN C. AVISE, and FRANCISCO J. AYALA, *Editors*

NATIONAL ACADEMY OF SCIENCES
THE NATIONAL ACADEMIES

THE NATIONAL ACADEMIES PRESS
Washington, D.C.
www.nap.edu

THE NATIONAL ACADEMIES PRESS 500 Fifth Street, NW Washington, DC 20001

This volume is based on the Arthur M. Sackler Colloquium of the National Academy of Sciences, "The Human Mental Machinery," held January 11–12, 2013, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, California.

The articles appearing in these pages were contributed by speakers at the colloquium and have been anonymously reviewed. Any opinions, findings, conclusions, or recommendations expressed in this volume are those of the authors and do not necessarily reflect the view of the National Academy of Sciences.

In the light of evolution / John C. Avise and Francisco J. Ayala, editors.
p. cm.
Vol. I based on a colloquium of the National Academy of Sciences, held December 1–2, 2006, in Irvine, California.
Includes bibliographical references.
ISBN-13: 978-0-309-29640-3
ISBN-10: 0-309-29640-4
1. Evolution (Biology)—Congresses. I. Avise, John C, 1948–. II. Ayala, Francisco José, 1934–.
III. National Academy of Sciences (U.S.)
QH359.I55 2007
576.8—dc22
2007032455

Additional copies of this book are available from the National Academies Press, 500 Fifth St., N.W., Lockbox 285, Washington, DC 10055; (800) 624-6242 or (202) 334-3313 (in the Washington metropolitan area); Internet, http://www.nap.edu.

Cover image: Evoking a sense of beauty and wonder, this limestone carving of Buddha's head is thought to have been part of a monumental statue from the cave temples of Xiangtangshan in China. Aesthetic values are one of the unique mental traits of humans, along with others such as self-reflection and ethics. Understanding the brain processes behind these traits and how they evolved is the topic of the Sackler Colloquium, In the Light of Evolution VII: The Human Mental Machinery. Photograph by John Tsantes (Image used with permission from the Freer Gallery of Art and the Arthur M. Sackler Gallery, Smithsonian Institution, Washington, DC).

Printed in the United States of America

THE NATIONAL ACADEMIES

Advisers to the Nation on Science, Engineering, and Medicine

The **National Academy of Sciences** is a private, nonprofit, self-perpetuating society of distinguished scholars engaged in scientific and engineering research, dedicated to the furtherance of science and technology and to their use for the general welfare. Upon the authority of the charter granted to it by the Congress in 1863, the Academy has a mandate that requires it to advise the federal government on scientific and technical matters. Dr. Ralph J. Cicerone is president of the National Academy of Sciences.

The **National Academy of Engineering** was established in 1964, under the charter of the National Academy of Sciences, as a parallel organization of outstanding engineers. It is autonomous in its administration and in the selection of its members, sharing with the National Academy of Sciences the responsibility for advising the federal government. The National Academy of Engineering also sponsors engineering programs aimed at meeting national needs, encourages education and research, and recognizes the superior achievements of engineers. Dr. C. D. Mote, Jr., is president of the National Academy of Engineering.

The **Institute of Medicine** was established in 1970 by the National Academy of Sciences to secure the services of eminent members of appropriate professions in the examination of policy matters pertaining to the health of the public. The Institute acts under the responsibility given to the National Academy of Sciences by its congressional charter to be an adviser to the federal government and, upon its own initiative, to identify issues of medical care, research, and education. Dr. Harvey V. Fineberg is president of the Institute of Medicine.

The **National Research Council** was organized by the National Academy of Sciences in 1916 to associate the broad community of science and technology with the Academy's purposes of furthering knowledge and advising the federal government. Functioning in accordance with general policies determined by the Academy, the Council has become the principal operating agency of both the National Academy of Sciences and the National Academy of Engineering in providing services to the government, the public, and the scientific and engineering communities. The Council is administered jointly by both Academies and the Institute of Medicine. Dr. Ralph J. Cicerone and Dr. C. D. Mote, Jr., are chair and vice chair, respectively, of the National Research Council.

www.national-academies.org

Arthur M. Sackler, M.D.
1913–1987

Born in Brooklyn, New York, Arthur M. Sackler was educated in the arts, sciences, and humanities at New York University. These interests remained the focus of his life, as he became widely known as a scientist, art collector, and philanthropist, endowing institutions of learning and culture throughout the world.

He felt that his fundamental role was as a doctor, a vocation he decided upon at the age of four. After completing his internship and service as house physician at Lincoln Hospital in New York City, he became a resident in psychiatry at Creedmoor State Hospital. There, in the 1940s, he started research that resulted in more than 150 papers in neuroendocrinology, psychiatry, and experimental medicine. He considered his scientific research in the metabolic basis of schizophrenia his most significant contribution to science and served as editor of the *Journal of Clinical and Experimental Psychobiology* from 1950 to 1962. In 1960 he started publication of *Medical Tribune*, a weekly medical newspaper that reached over one million readers in 20 countries. He established the Laboratories for Therapeutic Research in 1938, a facility in New York for basic research that he directed until 1983.

As a generous benefactor to the causes of medicine and basic science, Arthur Sackler built and contributed to a wide range of scientific institutions: the Sackler School of Medicine established in 1972 at Tel Aviv University, Tel Aviv, Israel; the Sackler Institute of Graduate Biomedical Science at New York University, founded in 1980; the Arthur M. Sackler Science Center dedicated in 1985 at Clark University, Worcester, Massachusetts; and the Sackler School of Graduate Biomedical Sciences, established in 1980, and the Arthur M. Sackler Center for Health Communications, established in 1986, both at Tufts University, Boston, Massachusetts.

His pre-eminence in the art world is already legendary. According to his wife Jillian, one of his favorite relaxations was to visit museums and art galleries and pick out great pieces others had overlooked. His interest in art is reflected in his philanthropy; he endowed galleries at the Metropolitan Museum of Art and Princeton University, a museum at

Harvard University, and the Arthur M. Sackler Gallery of Asian Art in Washington, D.C. True to his oft-stated determination to create bridges between peoples, he offered to build a teaching museum in China, which Jillian made possible after his death, and in 1993 opened the Arthur M. Sackler Museum of Art and Archaeology at Peking University in Beijing.

In a world that often sees science and art as two separate cultures, Arthur Sackler saw them as inextricably related. In a speech given at the State University of New York at Stony Brook, *Some reflections on the arts, sciences and humanities*, a year before his death, he observed: ''Communication is, for me, the *primum movens* of all culture. In the arts . . . I find the emotional component most moving. In science, it is the intellectual content. Both are deeply interlinked in the humanities.'' The Arthur M. Sackler Colloquia at the National Academy of Sciences pay tribute to this faith in communication as the prime mover of knowledge and culture.

Contents

Preface to the *In the Light of Evolution* Series

Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two urgent challenges, and opportunities, for 21st-century science are to gain deeper insights into the evolutionary processes that foster biotic diversity, and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought also extend into learned realms traditionally reserved for philosophy and religion.

In 1973, Theodosius Dobzhansky penned a short commentary entitled "Nothing in biology makes sense except in the light of evolution." Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have often been neglected, misunderstood, or purposefully misrepresented.

The central goal of the *In the Light of Evolution* (*ILE*) series is to promote the evolutionary sciences through state-of-the-art colloquia—in the series of Arthur M. Sackler colloquia sponsored by the National Academy of Sciences—and their published proceedings. Each installment explores evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the *ILE* series aims to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

The organizers and founding editors of this effort (Avise and Ayala) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory this *ILE* series is dedicated. May Dobzhansky's words and insights continue to inspire rational scientific inquiry into nature's marvelous operations.

John C. Avise and Francisco J. Ayala
Department of Ecology and Evolutionary Biology,
University of California, Irvine (January 2007)

Preface to *In the Light of Evolution, Volume VII: The Human Mental Machinery*

This book is the outgrowth of the Arthur M. Sackler Colloquium "The Human Mental Machinery," which was sponsored by the National Academy of Sciences on January 11–12, 2013, at the Academy's Arnold and Mabel Beckman Center in Irvine, CA. It is the seventh in a series of colloquia under the general title "*In the Light of Evolution*." The first six books in this series were titled *Adaptation and Complex Design* (Avise and Ayala, 2007), *Biodiversity and Extinction* (Avise et al., 2008), *Two Centuries of Darwin* (Avise and Ayala, 2009), *The Human Condition* (Avise and Ayala, 2010), *Cooperation and Conflict* (Strassmann et al., 2011), and *Brain and Behavior* (Striedter et al., 2013).

In his Notebook C, Darwin gave us one of his first insights into human nature. There, referring to the human being, Darwin wrote:

> He is Mammalian—his origin has not been indefinite—he is not a deity, his end under present form will come, (or how dreadfully we are deceived) then he is no exception.—he possesses some of the same general instincts, & moral feelings as animals.—they on the other hand cannot reason—but Man has reasoning powers in excess. Instead of definite instincts—this is a replacement in mental machinery—so analogous to what we see in bodily, that it does not stagger me. (Darwin, 1836–1844)

As Darwin noted, our mental machinery makes us different. For instance, it allows us to ask about ourselves, about what a human is. It enables us to question what we are and the ways in which we reached our current nature. One thing we have discovered is that humans possess certain unique mental traits. Self-reflection, as well as ethic and aesthetic values, is among them, constituting an essential part of what we call the human condition. The human mental machinery led our species to have a self-awareness but, at the same time, a sense of justice, willing to punish unfair actions even if the consequences of such outrages harm our own interests. Also, we appreciate searching for novelties, listening to music, viewing beautiful pictures, or living in well-designed houses.

But why is this so? What is the meaning of our tendency, among other particularities, to defend and share values, to evaluate the rectitude of our actions and the beauty of our surroundings? The human mental machinery obviously refers to the brain, so the answer to the preceding questions must come from neural considerations. What brain mechanisms correlate with the human capacity to maintain inner speech, or to carry out judgments of value? To what extent are they different from other primates' equivalent behaviors?

This collection of colloquium papers aims to survey what has been learned about the human "mental machinery" since Darwin's insights. The colloquium brought together leading scientists who have worked on brain and mental traits. Their 16 contributions focus the objective of better understanding human brain processes, their evolution, and their eventual shared mechanisms with other animals. The articles are grouped into three primary sections: current study of the mind–brain relationships; the primate evolutionary continuity; and the human difference: from ethics to aesthetics.

The explicit objective of this colloquium—improving our knowledge of the content of Darwin's mental machinery—constitutes an endless task. However, this book offers fresh perspectives coming from interdisciplinary approaches that open new research fields and constitute the state of the art in some important aspects of the mind–brain relationships. An intriguing contradiction seems sketched from the contributions to the colloquium. On the one hand, continuity at least exists between the mental machinery of humans and nonhuman primates. On the other hand, humans manifest conspicuous evolutionarily derived (i.e., exclusive) mental/neural traits. Darwin himself solved this apparent paradox. In chapters III, IV, and V of the *Descent of Man*, Darwin (1871) holds that human moral and mental faculties differ from those of animals, but not in an essential form. Coming back again to the Notebook C annotation (Darwin, 1836–1844), "[Man] possesses some of the same general instincts, & moral feelings as animals . . . but Man has reasoning powers in excess . . . this is a replacement in mental machinery."

Part I

CURRENT STUDY OF THE MIND–BRAIN RELATIONSHIPS

John Searle opens the proceedings with a philosophical introduction to the still-elusive question of consciousness. To discuss the eventual scientific approach to a theory of mind (ToM), the author analyzes the relationships between subjective feelings, such as mental issues, and objective (i.e., scientific) approaches to them. Distinguishing between ontologic and epistemic approaches to the subjectivity/objectivity issue, Searle holds that mental issues, such as consciousness, can be scientifically reached, concluding in this way: "I think the future of this entire discussion we have been having [in the colloquium] lies in a better understanding of the brain." Indeed, this is the objective that initially led to the organization of this Sackler Colloquium.

ToM is also the approach chosen by Robert Seyfarth and Dorothy Cheney in Chapter 2. As the authors state, a subconscious, reflexive appreciation of others' intentions, emotions, and perspectives lies at the roots of human ToM. The adaptive advantages of an attribution of thoughts and intentions to predict others' behavior mainly consist of helping to form strong, permanent social bonds. Empirical study of monkeys' relationships shows these bonds. Following this point, Seyfarth and Cheney give data on different kinds of social challenges among female baboons that are better solved by means of affiliative behavior.

Even if ToM is a good hypothesis to link close social relationships to mental constructs and reproductive success, an eventual border might separate human consciousness from nonhuman primates' more "instinctive" behaviors. George Mashour and Michael Alkire focus on this eventual difference in Chapter 3. On the grounds of a comparative review of neurobiology, psychology, and anesthesiology, the authors hold that the basic neurophysiologic mechanisms supporting consciousness in humans are found at the earliest points of vertebrate brain evolution. Mashour and Alkire propose to study this evolution by means of models coming from the recovery of consciousness after general anesthesia in animals.

1

Theory of Mind and Darwin's Legacy

JOHN SEARLE

We do not have an adequate theory of consciousness. Both dualism and materialism are mistaken because they deny consciousness is part of the physical world. False claims include (*i*) behaviorism, (*ii*) computationalism, (*iii*) epiphenomenalism, (*iv*) the readiness potential, (*v*) subjectivity, and (*vi*) materialism. Ontological subjectivity does not preclude epistemic objectivity. Observer-relative phenomena are created by consciousness, but consciousness is not itself observer relative. Consciousness consists of feeling, sentience, or awareness with (*i*) qualitativeness, (*ii*) ontological subjectivity, (*iii*) unified conscious field, (*iv*) intentionality, and (*v*) intentional causation. All conscious states are caused by lower level neurobiological processes in the brain, and they are realized in the brain as higher level features. Efforts to get a detailed scientific account of how brain processes cause consciousness are disappointing. The Darwinian revolution gave us a new form of explanation; two levels were substituted: a causal level, where we specify the mechanism by which the phenotype functions, and a functional level, where we specify the selectional advantage that the phenotype provides. Sociobiology attempted to explain general features of human society, ethics, etc. It failed. For the incest taboo, it confuses inhibition with prohibition. It did not explain the moral force of the taboo. To explain the function of consciousness we cannot ask, "What would be subtracted if we subtracted consciousness but left everything else the same?" We cannot leave everything else the same because consciousness is necessary

---

Department of Philosophy, University of California, Berkeley, CA 94720. E-mail: searle@berkeley.edu.

for higher functions of human and animal life. The unified conscious field gives the organism vastly increased power.

I have two objectives in this article: I want first to say something about our current understanding of the nature of the mind, particularly consciousness; and, secondly, I want to relate my account of the mind to Darwinian evolution. Many of the ideas in this chapter have appeared in preliminary form by me in various books and articles; particularly significant are Searle (1992, 1996, 2005).

THE "SCANDAL" OF CONSCIOUSNESS

Consciousness is something of a scandal because we do not have an adequate neurobiological theory of consciousness, and there are a rather large number of false claims made about it. Here, for a start, are half a dozen false claims made about consciousness in my intellectual lifetime. Several of these have been widespread and extremely influential.

Behaviorism

Consciousness as traditionally construed does not really exist, but rather there are just human and animal behaviors and dispositions to behavior (Skinner, 1992).

Computationalism (Strong Artificial Intelligence)

Consciousness as such does not really exist but is rather a program or a set of computer programs running in the brain (Minsky and Papert, 1987).

Epiphenomenalism

Consciousness does exist, but it cannot have any real effect on the world because it is a nonphysical phenomenon and as such cannot affect the physical world. It must be an epiphenomenon because the physical world is "causally closed." From an evolutionary point of view, it has no function (Chalmers, 1996).

The Readiness Potential

Consciousness does exist, but it has very little importance because research on the readiness potential in the supplementary motor cortex shows that our actions are initiated before our becoming consciously aware of what we are doing. The brain decides to perform an action before the conscious mind can be aware of it (Libet et al., 1983).

Objectivity and Subjectivity

Consciousness is not a suitable subject for serious scientific investigation; it is better left to theologians and philosophers. The reason is that science is by definition objective, and consciousness is by definition subjective; therefore, there cannot be a science of consciousness. This view is part of the oral tradition. When I was first interested in the neurobiology of consciousness, I discussed the issue with several neurobiologists, in both Europe and the United States. Several assured me that consciousness is not a suitable subject for serious scientific investigation because of its subjectivity.

Materialism

If consciousness is real, it must really be something else because the final inventory of the basic ontology of the world—an inventory that includes subatomic particles, gravity, electromagnetism, the weak and strong nuclear forces, and other fundamental features of reality—is entirely material and so will not include consciousness (Dennett, 1991).

I will argue that consciousness is a real biological phenomenon in the same sense as photosynthesis or digestion, and that all six of these views are more or less demonstrably false. However, that raises an interesting question: Why is there so much confusion about consciousness?

Why is it so hard for people to accept a naturalistic conception? We are the victims of two traditions that appear to be inconsistent with each other, but in fact they trade off on each other. One is the tradition of God, the soul, and immortality that says consciousness is not a part of the natural world. Consciousness is not even a property of the body or the brain. On the Cartesian view, it is a property of the soul and the soul is definitely not a part of the natural world. This thesis is why, incidentally, Descartes (1996) was forced to say that animals are not conscious because all the animal has got is a body. For Descartes, our bodies are not conscious, our brains are not conscious; only the soul is conscious. Now you might think that tradition is entirely dead, but it is not. Artificial intelligence (AI) in its strong AI version is an expression of the idea that the mind is not a part of the natural world. One of the adherents of the strong AI view wrote that the mind is something formal and abstract (Dennett and Hofstadter, 1981). The second tradition is usually mistakenly described as "materialism," and often its adherents simply deny that consciousness as qualitative, subjective states really exists. An extreme statement was given by John B. Watson, one of the founders of behaviorism: "the time has come for psychology to discard all reference to consciousness . . . it is neither a definable nor a usable concept, it is merely another word for the 'soul' of more ancient times. . ." (Watson, 1925).

Both traditions share a resistance to treating real consciousness—qualitative, subjective consciousness—as a real biological feature of the world.

OBJECTIVITY, SUBJECTIVITY, AND OBSERVER RELATIVITY

Before refuting these views and giving an account of consciousness, I need to make some distinctions. First, the distinction between objectivity and subjectivity looms very large in our intellectual culture, but unfortunately it is systematically ambiguous between an epistemic sense and an ontological sense ("epistemic" means having to do with knowledge and "ontological" means having to do with existence).

Epistemically, the distinction is between types of claims, those that can be settled as a matter of "objective fact" and those that cannot be so settled. So, if I say Van Gogh died in France, that is epistemically objective. You can settle that as a matter of objective fact. If I say Van Gogh was a better painter than Gauguin, that, as people like to say, is a matter of "subjective opinion." It cannot be settled as a matter of objective fact. However, in addition to that distinction, there is an underlying ontological distinction between modes of existence. Some entities have a mode of existence that is independent of anybody's attitudes or consciousness. Mountains, molecules, and tectonic plates are in that sense ontologically objective. However, some entities depend for their very existence on being experienced by a human or animal subject. In this sense, pains, tickles, and itches are ontologically subjective. Why is this distinction important? It is of crucial importance because the ontological subjectivity of a domain does not preclude epistemic objectivity of a science of that domain. You can have a completely adequate science of consciousness or mental life in general that is epistemically objective even though the entire domain is ontologically subjective.

Related to the distinction between objectivity and subjectivity is the distinction between those features of the world whose existence depends on human attitudes and those features that exist independently of anyone's attitudes. I call the former "observer relative" and the latter "observer independent" or "absolute." Observer-relative phenomena include money, property, marriage, nation states, universities, and summer vacations. Observer-independent phenomena include mountains, molecules, galaxies, and tectonic plates. In general, the natural sciences deal with observer-independent phenomena; the social sciences deal with observer-relative phenomena. The observer relativity of a phenomenon introduces an element of ontological subjectivity into its very existence. So the existence of money and language, for example, is observer relative and consequently contains an element of ontological subjectivity. However, and this is a crucial point, as we have already seen, the ontological subjectivity of a domain does not preclude an epistemically objective science of that domain. There can be epistemically objective sciences of economics and linguistics, although the objects of study of the disciplines are for the most part observer relative and thus at least in part ontologically subjective. All observer-relative phenomena are created by consciousness, but the consciousness that creates them is absolute and not observer relative. I will say something about the role of the unconscious later.

These distinctions already will enable us to answer several of the mistaken theories about consciousness. However, before I do that, I want to address the analysis of consciousness directly.

ANALYSIS OF CONSCIOUSNESS

What is consciousness? What are its features? Where do we stand in its scientific investigation? It is often said consciousness is hard to define. I do not think it is hard to define. We need to make a distinction between the scientific definition that comes at the end of an investigation and the commonsense definition that enables us to identify the target of the investigation. Think of water: the commonsense definition is that it is a clear, colorless, and tasteless liquid that flows in rivers and exists in lakes and falls out of the sky in the form of rain. The scientific definition comes at the end of the investigation: it is H_2O. With consciousness, we are still in the clear, colorless, tasteless liquid stage, and that is the sort of definition I am going to give you. Consciousness consists of all of our states of feeling or sentience or awareness. It begins when we wake from a dreamless sleep and continues until we go to sleep again or die or otherwise become unconscious. On this definition, dreams are a form of consciousness.

This then is the definition of consciousness. What are some of its features? There are many features, but, for the sake of brevity, I will confine myself to the five most important.

Qualitativeness

For every conscious state, there is a qualitative feel to that state, something it feels like to be in that state. Think of the difference between drinking wine, listening to music, and working on your income tax. Qualitativeness is not just a feature of bodily sensations and emotions but characterizes thought as well. You can see that the thought that 2 + 2 = 4 has a certain characteristic feel if you try thinking the same thought in French or German. To me at least, it just feels different.

Ontological Subjectivity

Because of this qualitative character, every conscious experience is ontologically subjective. It exists only insofar as it is experienced by a human or animal subject. This feature makes consciousness seem intractable; it makes it seem a difficult subject for scientific study.

Unity

A third feature of consciousness is that there is a remarkable unity to our conscious states. In giving a lecture, I do not just hear the sound of my voice and see the people in the audience and feel a slight headache from the wine I drank the night before; but I have all of those as part of a single unified conscious field. When we get to the topic of evolution, we will see the centrality of unity in enabling consciousness to perform its biological functions. You never just have a single conscious experience such as the taste of the wine or the smell of the rose, but each such experience occurs as part of a total large conscious experience, which consists of the entire ontologically subjective field of consciousness occurring at that moment.

I used to think that qualitativeness, subjectivity, and unity were separate features, but I now think they are just different aspects of the same feature, and it is the essence of consciousness. You cannot have qualitativeness without subjectivity and you cannot have subjectivity without unity. This feature, incidentally, is why the split-brain experiments are so interesting to us: because it looks like the unity of consciousness is partly disrupted if you cut the corpus callosum. So those are all three aspects of one feature, and it is the essence of consciousness.

There are two other features I want to mention.

Intentionality

Intentionality is that feature of the mind by which it is directed at objects and states of affairs (intending in the ordinary sense is just one type of intentionality, along with perception, belief, desire, fear, the emotions, etc.). Not all conscious states are intentional. Think of undirected anxiety, for example. However, most of them are, and this feature is really what gives importance to the previous features because intentionality is the way that the conscious organism has of relating to the environment.

Intentional Causation

The conscious mind functions causally in producing behavior, and, in conscious perception, the environment is causally presented to the consciousness of the agent. For example, in the presence of food, light reflected off the object will cause a conscious visual experience in the animal, and this experience will consciously motivate the animal to move toward the food.

SOLUTION TO THE "MIND–BODY PROBLEM"

Suppose that I am right so far and that consciousness consists of unified, qualitative subjectivity and that it enables us to cope with the environment by way of intentionality and intentional causation. How does such a phenomenon fit in with what we know about the rest of the universe? This, you will no doubt recognize, is the traditional mind–body problem. It is supposed to be frightfully difficult, maybe impossible, to solve. I think, at the level of the general relationships between the mind and the brain, it has a rather simple solution. The neurobiological solution turns out to be very difficult and complicated, but, at the level of describing the general relationships between consciousness and neurobiology, the solution is not complex. Here it is: all of our conscious states without exception are caused by neurobiological processes in the brain and they are all realized in the brain as higher level or system features. Consciousness is a feature of the brain in a way, for example, that the liquidity of the water is a feature of the system of H_2O molecules. It is not something squirted out by the H_2O molecules; it is the condition that the system of molecules is in. In the same way, my conscious state is the condition that my brain is now in. And just as a body of water can go from a liquid state to a solid state, depending on the behavior of the microelements—the H_2O molecules—so the brain can go from a conscious state to an unconscious state depending on the behavior of the microelements—the neurons.

If that is how it works in general, then why do we not get busy and figure out exactly how it works? Why is progress so slow? I do not know. I was asked to write an article for the *Annual Review of Neuroscience* (Searle, 2000) in which I surveyed a lot of the literature investigating the causation and the realization of consciousness in the brain. And it occurred to me that part of the difficulty is that the research techniques are at present inadequate to address the problems that really bother us. They tend to be either imaging techniques—functional MRI being the most influential, but other forms of scanning are important as well—or they tend to be single cell recordings. And much of the most exciting work, for example on binocular rivalry, tends to be focused on very local neurobiological structures, whereas it seems me that consciousness is more likely to be a global phenomenon. Our present research techniques make it extremely difficult to investigate how consciousness is caused in the brain as a large-scale phenomenon.

I distinguish between what I call the building-block approach, where we think of the total conscious field as made up of a set of separate conscious building blocks such as the specific types of perception, and what I call the unified field approach, where we think of specific stimuli such as perception as modifying a preexisting conscious field. There was a period when it seemed the crucial research task was to discover the neuronal correlate of consciousness. And indeed in this period a lot of neuronal correlates of specific forms of consciousness were discovered. However, these discoveries did not solve the problem of consciousness in a way that some people had hoped. Why not? The research on blind sight or binocular rivalry or gestalt switching was always on subjects who were already conscious. However, it did not answer the question: How does the subject's brain create an entire conscious field to begin with. Two rival pictures of this research exist: one is that perception creates consciousness; the second, to which I adhere, is that we should think of perception as modifying the preexisting conscious field. And the crucial question is: How does the brain create the conscious field?

Think of it this way. Imagine that you awake in a completely dark room in an unfamiliar environment. You can be totally awake and alert although you have zero or minimal perceptual stimuli. If you get up and move about, are you creating consciousness? In a sense, you are because you have conscious states you did not have before. However, I think it is best to think of these experiences as modifying the preexisting conscious field that came into existence when you became fully awake. Most of the research I am familiar with relies either on imaging techniques or single cell recordings. The difficulty is that neither of these seems adequate to get at global properties of the brain, and it may well be the case that the creation of the conscious field requires more powerful techniques than these.

REFUTATION OF THE MISTAKEN VIEWS

I promised at least a brief refutation of the six mistaken theories of consciousness and we now have enough material to do that.

Behaviorism

It should be an embarrassment to us that behaviorism was so influential for so long because it is obviously false. It denies the subjectivity of consciousness. Each of us knows from his or her own experience that our pain is one thing and the observable pain behavior is something else.

Computationalism

We know that the implemented computer program is not by itself sufficient for mental processes, whether conscious or unconscious, because the program is defined purely syntactically in terms of symbol manipulation, whereas mental processes have actual content. Syntax by itself is not sufficient for semantic content. I demonstrated this a generation ago with the so-called Chinese room thought experiment (Searle, 1980). Imagine that you are carrying out the steps in a program for answering questions in Chinese or some other language you do not understand. You might give the right answers, but, all the same, you do not understand Chinese. Carrying out the computational steps is not sufficient for understanding.

I think the argument is conclusive, but the material in this chapter gives us a much deeper argument. Except for computations carried out by a conscious agent, computation is observer relative. You cannot explain consciousness as computation because a process is computational only relative to some conscious agent. Either a conscious agent is carrying out a computation, such as adding 2 + 2 to get 4, or a conscious agent is using or can use a piece of machinery such as a calculator where he can interpret the results as arithmetical. Such computations are always observer relative. And, remember, observer relativity does not imply epistemic subjectivity. It is an epistemically objective fact that I am writing this using the Word program and that the program is implemented electronically, but "Word program" does not name an electrical phenomenon.

Epiphenomenalism

We have literally thousands of years of experiences of human and animal consciousness causing behavior. The problem is to explain how it could, given its subjective ontology. Here is how it works. Consider a simple act like raising my arm. My intention-in-action causes my arm to go up. However, we know independently that anything that causes my arm to go up in that way must cause the secretion of acetylcholine at the axon endplates of the motor neurons. No acetylcholine, no arm going up. However, that means that the conscious intention-in-action has to be a biochemical phenomenon. There is no way it is going to produce the secretion of acetylcholine unless it is itself realized in a biological structure. One in the same event, my conscious intention-in-action has a level of description where it is qualitative, subjective, and part of a unified subjective conscious field, and another level of description where it is a neurobiological process realized in the brain.

Part of our difficulty in understanding this point is that we are stuck with the traditional vocabulary that contains the traditional mistakes, the vocabulary of the mind and body, and dualism and materialism. What I am trying to convey with this very simple example is that, even for very simple conscious activities like raising your arm, the traditional categories are obsolete because you have to have the concept of a single event that has both subjective, qualitative, mentalistic features and biochemical features. And this phenomenon is familiar in nature, that you have the same phenomenon, the same system, with different levels of description. My car engine has a level of description where explosions occur in the cylinder that drives the piston and another level of description where individual hydrocarbon molecules oxidize. We find it difficult to appreciate these levels where the mind is concerned because one of those levels of description has such a sordid history. The dualistic tradition has given the mental level of description a bad name because it makes it appear that our mental life is not part of our ordinary biological existence.

Readiness Potential

In these experiments, subjects were asked to perform a trivial act such as pushing a button and to observe on a clock exactly when they undertook to do it. Some 200–300 ms before they were aware they had decided to do it, there was an increased activity in the supplementary motor area. Incredible claims were made for these data, such as for example that they disproved free will and showed that our brain decides to perform actions before our conscious mind does (Koch, 2012). Recent experiments show that the original experiments were flawed. If you ask the subjects to look at a clock and decide not to perform an action, you get the same readiness potential. As far as we can tell, the readiness potential was produced by watching the clock. Take away the clock and there is no readiness potential (Trevena and Miller, 2010).

I believe the history of the readiness potential is an unfortunate chapter in recent scientific history and it raises the question: Why were people so eager to believe these implausible conclusions? The answer I think is that they wanted to discredit consciousness. Consciousness has typically been an embarrassment to the natural sciences, and, in these cases, it looks like we have scientific proof that consciousness does not really matter very much for our behavior.

Objective/Subjective Argument

This argument is an obvious fallacy of ambiguity over the two senses of objective and subjective that I have explained. Science is indeed epistemically objective. However, there is nothing in epistemic objectivity that prevents the investigation of a domain that is ontologically subjective.

Materialism

These categories of materialism, mentalism, dualism, etc. have all become obsolete. Of course, ultimate reality is as described by the natural sciences and thus is "material." There is nothing in this concept of the material that prevents subjective, qualitative consciousness from being as much a biological phenomenon as digestion, mitosis, or photosynthesis.

THE DARWINIAN REVOLUTION

A remarkable thing about the development of knowledge is that we get not just new explanations but new forms of explanation. And, to me, one of the most fascinating things about the Darwinian revolution is that we got a form of explanation that previously was unknown or certainly unappreciated. The idea was that, in addition to the level of explanation of traditional Aristotelian biology, where you had a teleological explanation of a phenotype, we substituted for that explanation two different levels. Aristotle thought there were such things as final causes, teleological causes, where the explanation is given by specifying the goal, aim, or telos of the phenomenon to be explained. So, if you want to explain why fish have the shape they do, why are fish not shaped the way a brick is shaped, or why plants turn their leaves toward the sun, you point out that the purpose of all of this is to enable the fish to swim better or enable the plant to survive. And it is this teleological goal that provides the explanation. The Darwinian revolution produced a substitution of two different levels of explanation. Instead of saying the plant turned its leaves toward the sun because it has the goal of survival, we substitute two levels of explanation, a causal or mechanical explanation and a functional explanation. At the mechanical level, the plant has variable secretions of the growth hormone auxin, and these variable secretions of auxin turn the leaves toward the sun. And at the second functional level, plants that turn their leaves toward the sun are more likely to survive than plants that do not. Notice that survival still functions in the explanation, but survival is no longer the goal that the plant has; it is just something that happens. So, we have inverted the conditional. Instead of saying to survive, the plant has to turn its leaves toward the sun, we now say the plant will turn its leaves toward the sun because of the chemical secretions; and because it turns its leaves toward the sun, it is more likely to survive than if it did not. For the traditional Aristotelian final cause, or teleological cause, you substitute two levels. Survival still functions, but it no longer functions as the goal that explains the phenomenon; it is just something that happens. This feature introduces another element to the explanation: the diachronic element. This kind of explanation works only over periods of time.

FAILURE OF SOCIOBIOLOGY

There are limits with what you can do with Darwinian modes of explanation. Some decades ago, there was a movement called sociobiology, which was going to take this model of explanation and explain human culture, morality, civilization, philosophy, and pretty much everything else. The inventor of this was E. O. Wilson (1975); I had a chance to debate him and several other proponents, sometimes in print, but more often in conferences. The failure of sociobiology is revealing to us. I have just endorsed the Darwinian mode of explanation, but what are its limits? Why did sociobiology fail? It may sound question-begging to assume it failed, so I want to explain a little bit what its limitations were.

The crudest limitation that sociobiological methods had was that they were trying to explain specific features of human culture and society, thus the name sociobiology, but the mode of explanation had to be consistent with the fact that there has been no major change in the human gene pool over the past 30,000 years. That figure incidentally comes from physical anthropologists at the University of California, Berkeley, especially Sherwood Washburn (maybe the figures are inaccurate; I will discuss that in a moment), but now, if we are going to explain human societies, think of the enormous variations in human society over the past 30,000 years. So, if we want to explain things like the rise of fascism or the democratic society produced by the Enlightenment or the existence of the Enlightenment itself, then it looks like we have too crude an analytic tool to work with. Suppose the figure is wrong, suppose it is wrong by a factor of 10, and suppose the human gene pool is what it is over the past 3,000 years, the same problem still arises. There is still too much variety over the past 3,000 years for a single mode of explanation to explain it all.

It might seem the answer is to concentrate on cultural universals, and that is what Wilson did. For example, all societies have an incest taboo, and Wilson thought sociobiology provided an explanation for the taboo. Cultural anthropologists were somewhat outraged at this, and they pointed out, among other things, that the incest taboo takes many different forms in different cultures. In some cultures, it is forbidden to marry your cousin and in other cultures it is not. However, the answer I think is that the incest taboo always forbids brother–sister, father–daughter, mother–son sexual relations; and that is the core of the taboo. I debated Wilson once at the University of Michigan, and he claimed that sociobiology has shown why incest is evil: for the first time, we have an explanation of a universal feature of human morality; we have an explanation of why incest is evil. How is the explanation supposed to work on the analogy with the explanation I gave you of the two-level explanations for why plants turn their leaves toward the sun? Studies have shown that children brought up in close proximity to people of the opposite sex lack sexual desire for those. The favorite example comes from Israeli kibbutzim. It turns out that the children brought up in one kibbutz tend to lack sexual desire for other people brought up in that same kibbutz. They are bought up in very close proximity, especially in the communal nursery. In general, they tend to have greater sexual desires for people brought up in a different kibbutz on the other side of the hill. And Wilson said that what happens is that close proximity during the period of development leads to a type of aversion; this sexual aversion gives the mechanical or causal explanation of the incest taboo. What is the functional explanation? And to answer that we have to ask: Why do we have biparental reproduction in the first place? The answer is that you get a much better genetic result if you mix the genes. If we just reproduced like the amoeba by fission or with incest, we would not get the advantages of mixing the genes. So you have the functional level of explanation: the advantages of biparental reproduction and many of those advantages are lost if you reproduce by incest. And you have the causal level of explanation, which is the aversion.

This seems to me an inadequate explanation of a universal prohibition. To begin with, inhibition does not explain prohibition. If it were right that humans had an innate inhibition for sexual congress with people with whom they have been brought up in close proximity, then there would be little need for an incest taboo. There is, for example, no need for a prohibition against eating a lot of raw mud because we are just not inclined to do it. However, the absence of an inclination does not explain the power of prohibition. And the functional level does not give the specific intentional content to the prohibition. You do not get from "mixing the genes is useful" to "incest is evil." Furthermore, when Wilson said we have at last explained why incest is evil, it seems no such explanation was in fact given. At most, it would be an explanation of why it is a bad idea to have incestuous relations without taking precautions to prevent fertilization. However, the idea that the moral component in the incest taboo is explained by there being a functional advantage to biparental reproduction and a natural inhibition that occurs when people grow up in proximity seems to me much too weak. This is an illustration of where in the end sociobiological modes of explanation failed as an account of the general structure of human society or the structure of morality. That is not to say that we cannot do more than we have done with Darwinian modes of explanation, but this particular intellectual movement seemed to me doomed from the start.

EVOLUTIONARY FUNCTION OF CONSCIOUSNESS

However, then that point raises the question that I often hear when I talk about consciousness: What is the evolutionary function of consciousness? Maybe it does not have a function. There are two classes of people I have argued with about this. One class says: consciousness must be epiphenomenal because the physical world is causally closed, and on your own account consciousness is irreducibly subjective, and therefore it is not reducible to the objective world. I have already answered this claim. A second form of argument is more revealing. Consciousness does not have a function because we can easily imagine all of human and animal life going on as it does, only minus consciousness. We can easily imagine that we all existed as unconscious zombies but performed exactly the same actions that we now perform. This possibility shows that consciousness has no essential evolutionary function. (One frequently hears this objection in conferences on consciousness. I most recently was presented with this objection by several critics at the Turing Consciousness 2012 conference at the Université du Québec à Montréal.) This is a deeper mistake and I will answer it.

We tend to hear the question, “What is the evolutionary function of consciousness? What selectional advantage does it convey?” on analogy with such questions as “What is the selectional advantage of the vestibular ocular reflex (VOR)? What selectional advantage does it convey?” In the case of the VOR, the answer is simple: by stabilizing the retinal image, it improves visual perception. We arrive at this answer by mentally subtracting the VOR and seeing what difference it would make. The problem with trying to do this with consciousness is, if you subtract consciousness, you subtract roughly speaking all of our life, except such basic unconscious processes as breathing. What would be lost if we all suddenly went into a coma or had always been in a coma? Roughly speaking, everything. The reason that many people fail to see this is that they typically hear the question, “What would be lost if we subtracted consciousness?" as having the form "What would be lost if we subtracted consciousness but left everything else exactly the same?" However, of course, everything else would not be the same. In fact, pretty much nothing would be the same. I could not get up from the bed in the morning, eat my food, make my way around the surface of the earth, and deal with other people. It is even a mistake to think of consciousness having "a function." The question is like: What is the function of life? Everything in our life depends on being alive and just about everything in our lives depends on being conscious. The reason people tend to think that we might mentally subtract consciousness and leave everything else the same is that they are victims of residual dualism. They assume consciousness is not a part of the ordinary "physical" world, so we might just lift it off and leave everything else the same. However, that is not how nature works. For example, it does not show that birds' wings do not have a function, to argue that we can imagine a world in which birds are powered by rocket engines. The fact that we can imagine zombies that behaved like us without consciousness is like imagining that birds fly with rocket engines. It is irrelevant to giving an evolutionary explanation. The way that nature works for beings like us is that we have enormous power added by the existence of consciousness, by the existence of qualitative subjective conscious states.

Our typical vocabulary makes it difficult to state or appreciate this point because we tend to think in terms like "information" and "representation," and it is tempting to say things like "We have much more efficient information processing and more effective forms of representations than we would if we were unconscious." This formulation does not do justice to the power of consciousness. Our conscious perceptions and actions do not just give us representations. They give us direct presentations of the environment. Thanks to consciousness, I have an immediate awareness of the environment around me. And thanks to the unified consciousness field, I have a prodigious amount of presentational content in the conscious field. If you look around you for a moment and think how many things you can be consciously aware of right now, you would never know when to stop. And remember you have not only the immediate presentational character, but you also have an immediate sense of your most recent past and your intended future. You are constantly using the unified conscious field to change yourself and the environment.

I still have not adequately conveyed the enormous powers that consciousness gives us. The organism can coordinate an enormous number of simultaneous inputs within a single conscious field and can coordinate its behavior both in light of the sensory inputs and in light of its goals and the possible means for achieving its goals. It coordinates all of this in a way that simultaneously represents the past in the form of short-term and long-term memory and anticipates the future in the form of its plans, goals, and intentions. In the case of humans, consciousness also gives us the capacity for cooperating with conspecifics; and the specific form that human cooperation takes is the conscious use of language. The use of language gives us the distinguishing features of human civilization: money, property, government, social organizations, etc.—all of these are the results of conscious application of linguistic representations.

THE UNCONSCIOUS

What should we say about the unconscious? It is essential to distinguish unconscious mental phenomena from nonconscious neurobiological processes that make consciousness possible. For example, even when I am sound asleep I have an unconscious belief that George Washington was the first president. When I see anything, there are nonconscious feedback mechanisms between V1 and the lateral geniculate nucleus. These are essential to perception, but they have no psychological reality at all. What is the difference? The reason that we can say that my unconscious beliefs are psychologically real is that I am able to bring them to consciousness. So the notion of an unconscious mental state is parasitic on the notion of the conscious because an unconscious belief, if it genuinely has psychological reality, has to be the kind of thing that you could in principle bring to consciousness. I have to say "in principle" because access to consciousness may be blocked by brain damage or repression or forgetfulness or other things, but it cannot be something that is not even in principle accessible to consciousness because, if so, it has no psychological reality.

It is important to emphasize this point because, in the early days of cognitive science, the explanatory paradigm consisted in large part in attempts to get computational theories of cognitive capacities (Marr et al., 2010). We were told that the computational level has psychological reality, but it is at an intermediate level between that of commonsense psychology, conscious and otherwise, and the level of neurobiology. I want to say that there is no such level. You cannot make any sense of the idea that there is a psychological reality at that level if it does not have those features that constitute accessibility to consciousness in principle.

I think the paradigm is changing in cognitive science. I think we are moving away from a computational cognitive science to cognitive neuroscience. I welcome that move. I think the future of this entire research project lies in a better understanding of the brain.

2

Affiliation, Empathy, and the Origins of Theory of Mind

ROBERT M. SEYFARTH*‡ AND DOROTHY L. CHENEY†

To understand the evolution of a Theory of Mind, we need to understand the selective factors that might have jump-started its initial evolution. We argue that a subconscious, reflexive appreciation of others' intentions, emotions, and perspectives is at the roots of even the most complex forms of Theory of Mind and that these abilities may have evolved because natural selection has favored individuals that are motivated to empathize with others and attend to their social interactions. These skills are adaptive because they are essential to forming strong, enduring social bonds, which in turn enhance reproductive success. We first review evidence from both humans and other animals indicating that reflexive and reflective mental state attributions are inextricably linked and play a crucial role in promoting affiliative social bonds. We next describe results from free-ranging female baboons showing that individuals who show high rates of affiliative behavior form stronger social bonds with other females. These bonds, in turn, are linked to fitness. We then provide data from three different types of social challenges (male immigration, changes in grooming behavior after the death of a close relative, and responses during playback experiments), suggesting that females who manifest high rates of affiliative behavior may also be more motivated to anticipate challenges, react adaptively to setbacks, and respond appropriately to social interactions.

Departments of *Psychology and †Biology, University of Pennsylvania, Philadelphia, PA 19104. ‡To whom correspondence should be addressed. E-mail: seyfarth@psych.upenn.edu.

Do animals have a Theory of Mind (ToM)? Answers to this question have tended to focus on two properties that might characterize a cognitive process. First, is an animal's recognition of other individuals' mental states reflexive, and therefore perhaps immediate and unconscious? Or is it reflective, and therefore more likely to be ruminative and conscious? Second, to what kinds of mental states are animals attentive: more rudimentary psychological states, like another individual's gaze direction or its intentions, or more complex states, like another individual's knowledge or beliefs? These distinctions are not easy to draw, even in humans, where reflective, conscious mindreading about others' knowledge and beliefs is built on and develops gradually from reflexive, unconscious recognition of, for example, another's direction of gaze (Onishi and Baillargeon, 2005; Apperly, 2012).

There is considerable evidence that many animals are reflexively attuned to other individuals' gaze, intentions, and emotions; however, the degree to which they are also reflectively aware of others' knowledge and beliefs is less clear (Cheney and Seyfarth, 2007). Problems in assessment arise in part because whenever an animal behaves in ways that suggest an understanding of another's knowledge, its behavior can often also be explained by simpler mechanisms, including learned contingencies. A chimpanzee (*Pan troglodytes*) who takes food that a rival cannot see might do so because she understands the relation between seeing and knowing or because she has learned the behavioral rule that a rival is motivated to defend food at which he is looking. Although experiments have attempted to distinguish between these explanations (Kaminski et al., 2008; Bugnyar, 2011; Crockford et al., 2012; MacLean and Hare, 2012), results have not been easy to interpret. At the very least, they suggest that animals' understanding of others' psychological states is quite different and perhaps less subject to conscious reflection than adult humans'. Whatever the explanation, it is clear that attempting to identify precise, definitive benchmarks of mental state attribution in animals has proved to be more elusive and less productive than first hoped.

Here, we take a slightly different approach to the question of mental state attribution in animals and consider the selective factors that might have favored the evolution of a rudimentary ToM. We begin by assuming that a full-blown ToM evolved from more rudimentary, reflexive forms that were themselves adaptive in their own right. As a first step in understanding the evolution of a ToM, therefore, we need to understand the selective factors that might have jump-started these rudimentary forms. We argue that a subconscious, reflexive appreciation of others' intentions, emotions, and perspectives lies at the roots of even the most complex forms of ToM and that these abilities first evolved because natural selection favored individuals that were motivated to attend to other individuals' social interactions and empathize with them. These skills were favored by selection because they are essential to forming strong, enduring social bonds, which in turn have been shown to enhance reproductive success. We therefore propose that the evolution of a ToM ultimately derives from its role in facilitating the formation of social bonds.

We first review evidence from both humans and other animals indicating that reflexive and reflective mental state attributions are inextricably linked and play a crucial role in promoting affiliative social bonds. Then, using data on wild female baboons (*Papio hamadryas ursinus*), we suggest that individual variation in the motivation to attend to social interactions and react to social challenges is positively correlated with measures that have previously been shown to be linked to the formation of social bonds and, ultimately, enhanced reproductive success.

REFLEXIVE AND REFLECTIVE EMPATHY IN ANIMALS AND HUMANS

Any attempt to determine whether an animal does or does not understand what another individual knows or thinks is inevitably confounded by the fact that the reflective processes associated with higher levels of ToM are closely linked to—and often hard to distinguish from—the more automatic, reflexive processes that underlie them (de Waal, 2012; Hecht et al., 2012). Although we are consciously aware of the distinction between our own and others' mental states, we are often unaware of the many cues on which this awareness is based. For example, although higher cortical areas, like the prefrontal cortex, are activated when a human attempts to determine whether another individual can see something, initial responses to gaze direction and goal-directed behavior also activate more primitive areas of the brain, including the superior temporal sulcus (STS) and the amygdala. In both humans and rhesus macaques (*Macaca mulatta*), the STS is particularly sensitive to the orientation of another individual's eyes (Jellema et al., 2000; Klein et al., 2009).

The same is true of intentional behavior. Although we have conscious access to our reflections about whether someone's actions are accidental or intentional, many of the neuronal responses that contribute to our eventual decision are more subconscious. In both humans and monkeys, mirror neurons in the inferior parietal lobule are activated when an individual both performs a specific action and he observes someone else perform that action. Significantly, many neurons begin to fire before the other individual actually performs the action, suggesting that these neurons encode not only the specific motor act but also the actor's intentions (Fogassi et al., 2005; Rizzolatti and Fabbri-Destro, 2009). Thus, our ability to recognize that gaze has informative content, or to consider whether behavior is intentional, depends crucially on automatic, reflexive neuronal activity of which we are largely unaware.

Similar results emerge in studies of empathy. Reflective, explicit empathy involves the ability to recognize emotional states like grief or fear in others without necessarily experiencing the same emotions oneself (Hecht et al., 2012). However, reflective empathy evokes activity not just in the cortex but also more primitive areas of the brain shared with many animals, including the midbrain, the brainstem, and endocrine systems associated with reactivity, reward, and social attachment (Decety and Jackson, 2004; Decety, 2011). Although we can distinguish between our own and others' emotions, representations of emotions like pain, disgust, and shame in others also activate many of the same areas of the brain that are activated when we experience or imagine the same emotions ourselves (Rizzolatti and Fabbri-Destro, 2009). Feeling sympathy for or being nice to others is emotionally rewarding in part because it facilitates the release of dopamine, a neurotransmitter associated with personal reward (Decety, 2011). Trust, empathy, and sensitivity to others' affective states are all facilitated by neuropeptides associated with attachment, maternal behavior, and pair bonding in animals, particularly oxytocin (Carter et al., 2008; Snowdon et al., 2010). Thus, even the most reflective forms of empathy in humans are derived from and still strongly linked to more rudimentary forms.

Similarly, reflective imitation involves the ability to recognize the goals and intentions of another and to understand that, to achieve the same goal, one must copy that individual's actions. Human culture depends crucially on this ability, which is also shown to some degree by the great apes (Buttelmann et al., 2007). Even humans, however, are largely unaware of many of the behaviors in others that they routinely mimic. Like some animals, we have a reflexive, unconscious tendency to mimic the postures, mannerisms, and behavior of individuals with whom we are interacting.

As already noted, in the motor domain the same mirror neurons are activated when an individual performs a movement as when he observes another engaged in that movement. Similarly, both human and nonhuman primates reflexively follow the gaze of others (Shepherd et al., 2009), and both human and macaque neonates copy others' facial expressions (Meltzoff and Moore, 1977; Ferrari et al., 2006). The fact that such mimicking is associated with empathy is exemplified by the phenomenon of contagious yawning. It is well known that viewing others yawn can elicit spontaneous yawning in oneself. Even this apparently reflexive response, however, seems to vary according to an individual's sensitivity to more reflective behavior, including face recognition and understanding of others' mental states (Platek et al., 2003). Spontaneous yawning is rare or absent in children with autism spectrum disorder (Senju et al., 2007; Helt et al., 2010).

It also occurs at higher frequencies among kin and friends than among strangers, suggesting that contagious yawning is linked to and may also promote affiliation (Norscia and Palagi, 2011). These observations are not limited to humans: chimpanzees are also more likely to yawn in response to the yawns of familiar, as opposed to unfamiliar, individuals (Campbell and de Waal, 2011).

A variety of other observations on what has been termed the chameleon effect (Chartrand and Bargh, 1999) supports the view that reflexive mimicry is linked to the formation and maintenance of social bonds and has been favored by evolution because it promotes affiliation (Lakin et al., 2003). Experiments suggest that people unconsciously mimic others when attempting to foster rapport and increase their frequency of mimicry when they are excluded from a group (Lakin and Chartrand, 2003; Lakin et al., 2008). Being imitated increases helpful and affiliative behavior (Van Baaren et al., 2004) and activates areas in the brain associated with reward processing (Kühn et al., 2010). In contrast, not being imitated increases cortisol levels (Kouzakova et al., 2010).

Similar observations have been obtained in nonhuman primates. Captive capuchin monkeys (*Cebus apella*) are more willing to approach and exchange tokens with a human who mimics their actions than one who does not (Paukner et al., 2009). Male chimpanzees' long-distance pant hoots become more similar acoustically as individuals spend more time together (Mitani et al., 1999; Crockford et al., 2004), suggesting that call convergence is associated with, and may even promote, social affiliation.

In practice, it is almost impossible to distinguish reflective empathy from more reflexive forms and learned negative associations (de Waal, 2012). This problem is not surprising given neurological evidence that the two are closely linked. In an early experiment specifically designed to examine whether one monkey would respond to another's distress, rhesus macaques were trained to pull chains to obtain a food reward. The apparatus was then rigged so that a monkey in an adjacent cage received a shock each time a particular chain was pulled. Most of the monkeys soon stopped pulling the chain that delivered the shock, even though doing so deprived them of a reward. They were especially likely to avoid the chain if they had previously received shocks themselves (Masserman et al., 1964; Wechkin et al., 1964). Although the monkeys' responses might at first be interpreted as evidence for reflective empathy, it seems as likely that they became distressed when they saw the other monkey being shocked because it was linked to a negative association for themselves. However, because even the most reflective forms of human empathy also evoke activity in more reflexive, primitive brain systems, these alternative explanations may be impossible to disambiguate.

In a more recent experiment, macaques were given the option of delivering a reward to themselves, another monkey, or no one. Although subjects preferred to reward themselves over others, they nonetheless opted to reward their partner if the alternative was to reward no one. This preference was especially true if the partner was familiar (Chang et al., 2011). Significantly, the same brain areas that are activated in humans during such exchanges were also activated in monkeys (Chang et al., 2013), and again—as in humans (Guastella and MacLeod, 2012)—the monkeys' vicarious reinforcement was enhanced if they first inhaled oxytocin (Chang et al., 2012).

Finally, in another experiment rats were placed in an arena with a cagemate trapped in a translucent tube (Ben-Ami Bartal et al., 2011). The free rats quickly learned how to open the tube to liberate their cagemates, and they continued to do so even when given an alternative option to open a tube containing chocolate. (In the latter case, the rat opened both tubes and shared the chocolate.) It is possible that the free rats' responses may have been provoked in part by their own elevated stress at hearing their cagemates' alarm calls. However, given neurological evidence that witnessing distress in others activates many of the same brain areas as experiencing distress oneself, this distinction becomes difficult to disambiguate.

In sum, a variety of evidence suggests that reflexive empathy and imitation in both humans and other animals have evolved because they promote affiliation and social bonding. Joint attention and joint action activate areas of the brain associated with the processing of reward, and they are facilitated by the release of oxytocin. Importantly, what seems to be rewarding to animals is not physical contact per se but the specific identity of the social partner. In socially monogamous tamarins (*Saguinus oedipus*), strongly bonded pairs exhibit higher oxytocin levels than more weakly bonded pairs (Snowdon et al., 2010). Among wild chimpanzees, urinary concentrations of oxytocin are higher after individuals groom with a closely bonded partner (both kin and nonkin) than with a less closely bonded partner (Crockford et al., 2013). Evidently, grooming with a close friend or relative is more emotionally rewarding than engaging in the same behavior with a less preferred partner.

If empathy and affiliation have indeed been under strong selective pressure and lie at the roots of ToM, it should be possible to link these behaviors to fitness. Indeed, there is growing evidence that such a link can be made, because empathy and affiliation help individuals to form and maintain social bonds, and these bonds promote fitness.

Strong, enduring social bonds are a distinctive and adaptive feature of many animal societies. Such bonds are not limited to those formed by heterosexual mated pairs but extend to same-sex bonds formed between both kin and nonkin. Correlations between same-sex bonds and measures of health or reproductive success have been documented in rodents, horses, dolphins, chimpanzees, baboons, and humans (Seyfarth and Cheney, 2012). Strong bonds buffer individuals against stress and disease and perhaps as a result are correlated with longevity and offspring survival.

These observations suggest that natural selection has favored empathy and imitation, because they are part of the cognitive and emotional skills that an individual needs to recognize others' social relationships, understand their motives and intentions, and keep track of, anticipate, and react adaptively to social events and challenges. We now explore these questions in more detail, focusing on data derived from a long-term study of wild baboons living in the Okavango Delta of Botswana.

EMPATHY, SOCIAL BONDS, AND REPRODUCTIVE SUCCESS IN WILD FEMALE BABOONS

Social Bonds

Like many other species of Old World monkey, baboons live in large social groups (~75 individuals) composed of both kin and nonkin. Males emigrate from their natal group at adulthood. Females assume dominance ranks similar to their mothers', and the female dominance hierarchy typically remains stable for many years (Cheney and Seyfarth, 2007). Females form strong grooming relationships with a subset of other females, the strongest bonds occurring among close matrilineal kin (Silk et al., 2012).

Despite the fact that high-ranking females enjoy priority of access to resources such as food and mates, female reproductive success in baboons—like female reproductive success in humans and other animals—is influenced less by a female's dominance rank than by the strength and stability of her bonds with other females. We evaluated females' bond strength using two indices of sociality. The first index, the Composite Sociality Index (CSI), measured dyadic bond strength based on females' rates of approaches, groom presents, grooming initiations, and grooming durations with other females. The second index, the Partner Stability Index (PSI), measured females' retention of their top three partners across years. Over a 17-year period, offspring survival was significantly positively correlated with the CSI (Silk et al., 2009), whereas longevity was significantly correlated with a combination of the strength and stability of females' relationships with their top partners (Silk et al., 2010). Females also experienced lower stress (as measured by fecal glucocorticoid metabolites) when their grooming network was more focused (Crockford et al., 2008). Thus, the strength and stability of females' social partners were correlated with several measures of fitness. Interestingly, however, variation in the strength of social bonds was not fully explained by obvious demographic attributes like dominance rank or availability of kin. Although females established their closest bonds with kin, kin varied in the strength of their bonds, and some females without close kin established close bonds with others.

These observations suggest that some individuals are more motivated or skilled than others at establishing and maintaining social bonds and that variation in patterns of affiliation that are correlated with fitness may result in large part from variation in personality styles. We therefore attempted to determine whether different patterns of behavior were more or less associated with social bond strength.

Personality Styles and Social Bond Strength

We applied exploratory principal component analysis to the behavior of 45 female baboons over a 7-year period (Seyfarth et al., 2012). To construct the components that were used to identify personality dimensions, we calculated annual rates for several behaviors not considered in previous analyses of sociality. These behaviors included the frequency that females were alone, the rate at which they were friendly to other females, the rate at which they were aggressive to other females (corrected for dominance rank), and the frequency with which they grunted when approaching higher- and lower-ranking females. Among baboons, grunts serve as signals of benign intent and facilitate friendly interactions (Cheney et al., 1995). When females grunt to higher-ranking individuals, they are less likely to receive aggression. Conversely, when females grunt to lower-ranking individuals, those individuals are less likely to show submissive behavior. We were especially interested in the frequency with which females grunted to lower-ranking individuals, because such vocalizations do not benefit the signaler in any obvious way. Instead, they seem to function primarily to alleviate the anxiety of the recipient.

Our analysis identified three relatively stable personality dimensions, each characterized by a distinct suite of behaviors that could not be explained by dominance rank or availability of kin. Females scoring high on the Nice dimension were friendly to all females and often grunted to lower-ranking females, apparently to signal benign intent. Aloof females were aggressive, were less friendly, and grunted primarily to higher-ranking females. Loner females were often alone, were relatively unfriendly, and also grunted most often to higher-ranking females (Seyfarth et al., 2012). The baboons themselves apparently recognized these differences, because they approached females who scored high on Nice at high rates but approached females scoring high on Aloof and Loner at much lower rates (Seyfarth et al., 2012, table 1). Personality designations remained relatively stable over time.

Importantly, the different personality attributes were associated in different ways with measures of fitness. Females who scored high on Nice had strong social bonds (high CSI scores) and stable preferences for their top partners. Females who scored high on Aloof had lower CSI scores overall but very stable preferences with their top partners. In contrast, Loner females had significantly lower CSI scores, less stable partner preferences, and significantly higher glucocorticoid (GC) levels (Seyfarth et al., 2012, table 2).

These results suggest that there are costs and benefits associated with particular personality characteristics. For example, selection would seem to act against females scoring high on the Loner dimension, because these individuals were under more stress than others and formed weaker bonds that yielded low CSI scores and low partner stability. This observation begs the obvious question of why any female would adopt the Loner strategy. Loners were not isolated and unfriendly solely because of their subordinate status or lack of kin; although these demographic factors contributed to their scores on this component, their behavior exacerbated them. Moreover, some Loners did have close kin, whereas other females who consistently scored high on Nice did not. If Loners were often the victims of circumstances, what skills or motivation allowed some individuals and not others to overcome these circumstances?

In sum, female baboons varied not only in the strength and stability of their bonds but also in the personality traits associated with these bonds—particularly the ability or motivation to interact with others.

To test whether variation in personality traits was also associated with variation in females' ability and/or motivation to keep track of, anticipate, and react adaptively to social events, we examined females' responses to three different types of social challenges. We were interested not in females' responses to adversity itself—because we expected little individual variation in responses to real, ongoing threats—but their ability to anticipate adversity, respond adaptively to adversity after it had occurred, and keep track of social interactions that had the potential to influence their own relationships. Because previous research had shown that, as a group, most females responded positively to these challenges, we expected that any differences that did emerge would be small.

Personality Styles and Responses to Social Challenges

Male Immigration

In the Okavango Delta, male immigrants that achieve alpha status often commit infanticide (Cheney and Seyfarth, 2007). Perhaps as a result, both immigration and instability in the alpha male position cause a significant increase in females' GC levels. Lactating females are particularly likely to experience elevated GC levels, though during some immigration events females in all reproductive states show significant increases (Beehner et al., 2005; Engh et al., 2006b; Wittig et al., 2008). These responses are associated with a decrease in sociality among females (Wittig et al., 2008), which may reflect their heightened vigilance and reactivity.

We examined increases in females' GC levels from 2 weeks before to 2 weeks after four different immigration events in 2002, 2003, 2004, and 2005. All events involved the takeover of the alpha male position. We tested whether the magnitude of the GC changes of individual females was linked to their personality styles. Importantly, by focusing on GC changes in the 2 weeks immediately after the immigration event, we were able to assess females' anticipation of the threat of infanticide rather than their responses to the actual act.

Consistent with previous results, the majority (75 percent) of individuals showed an increase in GC levels after immigration. However, some of the variation in females' GC levels also seemed to be linked to their personality scores. The correlation between percent change in GC levels and Aloof scores was weakly negative ($\beta = -10.15$, SE = 10.5, $t = -0.962$, $P > 0.10$), as was the correlation for Loner scores ($\beta = -11.24$, SE = 11.62, $t = -0.968$, $P > 0.10$) (Fig. 2.1). In contrast, the correlation between Nice scores and change in GC levels was positive, though nonsignificant ($\beta = 5.278$, SE = 10.00, $t = 0.527$, $P > 0.10$) (Fig. 2.1). There were no significant effects of reproductive state.

Thus, individuals who scored high on Nice tended to show increases in GC levels in response to male immigration, whereas those who scored high on Aloof and Loner tended to be less responsive.

Changes in Grooming Behavior After the Death of a Close Relative

Females also experience elevated GC levels after the death of a close adult female relative, probably in part because the death results in the loss of a regular grooming partner. Previous analyses have shown that, in the 3 months after this loss, bereaved females increase both grooming rates and the number of female grooming partners (Engh et al., 2006a). These responses may facilitate the repair of females' social networks through the establishment of new bonds.

To examine individual differences in response to this challenge, we compared the number of each bereaved female's different grooming partners in the 3 months after the death of a close female relative with the mean number of grooming partners for unaffected females in the group during the same period (controlling for reproductive state). (This method was chosen to control for variation in sampling rates across time.) Whether

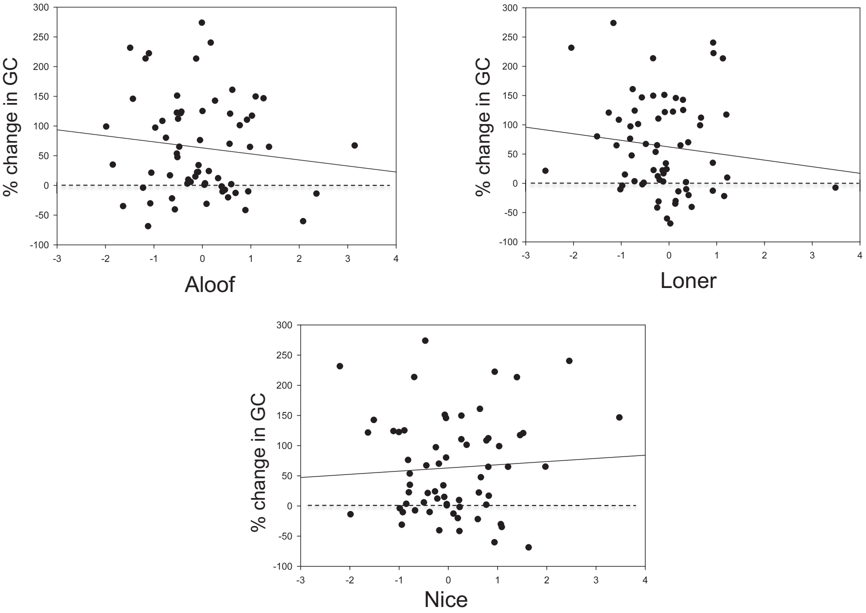


FIGURE 2.1 Percent change in females' GC levels from 2 weeks before to 2 weeks after the immigration of a potentially infanticidal male. Only immigration events in which an immigrant attained the alpha rank were included in analysis; *n* = 33 females present for 1–3 events for a total of 64 female events. Dashed lines indicate no change; solid lines indicate least-square regression (statistics and probability values given in the text). The *x* axis denotes females' scores on each of the three principal components (Aloof, Loner, and Nice) in the immigration year. Each point represents 1 female-year.

females had a higher or lower number of partners than unaffected females seemed to be related to their personality scores. Females scoring high on the Loner component had fewer grooming partners than unaffected females ($\beta = -1.138$, SE = 0.866, $t = -1.314$, $P = 0.203$). In contrast, correlations between the relative number of grooming partners were positive but nonsignificant for both Aloof ($\beta = 0.366$, SE = 0.624, $t = 0.586$, $P = 0.564$) and Nice ($\beta = 0.799$, SE = 0.509, $t = 1.569$, $P = 0.132$) scores (Fig. 2.2).

Thus, females who scored high on the Loner component had fewer grooming partners compared with unaffected females in the ensuing 3 months, suggesting that they were unsuccessful in rebuilding their social network. This decrease occurred despite the fact that females who scored high on the Loner component tended to show a greater increase in GC levels than other females in the 2 weeks after the death of a close relative, particularly when that relative was a mother or adult daughter ($r_s = 0.771$, $N = 6$, $P > 0.10$). In contrast, females who scored high on the Aloof and Nice components responded to the death of a close relative by grooming comparatively more females than unaffected individuals.

Variation in the Strength of Responses During Playback Experiments

Playback experiments are designed to test subjects' knowledge of other individuals' dominance ranks and kinship as well as their memory of recent social interactions and their participants. Consider reconciliation, for example. Baboons often grunt to their opponents after aggression, and these grunts serve to restore opponents to baseline levels of tolerance (Cheney and Seyfarth, 1997). In an experiment designed to determine

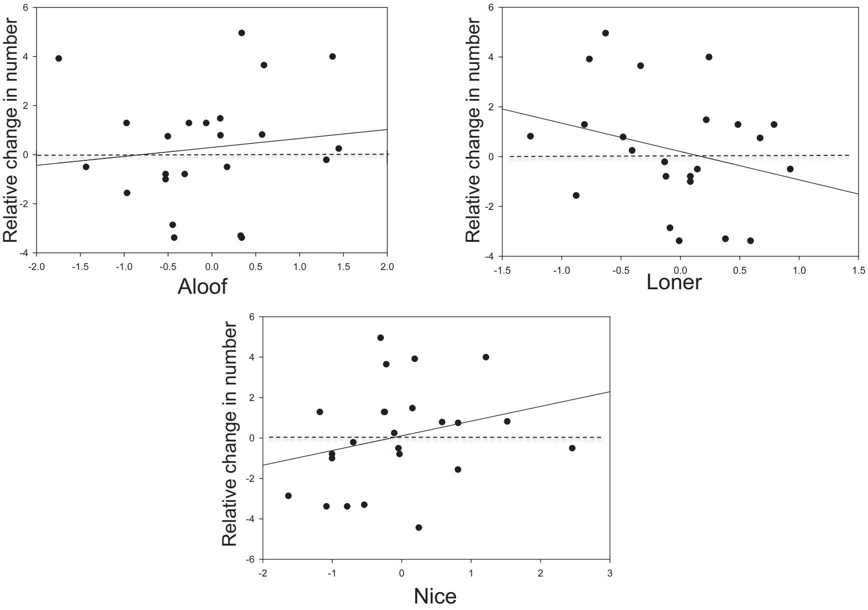


FIGURE 2.2 The relative number of a female's different grooming partners in the 3 months after the death of a close relative (mother, adult daughter, or sister) compared with the mean number of grooming partners for all other females in those months (controlled for reproductive state); $n = 18$ females who lost from one to three close relatives for a total sample of 24 female-years. One outlier was removed. Legend is the same as in Fig. 2.1.

whether reconciliation by kin could serve as a proxy for direct reconciliation, victims were played the grunt of the close relative of a recent opponent. Subjects were significantly more likely to approach their opponent after hearing a grunt from their opponent's relative (test condition) than after hearing a grunt from a female from a different matriline (control condition) (Wittig et al., 2007b). In so doing, subjects showed that they remembered not only the specific nature of a recent interaction and the identity of the participants but also the kinship relations (or close associates) of other females in their group. Thus, by responding more strongly during tests than control trials, subjects showed that they were not only reactive but also appropriately reactive, in the sense that they responded strongly only to relevant stimuli.

For this analysis, we considered variation in females' responses to playback stimuli in five previously conducted experiments that tested baboons' memory of recent social interactions and knowledge of other individuals' relationships (summary of the playback experiments used in the analysis is available from the authors) (Bergman et al., 2003; Engh et al., 2006c; Wittig et al., 2007a,b; Cheney et al., 2010). We used duration of looking toward the speaker in test compared with control trials as our dependent measure, because this response was used in all experiments. Because the strength of subjects' responses varied across experiments, we ranked each subject's duration of response in each experiment relative to response duration of other subjects. Thus, a subject who responded more strongly in the test vs. the control condition received a high positive ranking, whereas a subject that responded more strongly in the control condition received a negative ranking.

The correlations between strength of response and Aloof, Loner, and Nice scores were all positive, but only the Nice scores reached statistical significance (Aloof: $\beta = 0.381$, SE = 0.580, $t = 0.657$, $P > 0.10$; Loner: $\beta = 0.625$, SE = 0.634, $t = 0.986$, $P > 0.10$; Nice: $\beta = 1.250$, SE = 0.566, $t = 2.246$, $P = 0.027$) (Fig. 2.3). Thus, although most females responded more strongly during test than control trials, females who scored high on the Nice component were the most responsive.

Discussion: Social Challenges

Previous analyses (Seyfarth et al., 2012) showed that females scoring high on the Nice component have stronger social bonds with other females. The data presented here suggest that, by three independent measures, these individuals may also be more responsive to social challenges and more motivated to attend to social interactions within their group (Table 2.1).

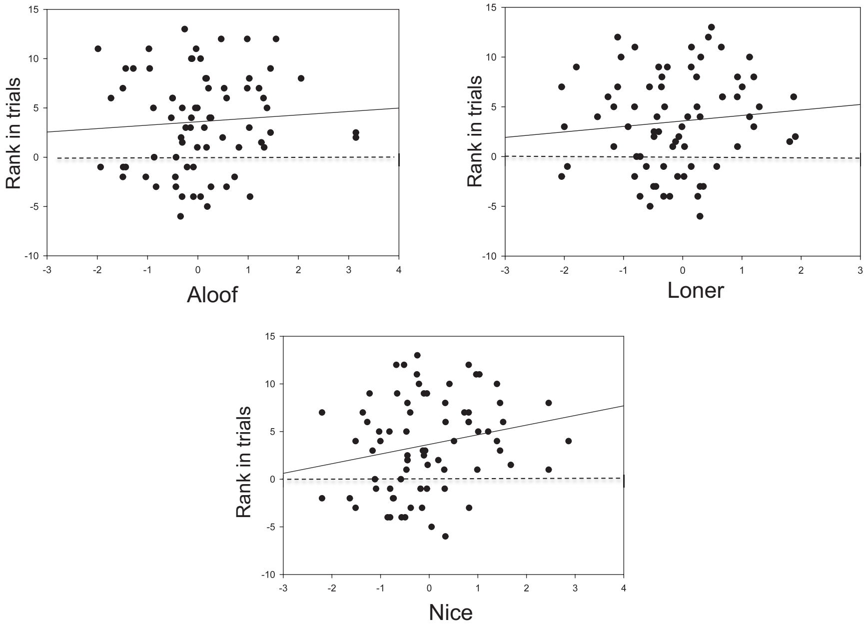


FIGURE 2.3 Variation in females' responses to playback stimuli in five different experiments. Subjects were ranked according to the strength of their response in experimental trials minus control trials; $n = 33$ females in one to five experiments for a total of 73 subjects. One outlier was removed. Legend is the same as in Fig. 2.1.

First, females who score high on Nice may better anticipate threats that have yet to occur. Such females showed a greater anticipatory increase in GC levels at the arrival of a potentially infanticidal immigrant, suggesting that they recognized the threat that such a male represented even before he attacked any infants. Second, females who score high on Nice may respond more adaptively to setbacks that have occurred. Females with high Nice and Aloof scores had more grooming partners than unaffected females after the death of a close relative, suggesting that they were attempting to identify new social partners. In contrast, females who scored high on Loner had fewer partners than other females, suggesting that they made no such effort. Finally, there was some indication that females who scored high on Nice were more appropriately reactive during playback experiments than other females, perhaps because they were generally more attentive to social interactions and events in their group.

It is important to emphasize that all of the observed differences were small. As a group, females responded positively to each of the three chal-

TABLE 2.1 Signs of the β Coefficients (Regression Slopes) of the Relation Between Personality Component Scores (Nice, Aloof, and Loner) and Three Social Challenges

Social Challenge	Nice	Aloof	Loner
Male immigration	+	–	–
Change in grooming partner number after relative's death	+	+	–
Playback experiments	+*	+	+

*$P < 0.05$.

lenges, so it is not surprising that individual variation in response strength was subject to a ceiling effect. The attributes associated with females who scored high on the Nice component were not unique to these individuals; rather, such females seemed more consistently to show strong anticipatory and reactive responses to challenges. Clearly, however, this hypothesis will need to be tested in future research.

Several recent studies of birds have investigated the relationship between problem-solving ability and fitness. Results suggest that variation in problem solving does not result solely from differences in motivation or reactivity but instead may reflect genuine differences in cognitive ability (Keagy et al., 2011; Cole et al., 2012; Cauchard et al., 2013). In contrast, we have no evidence that female baboons vary in their cognitive abilities—that, for example, Nice females are, by some measure, more skilled at problem solving. Instead, data suggest that differences in personality styles may be associated with greater responsiveness to social challenges and greater motivation to attend to, recall, and anticipate social interactions. In a somewhat similar study of captive rhesus macaques, males who scored high on a sociability index (defined as the motivation to seek out others) experienced better health. These males also coped better both physiologically and behaviorally during unstable social conditions, and they seemed more motivated than other males to manage unpredictable social circumstances (Capitanio, 2011). In contrast to males that scored low on the sociability index, they seemed to find social interactions rewarding rather than aversive. Similar differences were observed among Nice and Loner female baboons.

CONCLUSIONS

Human behavior during cooperative interactions is often contrasted with behavior of chimpanzees, which in captivity show little evidence of prosocial behavior. Indeed, experiments explicitly designed to compare the behavior of children and chimpanzees suggest that humans are unique not only in their motivation to participate in activities that involve shared goals and joint action but also their concern for the welfare of others (Tomasello et al., 2005; Warneken and Tomasello, 2009; Silk and House, 2011). Most forms of apparent prosociality and empathy in animals can be explained functionally in terms of parental behavior, nepotism, or direct benefit. There is little evidence in animals—even apes—for the kind of reflective empathy that permits an individual to disassociate his own emotions and needs from others' or be sensitive to another's welfare independent of his own (Cheney, 2011).

However, although cooperation among humans clearly differs from cooperation among animals in many nontrivial ways, more naturalistic studies suggest that the contrasts are not as stark as initially proposed. For example, wild chimpanzees engage in a variety of cooperative, sometimes risky ventures with long-term social partners, including grooming, food sharing, and border patrols (Mitani, 2006). These interactions seem to be emotionally rewarding. As already mentioned, both male and female chimpanzees experience elevations in urinary oxytocin after grooming with a preferred partner (Crockford et al., 2013), and males that share meat with others experience a significant drop in testosterone (Sobolewski et al., 2012). Thus, chimpanzees in the wild regularly engage in joint, cooperative action and seem to derive pleasure and reduced tension from what are, arguably, rather prosocial activities.

We have suggested that a full-blown ToM evolved from a rudimentary form that is reflexively attentive and sensitive to others' attention, emotions, and intentions. This rudimentary form of shared attention is widespread in many animals, still present in humans, and difficult to disambiguate—behaviorally and neurologically—from humans' more derived, reflective ToM. We can explain the evolution of rudimentary ToM by noting that it facilitates attentiveness to others' emotional states and thereby promotes the formation of strong social bonds, which are linked to fitness. Shared attention and sensitivity to others' emotions may promote bond formation, because they include a subconscious tendency to mimic individuals with whom we are interacting. When two individuals interact, imitation makes the behavior of each partner more predictable to the other, and predictability and control are major modulators of stress (Sapolsky, 2004). We may therefore find individuals who imitate us attractive in part because they are predictable.

In sum, a rudimentary ToM may have evolved because, in social animals, reflexive empathy and joint attention are both emotionally rewarding and adaptive. Individuals who are motivated to attend to others' behavioral, attentional, and emotional states are more likely to interact positively with others and form stronger social bonds. Strong social bonds, in turn, contribute to reproductive success. Individual variation in the strength of social bonds, stress levels, and responsiveness to social challenges may stem less from variation in cognitive ability than variation in the motivation to attend to and participate in social interactions.

METHODS

Data were derived from a long-term study of wild chacma baboons (*P. hamadryas ursinus*) in the Moremi Game Reserve, Botswana. The group had been observed since 1978. Maternal kinship was known for all individuals. The primary causes of mortality were infanticide and predation [details in Onishi and Baillargeon (2005)].

Statistical analyses were conducted using R statistical software (version 2.15; R Foundation for Statistical Computing). For exploratory principal component analysis, we used the principal function in the psych package with the default varimax rotation. To test for a relation between scores on principal components and dependent variables, we used linear mixed models (lmer in R), entering female identification and year as random factors.

ACKNOWLEDGMENTS

We thank the Office of the President, Republic of Botswana, and the Department of Wildlife and National Parks for permission to work in the Moremi Reserve. We thank J. Beehner, T. Bergman, C. Crockford, A. Engh, M. Heesen, L. Moscovice, R. Wittig, K. Seyfarth, C. Shaw, M. Mokopi, and A. Mokopi for assistance with data collection and J. Silk and two anonymous reviewers for comments. Research was supported by the National Science Foundation, the National Institutes of Health, the Leakey Foundation, the National Geographic Society, and the University of Pennsylvania. Research was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol No. 19001).

3

Evolution of Consciousness: Phylogeny, Ontogeny, and Emergence from General Anesthesia

GEORGE A. MASHOUR* AND MICHAEL T. ALKIRE[†][‡]

Are animals conscious? If so, when did consciousness evolve? We address these long-standing and essential questions using a modern neuroscientific approach that draws on diverse fields such as consciousness studies, evolutionary neurobiology, animal psychology, and anesthesiology. We propose that the stepwise emergence from general anesthesia can serve as a reproducible model to study the evolution of consciousness across various species and use current data from anesthesiology to shed light on the phylogeny of consciousness. Ultimately, we conclude that the neurobiological structure of the vertebrate central nervous system is evolutionarily ancient and highly conserved across species and that the basic neurophysiologic mechanisms supporting consciousness in humans are found at the earliest points of vertebrate brain evolution. Thus, in agreement with Darwin's insight and the recent "Cambridge Declaration on Consciousness in Non-Human Animals," a review of modern scientific data suggests that the differences between species in terms of the ability to experience the world is one of degree and not kind.

---

*Departments of Anesthesiology and Neurosurgery, Neuroscience Graduate Program, University of Michigan Medical School, Ann Arbor, MI 48109; and [†]Veterans Administration Long Beach Healthcare System, Department of Anesthesiology and Perioperative Care, Center for the Neurobiology of Learning and Memory, University of California, Irvine, CA 92697. [‡]To whom correspondence should be addressed. E-mail: malkire@uci.edu.

Evolutionary biology forms a cornerstone of the life sciences and thus the neurosciences, yet the emergence of consciousness during the timeline of evolution remains opaque. As the theory of evolution began to eclipse both religious explanations and Enlightenment doctrines regarding the singularity of human consciousness, it became clear that consciousness must have a point of emergence during evolution and that point likely occurred before *Homo sapiens.* "How," Darwin questioned, "does consciousness commence?" His post-*Beagle* research on this question evidently caused him violent headaches. One such headache can be expressed as the 20th century philosophical distinction of phenomenal consciousness and access consciousness (Block, 2007). Phenomenal consciousness relates solely to subjective experience, whereas access consciousness includes (among other processes) the ability to report such experiences verbally (other distinctions related to consciousness can be found in Table 3.1). Thus, the scientist looking for objective indices of subjective events is primarily limited to humans manifesting access consciousness, an obstacle in studying the evolution of consciousness antecedent to our species. We could, however, take solace in the dictum that ontogeny recapitulates phylogeny and search for clues in developing humans. Unfortunately, Haeckel's theory of recapitulation is not scientifically sound and, even if applicable in this case, we would still be constrained by the high probability that babies develop phenomenal consciousness before access consciousness. To overcome the limitations in identifying the birth of consciousness, we need a reproducible experimental model in which (*i*) consciousness emerges from unconsciousness at a discrete and measurable point, (*ii*) phenomenal consciousness and access consciousness are closely juxtaposed or collapsed, and (*iii*) assessment of neural structure and function is possible. In this chapter, we consider top-down and bottom-up approaches to consciousness, nonhuman consciousness, and the emergence of consciousness from general anesthesia as a model for the evolution of subjectivity.

TOP-DOWN AND BOTTOM-UP APPROACHES TO CONSCIOUSNESS

To locate the birth of consciousness on the evolutionary timeline, it will be beneficial to consider the basic neural machinery that is thought to be involved in human consciousness (Crick, 1994; Damasio, 1999; Edelman and Tononi, 2000; Tononi, 2004; Baars, 2005; Denton, 2005; Blumenfeld, 2011). The distinction between phenomenal and access consciousness was noted, but phenomenal consciousness itself reflects the dissociable neurobiological processes of awareness and arousal (Paus, 2000; Schiff and Plum, 2000; Jones, 2003; Laureys, 2005; Lydic and Baghdoyan, 2005)

TABLE 3.1 Definitions Relevant to Consciousness

Terms	Explanation
Easy vs. hard problem of consciousness	This distinction was drawn by philosopher David Chalmers. "Easy" problems of consciousness (which are easy in principle only) include understanding the neural basis of feature detection, integration, verbal report, etc. The hard problem is the problem of experience; even if we understand everything about neural function, it is not clear how that would explain subjectivity.
Awareness	Cognitive neuroscientists and philosophers use the term "awareness" to mean only subjective experience. In clinical anesthesiology, the term awareness is (inaccurately) used to include both consciousness and explicit episodic memory.
Wakefulness vs. awareness	Wakefulness refers to brain arousal, which can be manifest by sleep-wake cycles and can occur even in pathologic conditions of unconsciousness such as vegetative states. Thus, being awake is dissociable from being aware.
Phenomenal vs. access consciousness	Phenomenal consciousness is subjective experience itself, whereas access consciousness is that which is available to other cognitive processes (such as working memory or verbal report).
External vs. internal consciousness	External consciousness is the experience of environmental stimuli (such as the sound of an orchestra), whereas internal consciousness is an endogenous experience (such as a dream state).
Consciousness vs. responsiveness	An individual may fully experience a stimulus (such as the command "Open your eyes!") but not be able to respond (as when a patient is paralyzed but conscious during surgery).
Levels of consciousness vs. contents of consciousness	Levels of consciousness include distinctions such as alert vs. drowsy vs. anesthetized, whereas the contents of consciousness refer to particular phenomenal aspects such as a red rose vs. a blue ball.

(Table 3.1). Awareness refers to the content of consciousness (red apple vs. blue sky), whereas arousal refers to brain activation and level of consciousness (alert vs. drowsy vs. asleep vs. anesthetized). A number of current theories about consciousness propose that the cortex is the primary site containing the neural correlates of awareness (Tononi and Edelman, 1998; Van der Werf et al., 2002; Crick and Koch, 2003; Seth et al., 2005; Franks, 2008; Brown EN et al., 2011), whereas midline subcortical brain structures provide ascending arousal influences to the cortex (Van der Werf et al., 2002; Franks, 2008; Brown EN et al., 2011). Thus, we can explore both top-down and bottom-up approaches to consciousness.

Top-Down Approach

Seth et al. (2005) propose three main physiological reasons supporting the importance of the neocortex to the process of consciousness. First, the electroencephalogram of virtually all mammals and birds in the awake state is characterized by desynchronized, high-frequency, and low-amplitude activity. This pattern changes to one of low-frequency, high-amplitude activity during depressed levels of consciousness such as nonrapid eye movement (NREM) sleep, minimally conscious states, and anesthesia. Thus, a state-dependent change in the electrical firing properties of the neurons across the neocortex varies with the level of arousal and strongly supports the idea that neuronal activity in the brain (and particularly in the neocortex) is a necessary requirement for consciousness (Revonsuo, 2006).

Second, consciousness appears to be linked more specifically with neural activity in the thalamocortical system. In this view, the midline brain structures of brainstem and midbrain are thought to be important for keeping the cortex in an aroused or awake state, whereas the cortical regions are thought to serve as specific cognitive modules contributing to the contents of conscious experience. The idea that certain brain regions are more important than others for generating the contents of consciousness is further supported by a number of basic neurological facts. For instance, a person could suffer the loss of the cerebellum or large bilateral portions of the medial temporal lobes, including amygdala and hippocampus complex, and would not become unconscious. However, focal damage to specific areas of cortical tissue will change the contents of a person's consciousness in a way that matches the loss of function associated with the specific area damaged. Cortical lesions can thus result in such specific impairments of consciousness that one may no longer be able to speak, perceive color, or identify parts of themselves as their own (Aguirre et al., 1998). Damage to lower midline brain structures, on the other hand, will likely alter the level of consciousness (i.e., arousal) without necessarily changing its contents.

Thalamocortical oscillations have been posited to be of critical importance to consciousness because they help integrate functionally diverse and spatially distinct cognitive modules in the cortex (Saalmann et al., 2012; Schmid et al., 2012). The interplay of segregation and integration is a fundamental focus of the integrated information theory of consciousness (Tononi, 2004, 2012). The capacity of the thalamocortical system to achieve both integration and differentiation is reflected in higher levels of Phi, a proposed metric for consciousness (Tononi, 2004). Phi reflects the amount of information generated by an integrated system beyond the information contained within the components of the system. In principle, this measure captures the emergent property of the system (consciousness) that cannot be causally reduced to individual subsystems (particular brain regions). Phi is predicted to decrease during sleep and seizures; preliminary evidence suggests it also decreases during anesthesia (Lee et al., 2009b), possibly due to impaired long-range coupling of neural spike activity (Lewis et al., 2012). Although the integrated information theory of consciousness has yet to be definitively demonstrated, it is a guiding paradigm that can inform the evolution of consciousness from the network perspective. Creatures with brain network systems that are capable of generating high values of Phi are more likely to be conscious (Edlund et al., 2011).

Third, widespread brain activity appears correlated with conscious activity. Sensory input spreads quickly from sensory cortex to parietal, temporal, and prefrontal areas (Dehaene et al., 2003). This spread of cortical activity is also associated with recurrent local feedback occurring along the way, followed shortly thereafter by long-range feedback from anterior to posterior structures (Lamme, 2006). These long-range connections are thought to be important for the experiential aspects of consciousness (i.e., awareness) (Singer, 1993) and appear to be preferentially suppressed during general anesthesia (Lewis et al., 2012; Schröter et al., 2012). In particular, there is strong evidence that networks across the frontal and parietal cortices are associated with awareness across multiple sensory modalities (Gaillard et al., 2006; Fahrenfort et al., 2008; Blumenfeld, 2012). The lateral frontoparietal network plays a role in mediating consciousness of the environment, whereas the medial frontoparietal network plays a role in mediating internal conscious states such as dreaming and internally directed attention (Boly et al., 2007; Denton et al., 2009). It is becoming increasingly clear that the directionality of corticocortical network communication is relevant to conscious processing. Information processing from the caudal to rostral direction (feedforward) is associated with sensory processing that can occur in the absence of consciousness (e.g., general anesthesia, priming) (Imas et al., 2005; Gaillard et al., 2007). In contrast, information processing in the rostral-to-caudal direction (feedback or cortical reafference) is thought to be associated with experience itself and is preferentially inhibited by general anesthetics (Imas et al., 2005; Lee et al., 2009a; Ku et al., 2011).

The neocortical view of consciousness originates, in part, from early morphologic examination of brain differences across species that suggested the capacities of consciousness increased as brains evolved from more primitive reptilian organization, to mammalian (or, with a limbic system, paleomammalian), and then neo-mammalian organization, characterized by an intricately folded neocortex. This conceptualization of brain evolution occurring in stages during which more "advanced" brains—along with their expanded behavioral repertoire—were built on the structure of earlier forms was popularized by Maclean as "the triune brain" (Maclean, 1990). Importantly, this view of brain evolution is now largely considered erroneous (Emery and Clayton, 2005; Jarvis et al., 2005). It did offer an easy conceptualization for relating brain structure with function and suggested evolutionary time points for when various behaviors would have emerged. Newer findings, however, strongly refute the model of a triune brain, especially the concept of a later-developing neocortex (Fig. 3.1) (Emery and Clayton, 2005). As it turns out, a precursor of the neocortex was actually present in the earliest evolving vertebrates, a claim based on some aspects of connectivity and homology of early transcription factor expression (Striedter, 2005). The basic structural pattern of a brainstem, midbrain, and forebrain did not need to be completely reinvented as each new species emerged. Rather, as various ecological niches were exploited by various creatures, those brain regions best suited for enhancing survival in the local environment were emphasized for further development (Emery and Clayton, 2005).

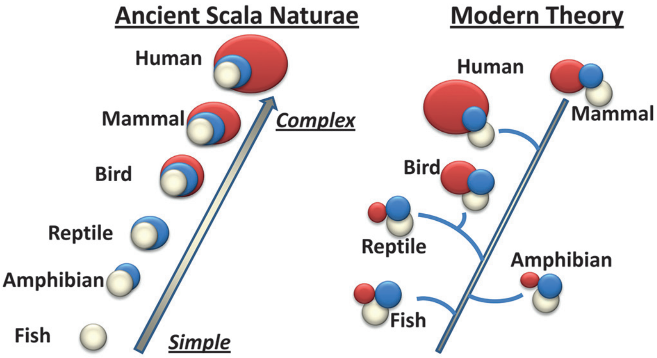


FIGURE 3.1 Theories of brain evolution. Ancient brain structure evolution theory of Scala Naturae showing brain development proceeding from simple to more complicated with the addition of new brain regions as evolution progressed. This erroneous view is compared with a modern understanding of brain structure evolution that reveals a basic common structure evolved in the vertebrate brain and various regions expanded to accommodate each specific animal's needs. Modified from Emery and Clayton (2005) with permission from Elsevier. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

Bottom-Up Approach

Since the discovery of the ascending reticular activating system by Moruzzi and Magoun in the late 1940s (Moruzzi and Magoun, 1949), the fundamental and permissive role for arousal in generating conscious states has been well established. It is now clear how a number of specific nuclei and specific cell types within the brainstem, midbrain, basal forebrain, and diencephalon send long-range axons throughout the cortex to enhance arousal and generate a neurochemical environment in the cortex that is capable of supporting consciousness (Lydic and Baghdoyan, 2005). The role of arousal in regulating overall levels of consciousness is clearly established in connection with depressed levels of consciousness as during sleep or coma (Laureys et al., 2004). How arousal machinery interacts with consciousness during more subtle cognitive and behavioral manipulations is the subject of much current research (Cahill and Alkire, 2003; Coull et al., 2004; Devilbiss et al., 2006). However, through the study of arousal as it relates to emotion (Paus, 2001; McGaugh, 2005), another link is made that puts some of Darwin's later investigations into a more modern light.

Darwin spent the later years of his career investigating the similarities and differences associated with emotional expression in man and animals (Darwin, 1872). He reasoned that if animals show emotion through behavioral expression, and man is an animal, then the behavioral expression of emotion in man must share a similar neurobiologic evolution with the other animals capable of expressing similar emotions. Put another way, years before behaviorism dominated neuroscience, Darwin saw how commonalities in emotional expression across species likely reflected the occurrence of similar underlying states of mind that only made sense within a theory of evolution. Modern study into the emotional lives of animals now reveals how fundamentally similar the brain structures are that support affective reactions in animals and humans (Panksepp, 2011).

Consciousness may not have emerged from the need to make an internal representation of the outside world, but rather as an extension of very basic primitive or primordial emotional influences. Such emotional influences would generate an arousal response in an organism and prepare its brain for action. This hypothesis is well elaborated by Denton (2005) in his book on primordial emotions. It posits that the most basic instincts, such as thirst, hunger for air, hunger for salt and food, and the desire for sex are the defining starting points for evolving a conscious brain (Denton et al., 2009). This idea holds within it the concept of intention, desire, and action selection, where the basic intention of a movement is in the service of fulfilling a desire. As noted by Darwin (1872), "So strongly are our intentions and movements associated together, that if we eagerly wish an object to move in any direction, we can hardly avoid moving our bodies in the same direction, although we may be perfectly aware that this can have no influence."

The basic behavior of an organism is driven by a fundamental physiologic need to maintain homeostasis. Those cells and systems used for monitoring and maintaining the internal milieu are referred to as interoceptors (Denton, 2005). The basic behaviors driving homeostasis are evident as far back as the first multicellular organisms that needed a vascular system to provide nutrients to those cells no longer exposed directly to the environment. Creatures that could meet their basic homeostatic needs are the ones that survived; those that did not suffered extinction. The brain structures needed for generating arousal and primitive emotional responses are generally located in the brainstem, midbrain, and limbic system and are as old as the vertebrate radiation itself (Jing et al., 2009).

Recent work on the lamprey, a jawless fish whose common ancestor forms the basis for all vertebrates more than 500 million years ago, has revealed just how ancient the neuroanatomy and neurochemistry needed for action selection is. Findings reveal that the lamprey's behavioral motor output system shows similar complexity to higher-level vertebrates who are capable of regulating behavior by both direct and indirect motor output pathways from the basal ganglia (Stephenson-Jones et al., 2012). In other words, the lamprey is capable of both selecting a motor output to perform and at the same time inhibiting the performance of other possible outputs. Thus, they are capable of making a choice depending on the situation with which they are confronted. This "reduction of uncertainty" (a classic definition of information) through action selection may be the precursor to the highly informative states of consciousness characteristic of humans. We address the relationship of motoric behavior and consciousness in the next section.

More complex neocortical abilities offered a survival advantage to more complex brains by giving organisms a larger grasp of their surroundings, but these systems developed over time and used sensory information from the environment or exteroreceptors (Denton, 2005). Denton illustrates his point with the example of a dehydrated frog placed next to a water source in the sun. The frog has only a limited capacity in its visual system and when placed next to a source of water it will usually die without moving, unless it stumbles on the water by accident. If, by chance, the frog finds the water, it will drink, which suggests functioning interoreceptors. In contrast, the more highly evolved visual system of the lizard allows that creature to see the water and immediately drink, suggesting that its more evolved brain more successfully couples its exteroreceptor-mediated perceptions with its interoreceptor-mediated needs. This coupling of an internally based need system with an externally based situational awareness system is likely the foundation for the emergence of consciousness, and it closely corresponds to the mental machinery seen in humans for generating awareness and arousal.

The brainstem arousal centers are, for the most part, juxtaposed with the sensory motor inputs and outputs of the cranial nerves that supply the head and neck with its ability to orient a creature to its environment and provide a stable platform for sensing its surroundings. The motor output of the cranial nerves is fundamentally linked with the expression of emotion in essentially all vertebrates, and this likely emanates from the oldest of the predator–prey relationships. In essence, an open mouth signifies a meal for the predator, and if the hunt is successful, it would likely be associated with internal sensations of goal/task completion that would serve to fulfill a basic need for food in the predator. This goal completion/desire fulfillment would likely have positive reinforcing value for an organism and might easily be hypothesized to lead to internal states comparable to a sense of pleasure (Panksepp, 2011). For the prey, an open mouth heading toward it would certainly be cause for alarm, prompting an immediate escape response that, if successful, might be associated with an internal state of heightened arousal and fear (Panksepp, 2011). Thus, the most basic emotions and arousal states are associated with internal feedback networks that serve to guide an organism's behavior toward its best possible situational outcome. This emotional arousal machinery underlies essentially all behavioral choices in the vertebrate brain.

CONSCIOUSNESS IN NONHUMAN SPECIES

If consciousness evolved in conjunction with cephalad development of the central nervous system, then its emergence should, in principle, be identifiable at a discrete point on the tree of evolution. Darwin reasoned that the cognitive differences between species must be one of degree and not kind. This conclusion is consistent with the recent Cambridge declaration that occurred on July 7, 2012, at the first annual Francis Crick memorial conference on consciousness. A group of prominent scientists formally declared in a document entitled the "Cambridge Declaration on Consciousness in Non-Human Animals" that the neurobiological structures needed to support consciousness are not uniquely human (Low, 2012). This declaration essentially states that the capacity for consciousness likely emerged very early in evolutionary terms, and those processes that support consciousness in humans are likely characteristic of many living creatures. In fact, according to the declaration, based on a number of considerations from comparative brain anatomy and current knowledge about the neurobiology of consciousness, it would seem almost certain that some form of consciousness is present in all mammals and could have emerged on the evolutionary timeline at the branch point of amniotes.

However, long before the Cambridge declaration, some thinkers expressed serious concerns about attributing higher levels of consciousness to all life. Indeed, René Descartes, often considered the philosophical father of the mind–body relationship, questioned whether a conscious self arose in the animal kingdom. He avoided ascribing a conscious self to a particular animal because by doing so he recognized that he might be compelled to ascribe a conscious self to all animals. This all-or-none approach did not reflect an evolutionary theory perspective, which raised the possibility of a conscious continuum. This continuum, however, also introduces difficulty. As pointed out by Gallup (1985), in discussing the emergence of consciousness in animals,

> Where do we draw the line? On the one hand, we could decide not to draw a line. This would presume that all living things are sentient, conscious, and mindful. While the data are admittedly incomplete, the issue should be taken seriously. Life on this planet consists of several million different species. Most are microorganisms, plants, and insects. I doubt that there is a paramecium, a rosebush, or a termite alive today which is aware of its own existence or has the capacity to become the object of its own attention.

With Gallup's statement, we begin to see the need for clarity in how or why we associate certain behaviors with subjective experience and the need for some operational definitions of the "consciousness" being studied.

To identify the origin of sentience along an evolutionary timeline, it is beneficial to consider a common element that might link consciousness across species, rather than focusing on the ostensibly unique qualities of human experience such as self-reflection. Furthermore, this common element should likely relate to a goal-directed behavior or response pattern that confers a survival advantage in a given environment. In line with philosophers such as Merleau-Ponty and neuroscientists such as Rudolfo Llinás and György Buzsáki, we support motility (also referred to in this context as motricity) as a strong candidate for the evolutionary anlage of consciousness (Cotterill, 2001; Goodrich, 2010). Consider, for example, the unicellular paramecium, which is covered with several thousand cilia. These cilia can serve both the function of sensing environmental stimuli and initiating motility responses (e.g., attraction, avoidance) based on the nature of those stimuli. This preneural example of a single structure (i.e., cilia and their coordinated activity) mediating both sensation and response is intriguing but does not establish the primacy of motility as a kernel of consciousness. Perhaps a more compelling case is that of the sessile sea squirt, which possesses neural structures only transiently during a larval stage (Llinás, 2001). Neural ganglia and primordial sensory processing allow the sea squirt to find a suitable local environment and underwater surface for attachment. However, after this goal is achieved the neural tissue is digested, suggesting a role related exclusively to movement. Although it is unlikely that paramecia and sea squirts have phenomenal experience, these early examples of sensation in the service of motility lead us to start the search for the neurobiological origins of consciousness in phylogenetically conserved structures.

WHAT IS THE NEURAL "CORE" OF CONSCIOUSNESS?

To identify which aspects of the mental machinery should be the focus of evolutionary consideration for consciousness, we need to identify the neural correlates of the most primitive core of human consciousness. The still emerging field of consciousness studies has been dominated in the last decade by a search for the neural correlates of consciousness, which have been defined as the specific and minimally adequate brain states that correspond to states of consciousness (Tononi and Koch, 2008). However, studies of the content of consciousness (e.g., the awareness of a red rose placed in your visual field) already assume a conscious brain; thus, the neural activity or structure identified in these paradigms corresponds to a specific content within a preexisting consciousness (Hohwy, 2009). Studying the level of consciousness (e.g., arousal states) is also beset with difficulties. For example, the transition from a fully conscious to unconscious state will inform us primarily of correlates required for the full spectrum of waking human consciousness rather than the minimal or core requirements. Furthermore, we must also grapple with how to identify the true correlate (or substrate) of consciousness vs. neural prerequisites or neural consequences of consciousness (Aru et al., 2012; de Graaf et al., 2012).

To address some of these difficulties, a recent study explored the neural correlates of the primitive form of consciousness that arises during emergence from general anesthesia (Långsjö et al., 2012). With anesthesia, the level of consciousness can be manipulated as an experimental variable, and the resultant changes in brain activity can then be determined with various neuroimaging and neurophysiologic techniques. Numerous studies have now examined what happens to brain activity when consciousness is removed by anesthesia (Alkire et al., 2008; Brown et al., 2010); however, fewer studies have investigated the correlates of consciousness associated with its return following a period of anesthesia (Friedman et al., 2010; Lee U et al., 2011; Xie et al., 2011; Bonhomme et al., 2012). In one recent study of healthy male volunteers, positron emission tomography (PET) was used to investigate the neural correlates of the recovery of consciousness from the i.v. anesthetics propofol and dexmedetomidine (Långsjö et al., 2012). The order of the state transition is important because the investigation of consciousness to unconsciousness may yield a variety of nonspecific deactivations due to drug effects that do not necessarily play a core role in consciousness. The emergence of consciousness (as judged by the return of a response to command) was correlated primarily with activity of the brainstem (locus coeruleus), hypothalamus, thalamus, and anterior cingulate (medial prefrontal area). Surprisingly, there was limited neocortical involvement that correlated with this primitive form of consciousness. Frontal–parietal connectivity appeared to be the key cortical response, which has been confirmed by studies of consciousness and anesthesia using electroencephalography (Lee U et al., 2011). Similar findings were seen in another imaging study investigating the emergence of consciousness from sleep (Balkin et al., 2002). In the sleep study, midline arousal structures of the thalamus and brainstem also recovered function well before cortical connectivity resumed. Thus, the core of human consciousness appears to be associated primarily with phylogenetically ancient structures mediating arousal and activated by primitive emotions (Liotti et al., 2001; Denton et al., 2009), in conjunction with limited connectivity patterns in frontal–parietal networks (Merker, 2007; Brusseau, 2008) (Fig. 3.2).

The emergence from general anesthesia may be of particular interest to evolutionary biology, as it is observed clinically to progress from primitive homeostatic functions (such as breathing) to evidence of arousal (such as responsiveness to pain or eye opening) to consciousness of the environment (as evidenced by the ability to follow a command) to higher cognitive function. Unlike the emergence of consciousness over millions of years in phylogeny or months during the gestational period in ontogeny, the emergence of consciousness from the anesthetized state is a reproducible model system that can be observed in real time over the course of hours. Multimodal investigation using neuroimaging and neurophysiology, in conjunction with clinical observation and cognitive evaluation, could uncover key shifts of neural activation or network organization that support conscious processing. For example, high-density electroencephalography could be used during recovery from general anesthesia to measure Phi to help delineate in humans the threshold for emerging consciousness. Such a threshold could then be compared with other species in the waking state to determine the relative value with reference to the neural core of human consciousness. This approach could be applied to any number of brain network properties, as assessed quantitatively through graph theoretical methods (Stam and van Straaten, 2012b).

Network approaches—which have broad applicability in mathematics, biology, computer science, and sociology—might be particularly attractive to test hypotheses across species, where functionally similar cognitive systems may arise from neurobiologically distinct structures.

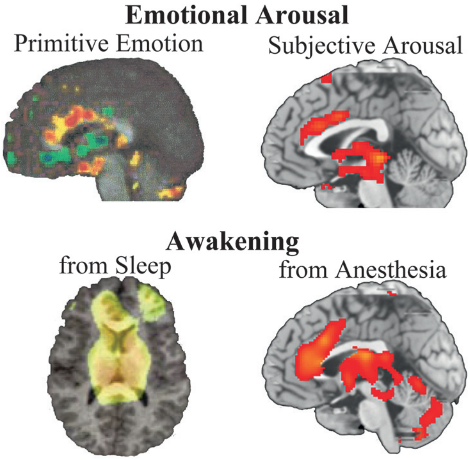


FIGURE 3.2 Brain structures functionally related to primitive emotional arousal and the return of consciousness following sleep or anesthesia. The primitive emotional response of air hunger shows activations in brainstem and anterior cingulate regions; thalamic changes are also seen (Liotti et al., 2001). Subjective emotional arousal activates similar regions in an event-related functional MRI study of picture viewing. Reproduced with permission from Hayama et al. (2012). Midline thalamic and anterior cingulate arousal is seen with PET neuroimaging when consciousness first reemerges following sleep or anesthesia. Reproduced with permission from Balkin et al. (2002) and Långsjö et al. (2012). A common brainstem, thalamic, cingulate neuroanatomy associated with conscious brain activity is seen. Images used with permission. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

For example, the mammalian cortex and avian pallium are histologically distinct (Table 3.2) (Butler, 2008), but may subserve similar network functions that can be quantitatively assessed and compared with human findings. General anesthesia represents a way of turning back the evolutionary clock of cognitive function in humans and—depending on the "depth" and length of anesthetic exposure—allows investigators to observe the return of neural function in a way that could recapitulate phylogeny. Although not without difficulties (including the contamination of access consciousness, because language is involved in assessing return of consciousness after anesthesia), advantages of emergence from anesthesia as a model system for the evolution of consciousness include convenience, reproducibility, real-time observation, possibility of subjective report of experiences (with experiments in humans), and amenability to neuroscientific investigation across multiple species.

TABLE 3.2 Comparison of Neocortex and Pallium with Respect to Requirements for Cell Assemblies

Requirements for Hebbian Cell Assembly	Structure of Mammalian Neocortex	Structure of Avian Pallium
Many neurons of the same kind	About 85% pyramidal cells	High number of multipolar cells
Connections with each other	Most synapses are between pyramidal cells	Many synapses between multipolar cells
Excitatory connections	About 90% of synapses are type 1 (excitatory)	Many synapses excitatory
Modifiable connections	About 75% of synapses are on spines	Dendrites are densely spiny
Individual neurons connected to as many other neurons as possible	About 8,000 synapses per neuron	Many synapses per neuron
Distant connections across the network	Large amount of white matter	Axons more interspersed with neurons

SOURCE: Modified from Butler (2008) with permission from Elsevier.

WHEN DOES CONSCIOUSNESS OF THE WORLD ARISE?

The recent experiments with general anesthesia in humans suggest that phylogenetically ancient structures in the brainstem and diencephalon—with only limited neocortical involvement—are sufficient to support primitive consciousness. Where, then, does consciousness arise on the evolutionary timeline? One might be tempted to conclude that consciousness commenced as our mammalian ancestors evolved just beyond reptiles and their predominantly subcortical brains. However, paleontological findings suggest that the synapsid line that gave rise to mammals and the sauropsid line that gave rise to reptiles and birds both diverged from the primitive anapsid line at a single point ~315 million years ago (Warren et al., 2008). Furthermore, there is significant evidence that avian species are capable of higher cognition and even consciousness itself (Butler and Cotterill, 2006). For example, birds demonstrate evidence of explicit episodic recall (i.e., conscious memory of an event) (Emery and Clayton, 2004) and theory of mind (i.e., attribution of subjective mental events to another being) (Emery and Clayton, 2001). Thus, it would be misguided to try to identify a single point at which consciousness emerged because evidence suggests that consciousness evolved along two independent lineages. As pointed out by Butler et al. (2005), birds and mammals share a number of homologous traits despite this evolutionary divergence, including a dramatic increase in their brain–body ratios (compared with reptiles), homeothermy, extended parental care of offspring, habitual bipedalism, distinct sleep stages, and complex social interactions. The neurobiology also reflects homologous advances, particularly in the mammalian neocortex and the avian pallium (Table 3.2). These advances include the emergence of recurrent or feedback processing, which is not found in reptiles. Thus, both birds and early mammals are equipped with a neural substrate consistent with conscious processing: phylogenetically conserved brainstem, diencephalic structures such as thalamus and hypothalamus, and association neocortex (or equivalent) capable of recurrent processing. All of these structures appear to play a role as the neural core for primitive consciousness in humans, as evidenced by experiments with general anesthesia.

The critical role of subcortical structures in consciousness has been further argued based on clinical observations of hydranencephalic children, who are essentially devoid of neocortex and yet who still demonstrate some behavioral signs of consciousness (Merker, 2007). Others have attempted to link the arousal-related components of consciousness with the contents of consciousness by placing emphasis on the dynamic recurrent activity that occurs in the thalamus or through the thalamic reticular nucleus when consciousness is present (Min, 2010; Ward, 2011). As such, the PET study showing that the emergence of consciousness is correlated with increased activity in "primitive" brain regions may reflect an arousal-related response to the test stimulus itself rather than a direct awareness of the stimuli that are occurring in the thalamus. In either event, the data clearly show that the neurocircuitry associated with arousal is fundamental to consciousness. A further recent study investigating long-term memory encoding also imaged the neural correlates of subjective emotional arousal. As shown in Fig. 3.2, the neural correlates for awareness of subjective arousal induced by viewing of emotional stimuli involve the same midbrain arousal structures seen with activation of primordial emotions (Hayama et al., 2012).

Regarding ontogeny of *H. sapiens*, peripheral sensory receptors are thought to be present from 20 weeks of gestation in utero. The developmental anlage of the thalamus is present from around day 22 or 23 postconception, and thalamocortical connections are thought to be formed by 26 weeks of gestation (Brusseau, 2008). Around the same time of gestation (25–29 weeks), electrical activity from the cerebral hemispheres shifts from an isolated to a more continuous pattern, with sleep-wake distinctions appreciable from 30 weeks of gestation. Thus, both the structural and functional prerequisites for consciousness are in place by the third trimester, with implications for the experience of pain during in utero or neonatal surgery. It is of interest to note that the third trimester of human development is thought to be the period in which the maximal proportion of time spent in REM sleep occurs across the lifespan (Birnholz, 1981). This finding supports the ontogenetic theory of REM sleep as a process of internally driven neuronal activation that prepares the developing cortex for the coming influx of sensory stimuli at birth. The theory of REM sleep as a form of protoconsciousness has recently undergone further elaboration (Hobson, 2009).

WHEN DOES CONSCIOUSNESS OF THE SELF ARISE?

One component of consciousness that seems linked to higher cognitive abilities is awareness of the self rather than simply awareness of the environment. One way to test for this possibility is to use what is known as the mirror self-recognition (MSR) test (Keenan et al., 2003). In 1970, Gallup found that chimpanzees, but not monkeys, were able to pass the MSR test (Gallup, 1970). This test presupposes that the experimental subject has sufficient cognitive ability to be aware of itself as an entity that is distinct from another conspecific. This ability then defines one form of consciousness (i.e., the ability to have awareness of one's own awareness or self). In Gallup's well-controlled experiment, the animals were first allowed ample time with mirror exposure to allow social responses to their reflected images to diminish greatly. The number of social responses and the number of self-directed responses were measured before the animals had a mark covertly placed on their forehead or ear while they were briefly anesthetized. The animals were then allowed to recover from anesthesia, and some hours later a mirror was reintroduced. On seeing themselves in the mirror, the marked chimpanzees—but not the marked monkeys—exhibited mark-directed responses by spending time investigating the area of the mark and examining their fingers after touching the mark. The findings led Gallup to conclude "insofar as self-recognition of one's mirror image implies a concept of self, these data would seem to qualify as the first experimental demonstration of a self-concept in a subhuman form." Regarding the difference between chimpanzee and monkey, he further concluded, "Our data suggest that we may have found a qualitative psychological difference among primates, and that the capacity for self-recognition may not extend below man and the great apes." The distinction among primates suggests that the qualitative nature of the conscious experience varies greatly across species and the introspective nature of human consciousness may be evolutionarily quite rare. The MSR test has now been used to examine the ability of other species to show evidence of self-awareness. Primates that have passed the MSR test include chimpanzees, orangutans, and bonobos. The case for the gorilla is equivocal with mostly negative findings; several studies have suggested that more socialized gorillas might be able to pass the test. Humans begin to develop a sense of self and pass the MSR test starting around 18 months of age, and by 24–36 months, almost all western children will show a positive MSR response (Amsterdam, 1972). The distinction between great apes and monkeys would seem to provide a clear demarcation in the capacity for consciousness between species. Numerous studies have supported this demarcation, with multiple failed attempts to detect self-awareness in monkeys, despite one recent report to the contrary (Rajala et al., 2010). However, a number of methodological concerns limit enthusiasm for the one contrary study, and overall the data continue to suggest that macaques do not evidence MSR behavior (Anderson and Gallup, 2011). In evolutionary terms, if objective evidence of self-awareness can be taken as evidence for consciousness, then consciousness as it occurs in the primate with their more fully developed cortex may have evolved ~5 million years ago, at around the time when great apes split off from the lesser apes.

Mirror self-recognition may not be limited to the relatively big-brained great apes. More recent work with other big-brained creatures suggests the possibility that dolphins, and at least one African elephant, may also be capable of this response (Delfour and Marten, 2001; Reiss and Marino, 2001; Plotnik et al., 2006). As apes, elephants, and cetaceans have a very remote common ancestor, these findings would seem to suggest that the mental machinery prerequisite for self-awareness must be at least as old as the development of the placental divide in mammals (Wildman et al., 2007). However, we may be able to take this idea on another path in evolutionary time. As noted, the cognitive abilities of some birds are now thought to be comparable to the abilities of some primates (Emery and Clayton, 2004). Evidence suggests that the brain development of the bird, which evolved on a different path from mammals, still has a conceptually similar thalamocortical structure that can be delineated (Jarvis et al., 2005). The cognitive abilities of various birds seem to correlate with the relative size of the analogous avian prefrontal cortex. Indeed, the crow-like Corvidae (crows, ravens, magpies, rooks, jackdaws, and jays) appear to have the most advanced behavioral repertoire, as well as the largest prefrontal cortex (pallium) (Emery, 2006). Importantly, a recent report shows magpies (having a relatively large prefrontal cortex) exhibit behavior consistent with MSR (Prior et al., 2008). This finding, coupled with the current understanding of avian neuroanatomy and its well-developed thalamocortical structure, suggests that the foundations required for both consciousness of the world and consciousness of the self may have formed as early as the amniote radiation (Warren et al., 2008).

From a cognitive perspective, the meaning of self-awareness behaviors in a mirror remains somewhat controversial (Morin, 2011). Some argue that the mirror behavior could be more easily explained by simple knowledge of one's body. The neurobiology of having a body sense is something that is highly linked with a sense of consciousness (Damasio, 2003). Perhaps, as stated by Morin (2011), "all an organism requires to self-recognize is a mental representation of its own physical self; the organism matches the kinaesthetic representation of the body with the image seen in the mirror and infers that 'it's me.'" A number of other arguments against overinterpreting MSR have been made, yet despite these relevant concerns, from an evolutionary point of view the presence or absence of a MSR response is at least a starting point for considering what having such a response might mean as a basis for the evolution of consciousness. The MSR response allows one to question what is functionally and structurally different about brains that can self-recognize vs. those that cannot.

WHY IS HUMAN CONSCIOUSNESS UNIQUE?

We have argued that the brainstem, diencephalon, and limited association cortex capable of recurrent processing is consistent with a core or primitive consciousness. However, what accounts for the richness of human experience in contrast to those of early mammals or birds? Drawing on the integrated information theory of consciousness, the evolution of more complex brain networks capable of synthesizing the outputs of more functionally diverse modules would result in a higher capacity for consciousness. Indeed, integration of information appears to correlate positively with fitness in artificial agents (animats) (Edlund et al., 2011). It is unknown in biology, however, whether it is the level or quality of consciousness that differs across species. Although *H. sapiens* may have more advanced cognition, it is difficult to imagine that a sedentary human has a higher level of consciousness than a highly alert beast in pursuit of prey; the richness of conscious experience may be what differs. Alternatively, it is possible that advanced symbolic processing in human cognition eclipses the subjective characteristics of experience. In other words, cognition may be potentially opposed to phenomenal consciousness. Despite these considerations, human consciousness—especially the capacity for self-consciousness and reflection/projection in time—seems unique. Although evidence suggests that the core of consciousness is rooted in phylogenetically older structures such as the brainstem and diencephalon (Merker, 2007), the evolution of that which is particular to human consciousness may be more closely associated with the development of the frontal cortex. The relative size of the frontal lobes with respect to the total neocortex is roughly the same in modern humans and great apes, but richer interconnectivity might account for advanced cognition in *H. sapiens* (Semendeferi et al., 2002). In particular, directed anterior-to-posterior connectivity has been associated with conscious perception and is dominant in humans (Ku et al., 2011) but not in rodents (Imas et al., 2005; Nieder, 2009) (Fig. 3.3). It has been suggested that the afferent information from the periphery converging at the hub of the posterior parietal cortex becomes, with the expansion of the frontal cortex, dominated by a strong anterior-to-posterior reafference (Noack, 2012). Indeed, a recent neural mass model based on structural connectivity data from diffusion tensor imaging in humans predicts an information flow from the frontal to the posterior parietal cortex (Stam and van Straaten, 2012a). In essence, this information flow reversal suggests that human consciousness is more defined by internal dynamics than external stimuli. This level of information flow reversal may help explain, in part, those animals capable of an MSR response. According to one theory, human consciousness is a closed system or "oneiric" (dream-like) state that is simply modulated by environmental input (Llinás and Ribary, 1993), a theory consistent with REM sleep as a building block for human consciousness. The relative independence from environmental determination of conscious content would potentially permit a greater diversity or richness of experience in comparison with species without dominance of anterior-to-posterior flow. This independence would also facilitate the projection and simulation associated with future plans, of clear relevance to survival. It is important to note, however, that the role of information flow in consciousness is unclear at this time and requires further neuroscientific investigation.

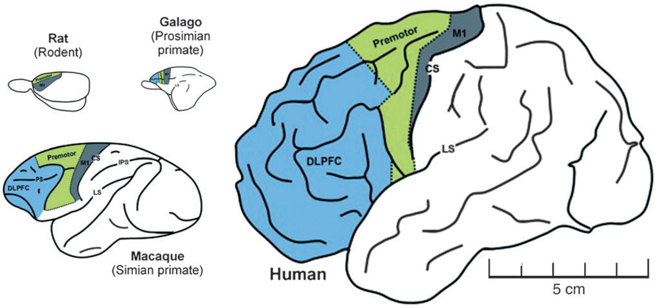


FIGURE 3.3 Schematic showing relative size of frontal lobe across different species and the potential capacity for anterior-posterior information flow. The DLPFC (blue) areas represent the prefrontal cortex, and the schematic shows how the prefrontal cortex proportionally increases in size with increasing brain size across species. Relative brain size is scaled to the human brain. Modified from Nieder (2009) with permission from Elsevier. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

CONCLUSION

The emergence of consciousness on the evolutionary timeline has been scientifically considered at least since the time of Darwin. The emergence of consciousness from the anesthetized state may provide a practical and reproducible model for characterizing the real-time evolution of the core neural correlates required for consciousness of the world and of the self. Using recent data from general anesthesia in humans, we suggest that the arousal centers in the brainstem and diencephalon—in conjunction with even limited neocortical connectivity and recurrent processing—can result in primitive phenomenal consciousness. By "reverse engineering," we postulate that early mammals and birds possessing these structures (or their equivalents) are capable of phenomenal consciousness. However, the increased complexity of networks and a functionally dominant prefrontal cortex in the brain of *H. sapiens* likely accounts for the unique richness of the human experience.

ACKNOWLEDGMENTS

G.A.M. is supported by National Institutes of Health Grant 1R01 GM098578 and the James S. McDonnell Foundation.

Part II

THE PRIMATE EVOLUTIONARY CONTINUITY

Shared neurologic mechanisms are the main argument in favor of continuity between nonhuman and human primates' minds. Several contributors to this Sackler Colloquium have studied these common mechanisms in the field of memory and its brain counterparts. In Chapter 4, Robert Clark and Larry Squire offer a history of the scientific debate provoked by Owen's (1859) proposal of a lack of evolutionary continuity between human and other primates on the grounds of several brain traits, hippocampus minor (HM) among them (Scoville and Milner, 1957). Since HM was proposed to have a strong role in the organization of memory, the possibility of using animal models appeared, thus supporting evolutionary continuity for the neuroanatomy of human memory. Clark and Squire examine such cross-species similarities in the field of the multiple-memory systems paradigm, offering challenges to the animal model when concurrent discrimination tasks are considered in both humans and monkeys.

Two chapters in this book focus on the evolution of memory. Peter Carruthers points out in Chapter 5 that, despite being fundamental to learning, speech, reading comprehension, prospection and planning, as well as to reflective serial conscious reasoning, working memory (WM) has been scarcely investigated under the across-species perspective. On the grounds of current research, Carruthers holds that WM is a homologous trait shared by humans and nonhuman primates, although our species is unique in aspects like inner speech. Also, humans may be unique in making frequent task-independent use of their WM abilities. However, in the absence of direct comparative studies, claims on the WM continuity or discontinuity remain somewhat speculative.

Next, in Chapter 6, Timothy Allen and Norbert Fortin offer a complementary analysis of the large body of research on the evolution of episodic memory (EM). The authors propose that protoepisodic memory systems link avian and human phylogenies, supporting the homologous character of traits, such as hippocampal–parahippocampal–prefrontal pathways that would be shared from a common neural ancestry, as opposed to the alternative possibility of evolutionary convergence. Despite this shared capacity, Allen and Fortin discuss eventual divergences, such as with regard to human language, self-consciousness, empathy, and Theory of Mind, holding that these constitute species-specific attributes associated with the expansion in human brains of prefrontal areas.

Differences in social behavior between species rely in part on the neuromodulatory regulation of neural circuits. In Chapter 7, Steve Chang and his coworkers offer clues on how biological specializations for social function transform ancestral mechanisms by means of duplication, repurpose, or differential regulation at multiple levels of organization, from neurons and circuits to hormones and genes. Social behavior shapes the structure and function of these mechanisms in a feedback way. Therefore, the authors hold that a neuroethological approach to the study of human and nonhuman primate social behavior might clarify the phylogeny of interactions between social behavior and neuromodulatory regulation.

The counterpart of phylogeny is ontogenetic development. Comparisons between human and macaque neocortical development show differences that might relate the relatively prolonged neuronal maturation in humans to the enhancement of social learning and transmission of cultural practices, including language. However, few data exist on the ontogenetic neural development of the apes that are more closely related to humans. By means of an experimental analysis, Serena Bianchi and her coworkers, in Chapter 8, show for the first time how *Pan paniscus* synaptogenesis matches the human case, with a peak of synapse density during the juvenile period (2–5 years of age). Also, chimpanzees and humans share a late development of dendrites of prefrontal pyramidal neurons, compared to sensorimotor areas, offering a common potential for enhanced developmental plasticity. The authors hold that their findings suggest that several key features of human brain ontogeny emerged prior to the divergence of the chimpanzee and human lineages.

4

Similarity in Form and Function of the Hippocampus in Rodents, Monkeys, and Humans

ROBERT E. CLARK[*,†,‖] AND LARRY R. SQUIRE[*,†,‡,§]

We begin by describing an historical scientific debate in which the fundamental idea that species are related by evolutionary descent was challenged. The challenge was based on supposed neuroanatomical differences between humans and other primates with respect to a structure known then as the hippocampus minor. The debate took place in the early 1860s, just after the publication of Darwin's famous book. We then recount the difficult road that was traveled to develop an animal model of human memory impairment, a matter that also turned on questions about similarities and differences between humans and other primates. We then describe how the insight that there are multiple memory systems helped to secure the animal model and how the animal model was ultimately used to identify the neuroanatomy of long-term declarative memory (sometimes termed explicit memory). Finally, we describe a challenge to the animal model and to cross-species comparisons by considering the case of the concurrent discrimination task, drawing on findings from humans and monkeys. We suggest that analysis of such cases, based on the understanding that there are multiple memory systems with different properties, has served to emphasize the similarities in memory function across mammalian species.

---

[*] Veterans Affairs Medical Center, San Diego, CA 92161; and Departments of [†] Psychiatry, [‡] Neurosciences, and [§] Psychology, University of California at San Diego, La Jolla, CA 92093.
[‖] To whom correspondence should be addressed. E-mail: reclark@ucsd.edu.

Here, we describe the successful development during the past few decades of a model of human memory and human memory impairment in monkeys and rodents. This work, which focused on the hippocampus and anatomically related brain regions, provides a robust illustration of similar neuroanatomy and function across species. The expectation that the study of experimental animals should yield insights into the organization of human memory is certainly reasonable when considered in the light of evolution and evolutionary theory. Indeed, the central idea behind the study of nonhuman mammals is the notion that what can be learned about mammalian behavior and mammalian brains can improve understanding of the human brain and the human condition. However, this perspective was not so easily attained. We begin by describing an historical scientific debate in which this fundamental idea (continuity between nonhumans and humans) was challenged on the basis of supposed neuroanatomical differences between humans and other primates. The debate took place in the early 1860s, just after the 1859 publication of Darwin's (1859) *On the Origin of Species*. We then describe the difficult road that was traveled to develop an animal model of human memory impairment.

HIPPOCAMPUS MINOR AND BRAIN ANATOMY

In 1859, Sir Richard Owen (1804–1892), the renowned British comparative anatomist and paleontologist, and superintendent of the Natural History Department of the British Museum, member of the Royal Society, and author of more than 600 scientific publications, published a provocative and controversial paper (Owen, 1859). He argued that humans should be reclassified as distinct and separate from other primates. Up to this point, Linnaeus classification had placed humans, apes, and monkeys into the single order Primates. Owen's new classification created not only a new order for humans (Bimana "two-handed ones") but a new subclass for humans (Archencephala "ruling brain"), which placed humans well apart from other primates. On the final page of his essay, Owen provided the following summary: "Man is the sole species of his genus, the sole representative of his order and subclass. Thus I trust has been furnished the confutation of the notion of a transformation of the ape into man, which appears from a favourite old author to have been entertained by some in his day" (Owen, 1859).

It has been argued (Gross, 1993a) that this reclassification must have been due, at least in part, to Owen's knowledge of the forthcoming publication of Charles Darwin's (1859) *On the Origin of Species*. It was well known even before publication that Darwin's book would emphasize a clear physiological and anatomical relationship among species and argue that all species descended from common stock (in addition to proposing the theory of "natural selection" as the mechanism for driving evolution).

Owen based his new classification on three ostensible neuroanatomical differences in brain structure between humans and other animals, including nonhuman primates. He suggested that these three anatomical features were fundamental because these structures were not just different in humans and other primates but were found uniquely in the human brain (Owen, 1859). According to Owen, the first fundamental difference between humans and animals was that only in humans was there a posterior lobe. Specifically, only the human cerebrum extended over and beyond the extent of the cerebellum. The second difference was that only humans have a posterior horn or cornu of their lateral ventricles (a portion of the lateral ventricle that extends posteriorly and laterally). The third and most important difference was that only humans have a hippocampus minor.

Within the floor of the lateral ventricles are two prominent structures: a large structure referred to at that time as the hippocampus major (now known simply as the hippocampus) and a smaller structure known then as the hippocampus minor. The hippocampus minor is a ridge in the floor of the posterior horn of the lateral ventricle. The original term for the hippocampus minor, and the term in current use, is the calcar avis. The calcar avis is a Latin term meaning "cock's spur" due to its resemblance to the spurs found on rooster legs.

Owen's reclassification was met with a vigorous opposition, led principally by Thomas Henry Huxley (1825–1895). Huxley was a British biologist, paleontologist, and anatomist. In his lifetime, he served as president of the Royal Society, president of the Geological Society, and president of the British Association for the Advancement of Science, and he was one of Darwin's most vocal scientific supporters. The debate between Owen and Huxley was anticlimactic in one sense because Huxley was easily able to demonstrate that Owen's three criteria, including the hippocampus minor, were not only identifiable in all primate species available for study but that the relative size of the hippocampus minor was larger in some primate species than in humans (Huxley, 1861a,b, 1863). During the course of his investigations, Huxley also discovered that the hippocampal fissure in primates actually consisted of two separate fissures. The more anterior fissure retained the name hippocampal fissure, whereas the more posterior fissure was renamed by Huxley as the calcarine sulcus because the calcar avis, or hippocampus minor, is, in fact, formed by the deep inward penetration of the calcarine sulcus (Huxley, 1861a). The hippocampus minor debate can be said to have concluded when Sir Charles Lyell, Great Britain's leading geologist and one of its most eminent scientists, reviewed in detail the hippocampus minor debate (Lyell, 1863). Lyell authoritatively concluded, without reservation, that the hippocampus minor debate was settled in Huxley's favor. Lyell's conclusion was all the more compelling because Lyell had not fully embraced Darwin's theory of evolution.

Despite its brief lifetime, the debate over the hippocampus minor was important. It has been suggested by some historians (Desmond, 1984; Gross, 1993b) that Huxley intended to show not only that Owen was incorrect but that he must have been intentionally obfuscating the facts. Huxley admitted as much in a letter he sent to Sir Charles Lyell on August 17, 1862 [the letter is reproduced in Huxley (1900)]. In this letter, Huxley references a line from a well-known poem by the noted paleontologist, Sir Philip Egerton. Huxley wrote: "I do not think you will find room to complain of any want of distinctness in my definition of Owen's position touching the Hippocampus question. I mean to give the whole history of the business in a note, so that the paraphrase of Sir Ph. Egerton's line 'To which Huxley replies that Owen he lies,' shall be unmistakable." Huxley's effort damaged the scientific reputation of perhaps the most prominent antievolutionist of the time and helped pave the way for the broad scientific acceptance of evolution by scientists during the following decades [excellent reviews of the hippocampus minor debate are provided by Gross (1993a,b)].

In the end, the hippocampus minor debate provided another example of the similarities in neuroanatomical organization among all primate species, including humans. The same would later prove to be true for hippocampal function and for the organization of long-term memory across species ranging from rodents to primates. However, as described in the sections that follow, the continuity of memory function across species was in serious doubt for nearly two decades.

HIPPOCAMPUS AND THE MODERN ERA OF MEMORY RESEARCH

The modern era of memory research, and the first insights about the hippocampus and the organization of memory, began with the description of patient H.M. by William Beecher Scoville and Brenda Milner. Patient H.M. had a history of minor and major seizures that were unresponsive to antiepileptic medication. Eventually, with the consent of the family, the surgeon Scoville attempted to relieve the seizures with an experimental surgical intervention that involved resecting the medial aspect of the temporal lobe bilaterally. Subsequently, MRI scans showed that the lesion was bilaterally symmetrical and included the medial temporal polar cortex, virtually all the entorhinal cortex and amygdaloid complex, and the anterior half of the intraventricular aspect of the hippocampal formation [i.e., dentate gyrus (DG), hippocampus, subicular complex]. The perirhinal cortex was substantially damaged as well, with some sparing of its ventrocaudal aspect (Corkin et al., 1997). The surgery succeeded in that it reduced the frequency and severity of the seizures, but it left H.M. with profound amnesia.

The subsequent systematic evaluation of H.M. and other patients with similar damage established three fundamental principles (Squire, 2009). First, memory is a distinct cerebral ability that is separate from other cognitive functions, such as perception, intelligence, personality, and motivation. Second, short-term memory and long-term memory are distinct functions, because H.M. had severely impaired long-term memory. However, he could maintain and use information for a short time in immediate memory (and working memory) so long as the material could be effectively rehearsed. With distraction, the information was lost. Third, medial temporal lobe structures are not the ultimate repository of long-term memory because H.M.'s memory for remote events remained largely intact.

At the time that H.M. was first described, the anatomy of the medial temporal lobe was poorly understood and it was not known what specific damage (within the large region included in his surgery) was responsible for his memory impairment. Accordingly, efforts were begun to address this question in experimental animals. In fact, these efforts began almost immediately when Scoville himself went to Montreal and performed the same surgery in monkeys that he had performed with H.M (Correll and Scoville, 1965). However, these monkeys and others with medial temporal lobe lesions were able to learn tasks that seemed similar to tasks that H.M. could not learn.

The difficulty was that it was not yet appreciated that humans and experimental animals can approach ostensibly similar tasks using different strategies (*Multiple Memory Systems*). For example, monkeys learn visual discrimination tasks gradually over many trials in a fashion that is now referred to as habit learning. In the monkey, this kind of learning depends on the basal ganglia rather than the medial temporal lobe (Mishkin et al., 1984; Teng et al., 2000). By contrast, humans learn the same task by directly memorizing the stimulus material. In the decade that followed H.M.'s initial description, extensive work in rats with hippocampal lesions also failed to reproduce H.M.'s impairment. For example, rats with hippocampal lesions, like monkeys, performed normally on simple visual discrimination problems (Kimble, 1963). Lesioned rats were also unimpaired at learning to press a bar for food and at various shock avoidance tasks [reviewed by Douglas (1967)]. In short, it was clear from the work carried out during the 1960s that the behavioral impairments observed in rats with hippocampus lesions did not provide an adequate description of the memory impairment seen in humans with hippocampal damage.

Accordingly, investigators studying rats tended not to relate their work to studies of memory-impaired patients and were more likely to interpret their findings within the framework of response inhibition as first outlined by Pavlov (1927). In fact, in a review of the literature on the hippocampus and behavior published a decade after the description of H.M., Robert Douglas (1967) wrote:

> Hippocampal lesions obviously do not impair learning in general, even when the learning involves retention for long periods of time. Thus, the animal and human data would appear to be in contradiction. This contradiction could be "resolved" by postulating that the hippocampus has a different basic function in man and beast. Such a solution to this problem is generally unacceptable to physiological psychologists, however. Another possible resolution of this paradox is that the recent memory loss in man is a secondary effect of a different type of primary disorder. The author has chosen the latter course, and suggests that the recent memory loss in man is a genuine phenomenon, but that it is a byproduct of interference during storage and not due to a lack of ability to store, per se.

These comments made it clear that a large animal literature was substantially out of register with the human work and that experimentalists were beginning to doubt the basic idea that medial temporal lobe damage produced an impairment in memory. Furthermore, if one did suppose that medial temporal lobe damage in humans impaired memory, then to understand the data from animals, one must consider the possibility, however unsatisfactory, that memory is organized differently in humans and other animals.

MULTIPLE MEMORY SYSTEMS

During the 1960s and 1970s, it was not yet understood that different tasks of learning and memory could be supported by different brain systems. Many of the tasks given to animals with hippocampal lesions were, in fact, skill-based tasks that amnesic patients would have been able to acquire (Milner, 1962), or they were tasks that animals could learn as a skill even if humans tended to learn the task by memorizing the material. Establishing an animal model of human memory impairment would require developing tasks for animals that assessed the same kind of memory that is impaired in humans after medial temporal lobe damage.

The kind of memory that is impaired is now typically referred to as declarative memory (Cohen and Squire, 1980). Declarative memory is flexibly expressed and provides conscious access to facts and events. It is impaired when structures of the medial temporal lobe are damaged. In contrast, the term nondeclarative memory refers to various acquired skills and abilities that are not accessible to conscious knowledge but are expressed through performance and depend on different brain systems (Squire, 2004). Nondeclarative memory is independent of the medial temporal lobe.

A key advance in establishing a model of human medial temporal lobe amnesia was the development of one-trial memory tests for the monkey. In 1974, Gaffan suggested that many tests of memory in animals with hippocampal damage might not be similar to the tests that reveal memory impairment in patients. Accordingly, if one intends to relate work in animals to work in humans, it is not adequate to use any convenient task in which an animal must utilize memory. Rather, one must use "specifically designed animal analogs of those tests that do reveal impairment in human amnesiacs" (Gaffan, 1974). One of the tests that Gaffan used was a one-trial test of visual recognition memory, which had been refined for use in monkeys by Benjamin Weinstein (1941). In this test (initially referred to as the "matching-from-sample delayed reaction procedure"), monkeys were presented with a single object that they displaced for a food reward (the sample phase). Memory for the sample object was then tested after a delay by presenting the sample object together with a new object (choice phase). The monkey was trained to select (i.e., match) the object that had been presented previously during the sample phase. Unique objects were used on each trial so that judgment of familiarity was sufficient to identify the correct object. The demand on memory could be increased by increasing the delay between the sample and choice phases. This task became known as the "delayed matching to sample" (DMS) task. Monkeys with lesions of the fornix, thought to mimic the effects of hippocampal damage, impaired performance in a delay-dependent fashion. Performance was intact at a delay of 10 seconds but impaired at delays of 70 seconds and 130 seconds (Gaffan, 1974).

An alternative version of the DMS task was also developed and referred to as the delayed nonmatching to sample (DNMS) task (Mishkin and Delacour, 1975). In this case, monkeys were trained to select the new object during the choice phase (i.e., nonmatch the sample object). In a critical experiment (Mishkin, 1978), monkeys were given lesions designed to mimic the damage sustained by H.M. The key group received hippocampus plus amygdala lesions, together with the cortex underlying these two structures. Other monkeys received smaller lesions of the hippocampus (and underlying cortex) or lesions of the amygdala (and underlying cortex). Note that the underlying cortical areas damaged by surgery were not specifically targeted but were damaged during the surgical approach to the hippocampus and amygdala. Postoperatively, the animals reacquired the nonmatching rule, and the delay between the sample and choice phases was then increased progressively from 10 seconds to 30 seconds, 60 seconds, and 120 seconds. The result was that hippocampal or amygdala lesions (combined with the underlying cortical areas that were damaged in this study) yielded only a mild impairment but that the combined lesion (hippocampus plus amygdala and underlying cortex) produced a marked, delay-dependent deficit that was especially severe at the longer delays.

The demonstration of delay-dependent impairments in performance was critical for identifying this impairment as a memory impairment. When performance is spared at short delays and selectively impaired at longer delays (when the demand on memory is greatest), one can rule out a variety of alternative explanations for the impairment (e.g., the ability to identify objects; motivational changes; as well as secondary effects of the lesion, such as hyperactivity, increased distractibility, motor impairments, and other nonspecific effects). This study, and subsequent studies, that relied especially on the DNMS task (Zola-Morgan et al., 1982), documented the successful establishment of an animal model of human medial temporal lobe amnesia.

The DNMS task with trial-unique stimuli was subsequently adapted for use with rats (Mumby et al., 1990). This new task used trial-unique objects that could be displaced to obtain food rewards just as in the version developed for monkeys (Mumby et al., 1990). Additionally, the test apparatus was designed so that the delay between the sample and choice phases could be as short as 4 seconds. Work with this task demonstrated that lesions of the hippocampus, or lesions of the cortical regions adjacent to the hippocampus, produced a delay-dependent memory impairment similar to what had been reported in the monkey (Mumby and Pinel, 1994). Thus, this new task successfully extended the animal model of medial temporal lobe memory impairment to the rat. Further work with this task demonstrated that the impairment in rats with hippocampal lesions was unambiguously a delay-dependent memory impairment (Clark et al., 2001) and that delay dependence was not a simple consequence of the large amount of training given at the short delay during learning of the nonmatching rule (Ringo, 1993).

Since the successful establishment of the DNMS task, another memory task has become widely used. This task allows one-trial learning to be studied in humans and experimental animals in a straightforward and simple way (Clark and Squire, 2010). The visual paired-comparison (VPC) task was initially developed to study the development of vision in human infants (Fagan, 1970). In this task, two identical stimuli are presented side-by-side for a period (e.g., 1–2 min). Immediately afterward, the infant is presented with the recently viewed stimulus along with a novel stimulus. The finding is that infants preferentially look at the novel stimulus, presumably because they remember the already presented and now less interesting stimulus. This work established the VPC task as a reliable test of visual recognition memory. The task takes advantage of a spontaneous preference for novelty (which is preserved across mammalian species), and it has the advantage of not requiring any verbal instruction or rule learning. This feature makes the task an excellent tool for studying preverbal human infants and experimental animals.

The VPC test was subsequently adapted for the monkey (Bachevalier et al., 1993), the rat (Ennaceur and Delacour, 1988), and the mouse (Tang et al., 1999). When used with primates, this task is generally referred to as the VPC task, because it is a test of visual recognition memory. In the rat and mouse, the animal physically explores the objects so that visual, olfactory, and tactile information can be used to guide performance during the test phase. Accordingly, in the rodent, this task is typically referred to with other descriptors, such as "novel object recognition" (NOR), "novel object preference," "spontaneous object preference," or "spontaneous object recognition." Here, we refer to it as the NOR task.

Recent findings with the VPC and NOR tasks are consistent with findings using the DNMS task. For example, memory-impaired patients with damage that included the hippocampus exhibited memory impairment on the VPC test (McKee and Squire, 1993). Furthermore, monkeys (Zola et al., 2000), rats (Clark et al., 2000), and mice (Hammond et al., 2004) with selective hippocampal damage, or transient disruption of hippocampal function, exhibited delay-dependent memory impairments when tested with the VPC/NOR task [a summary of the work in animals with hippocampal lesions is provided in Clark and Martin (2005) and Squire et al. (2007)]. The NOR task has now largely replaced the DNMS task for the assessment of recognition memory in the experimental animal (Clark and Martin, 2005; Winters et al., 2008).

ORGANIZATION OF LONG-TERM DECLARATIVE MEMORY

Work in the experimental animal during the past three decades used these tasks to identify a system of anatomically connected structures in the medial temporal lobe that, when damaged, produce memory impairment like the impairment first revealed by the study of H.M. [reviewed in Clark and Squire (2010)]. The system of structures important for memory includes the hippocampus and the adjacent entorhinal, perirhinal, and parahippocampal cortices (Squire and Zola-Morgan, 1991). The amygdala is not part of this system. Note also that in the rat, the parahippocampal cortex is referred to as the postrhinal cortex; however, anatomical organization is preserved across the three species (Fig. 4.1).

The hippocampus, defined here as the DG, cornu ammonis (CA)3, and CA1, is anatomically situated to receive highly processed information from widespread neocortical regions through three cortical areas, the ento-

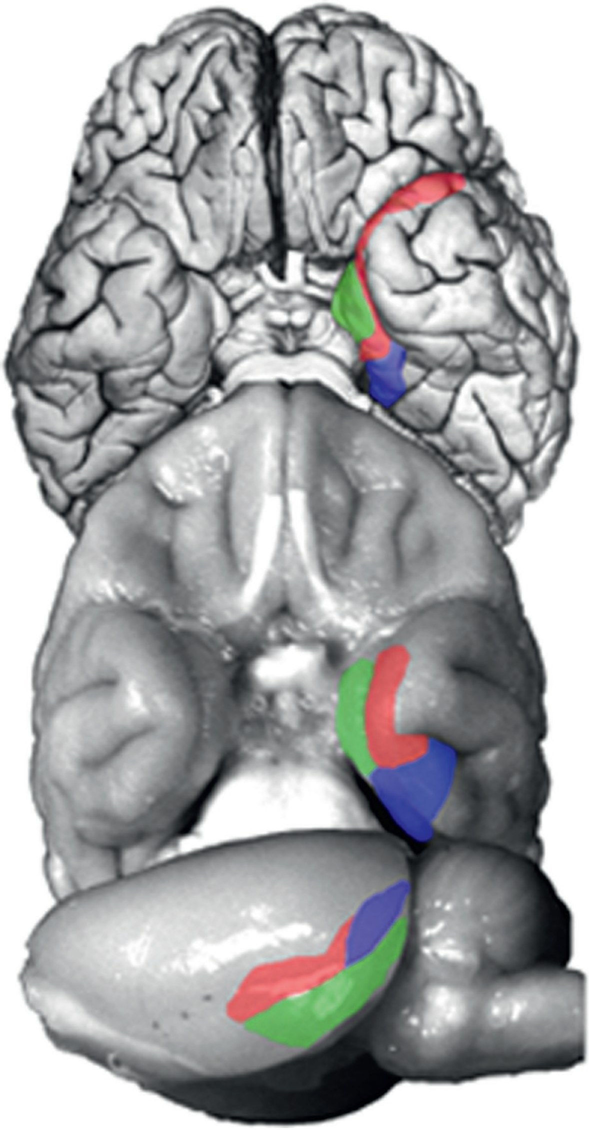


FIGURE 4.1 Ventral view of a human brain (*Top*), ventral view of a monkey brain (*Middle*), and lateral view of a rat brain (*Bottom*). The major cortical components of the medial temporal lobe are highlighted [perirhinal cortex (red), parahippocampal/postrhinal (blue), and entorhinal cortex (green)]. The organization and connections of these structures are highly conserved across these species. Brains are not drawn to scale. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

rhinal, perirhinal, and parahippocampal cortices, as well as through other direct projections to the entorhinal cortex from outside the temporal lobe (Fig. 4.2). The main pathway for the transmission of sensory information to the hippocampus is the entorhinal cortex. Layer II of the entorhinal cortex provides its major input. This unidirectional projection, forming part

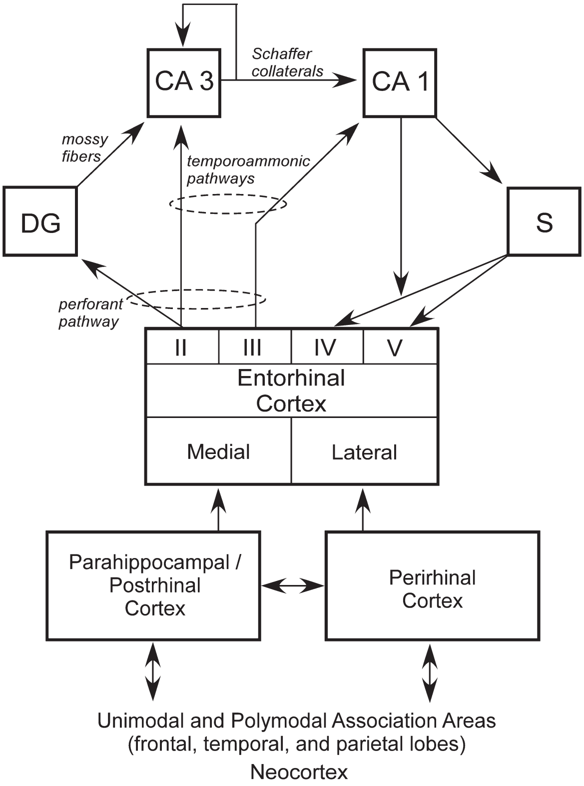


FIGURE 4.2 Schematic view of the connections within the medial temporal lobe memory system. The hippocampus, defined here as the DG, CA3, CA1, and subiculum (S), is anatomically situated to receive highly processed information from widespread neocortical regions through three temporal cortical areas, the entorhinal, perirhinal, and parahippocampal cortices (in the rat, the term postrhinal cortex replaces the term parahippocampal cortex), as well as through other direct projections to the entorhinal cortex from areas outside the temporal lobe. The figure shows a simplified view of the way in which information enters the hippocampus from the superficial layers (II and III) of the entorhinal cortex and then flows in a largely unidirectional feed forward direction to return (predominantly) ultimately to the deep layers of entorhinal cortex (IV and V). The output and input layers refer to the entire entorhinal cortex and not to its medial or lateral subdivisions.

of the perforant pathway, provides a substantial input to the DG, which, in turn, provides the major input to CA3 via the mossy fiber projection. There is also a smaller unidirectional projection to CA3 from layer II of the entorhinal cortex. CA3 provides the major input to CA1 via the Schaffer collateral/commissural pathway, but there is also a substantial recurrent associational projection within the CA3 field. CA1 also receives a direct projection from layer III of the entorhinal cortex, as does the subiculum (the temporoammonic pathway). Both the Schaffer collateral and temporoammonic projections to CA1 are unidirectional. CA1 primarily projects to the subiculum but also sends a projection to layer V of the entorhinal cortex. The subiculum sends projections primarily to layers IV and V of the entorhinal cortex (Witter and Amaral, 2004).

The hippocampus can be viewed as residing at the end of the processing hierarchy of the medial temporal lobe, receiving input from both the perirhinal and parahippocampal cortices, as well as the entorhinal cortex (Fig. 4.2). Guided by the anatomy, it seems plausible that the hippocampus extends and combines functions performed by the structures that project to it (Squire et al., 2007). Note also that anatomical connections from different regions of neocortex enter the medial temporal lobe at different points. Thus, the higher visual areas TE and TEO project preferentially to the perirhinal cortex. Conversely, spatial information that comes to the medial temporal lobe from parietal cortex arrives exclusively at the parahippocampal cortex. Consistent with these anatomical facts, damage to parahippocampal cortex was found to impair spatial memory more than did damage to perirhinal cortex (Parkinson et al., 1988; Malkova and Mishkin, 2003), and damage to perirhinal cortex impaired performance on the visual DNMS task more than did damage to parahippocampal cortex (Zola-Morgan et al., 1994). Finally, the relative segregation of visual and spatial information appears to be maintained within the entorhinal cortex, such that the lateral entorhinal cortex processes more visual information and the medial entorhinal cortex processes more spatial information.

CHALLENGE TO THE ANIMAL MODEL AND TO CROSS-SPECIES COMPARISONS

As discussed earlier, during the 1960s and early 1970s, the development of an animal model of human memory and human memory impairment was challenged by the fact that animals could use nondeclarative memory to solve some memory tasks that humans typically approached using declarative memory. It therefore became important to understand under what conditions this occurs and to identify what kind of memory is used in each case.

This issue can be illustrated by considering concurrent discrimination learning, a standard task that has been used to study mammalian memory for more than 50 years. In a common version of the task, eight pairs of objects are presented side-by-side five times each day, one pair at a time in a mixed order, for a total of 40 trials. One object in each pair is always correct, and a choice of the correct object yields a reward. The left/right position of the correct object varies randomly across trials. Humans readily learn this task, performing at a level better than 80 percent correct after only 1 or 2 days of training (Squire et al., 1988). That performance ordinarily depends on declarative memory, and on memorizing which object is correct in each pair, is demonstrated by the fact that task performance was correlated highly with the ability to describe the objects and by the fact that memory-impaired patients performed poorly during the period that their controls mastered the task. In contrast, this same task was acquired at a normal rate by monkeys with hippocampal lesions (Teng et al., 2000). Importantly, monkeys with hippocampal damage that also included damage to the caudate nucleus (Teng et al., 2000) or monkeys with selective damage to the caudate nucleus (Fernandez-Ruiz et al., 2001) were severely impaired at learning the task. These findings suggested that monkeys learn the concurrent discrimination task via a trial-and-error stimulus/response strategy that relies on nondeclarative memory. If so, the question naturally arises as to whether humans also have a similar capacity for nondeclarative memory that could support learning of this same task.

To address this question, patients with large lesions of the medial temporal lobe, and essentially no residual declarative memory, were given extended training on the concurrent discrimination task over a period of several weeks (Bayley et al., 2005). Fig. 4.3*A* shows the performance of four control participants on the task. The controls learned the task easily within three sessions. One key feature of declarative memory is that it can be expressed flexibly. To demonstrate this feature, the controls were given a sorting task 3–6 days after learning. The 16 objects used in this task were placed together on a table, and participants were told that some of the objects had been consistently designated as correct. They were then asked to sort the objects, placing the correct objects to one side of the table and the other objects to the other side. Fig. 4.3*A* shows that controls had no difficulty with this modification of the task.

By contrast, patient E.P. gradually learned the object pairs across 36 test sessions (Fig. 4.3*B*) but then failed the sorting task altogether 5 days later. Nonetheless, immediately afterward, E.P. performed well in the standard task format (Fig. 4.3*B*). Seventeen days later, E.P. again failed the sorting task but performed well in the original task format. The results for patient G.P. were essentially the same as for E.P. (Fig. 4.3*C*).

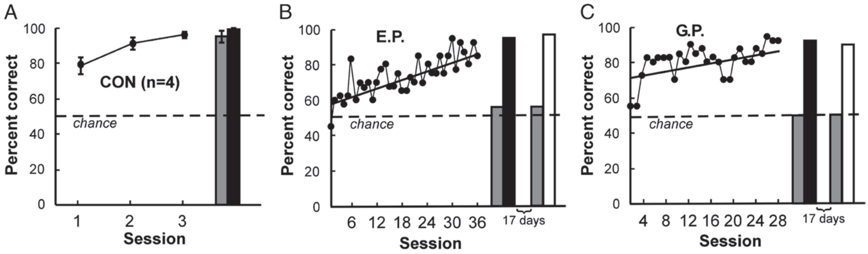


FIGURE 4.3 Performance on the concurrent discrimination task. (*A*) Controls (*n* = 4) learned the task easily within three sessions and performed well on the sorting task 3–6 days later (gray bar). The black bar shows performance immediately afterward, when participants were asked to verbalize their choices rather than reach for objects. Results are means ± SEM. (*B*) Patient E.P. gradually learned the object pairs across 18 weeks. Five days later, he failed the sorting task (gray bar) but then, immediately afterward, performed well in the standard task format while verbalizing his responses (black bar). Seventeen days later, E.P. again failed the sorting task (gray bar) but performed perfectly when 40 trials were given exactly as in original training (white bar). (*C*) Patient G.P. learned the object pairs gradually during 14 weeks. Like E.P., he failed the sorting task on two different occasions, 5 days after training and again 17 days later. In both instances, he performed well immediately afterward when the original task format was reinstated [verbalizing (black bar), standard task (white bar)]. The dashed line indicates chance performance (50% correct). Reproduced from Bayley et al. (2005).

Some informal observations are informative. At the beginning of each testing day, the patients were asked about the objects and about what had occurred on previous visits. However, they were never able to remember anything about earlier test sessions and could not describe how the objects had been used. Nonetheless, as training proceeded from day to day, both patients (without explicit instructions about what to do on each trial) readily picked up one of the objects in each pair and turned it over to receive feedback (the word "correct" or "incorrect" was printed under the base of each object).

Thus, both patients gradually acquired the standard eight-pair object discrimination task over many weeks; however, at the start of each session, they could not describe the task, the instructions, or the objects. The acquired knowledge was rigidly organized, and performance collapsed when the task format was altered. The findings indicate that humans possess a robust capacity for gradual trial-and-error learning that can operate outside awareness for what is learned and independent of the medial temporal lobe. What is acquired is inflexible and altogether different from declarative memory. These findings show that humans possess a nondeclarative learning system like other primates and suggest what the characteristics of this system are likely to be (e.g., inflexible, inaccessible to awareness).

In summary, the development of a model of human memory and human memory impairment in the monkey and rat is a success story, and the work has provided important insight into the anatomy and organization of mammalian memory. Still, challenges can arise because these species have evolved under different selection pressures that can bias them to approach tasks with different strategies than the strategies used by humans. Analysis of such cases, based on our understanding that there are multiple memory systems with different properties, has, in the end, served to emphasize the similarities in memory function across mammalian species.

ACKNOWLEDGMENTS

This work was supported by the Medical Research Service of the Department of Veterans Affairs, National Science Foundation Grant 1120395, and National Institute of Mental Health Grant 24600.

5

Evolution of Working Memory

PETER CARRUTHERS

Working memory (WM) is fundamental to many aspects of human life, including learning, speech and text comprehension, prospection and future planning, and explicit "system 2" forms of reasoning, as well as overlapping heavily with fluid general intelligence. WM has been intensively studied for many decades, and there is a growing consensus about its nature, its components, and its signature limits. Remarkably, given its central importance in human life, there has been very little comparative investigation of WM abilities across species. Consequently, much remains unknown about the evolution of this important human capacity. Some questions can be tentatively answered from the existing comparative literature. Even studies that were not intended to do so can nonetheless shed light on the WM capacities of nonhuman animals. However, many questions remain.

The nature of human working memory (WM) has been extensively investigated, with thousands of articles and books on the topic produced over the last half-century. Some of the main findings of this research will be outlined shortly. However, we know hardly anything about how WM evolved. For that (if we are to go beyond plausible speculation), we need detailed comparative studies. However, remarkably few

---

Department of Philosophy, University of Maryland, College Park, MD 20742. E-mail: pcarruth@umd.edu.

such studies have been conducted, as we will see. Nevertheless, the emerging consensus about the nature of human WM allows us to frame a series of questions or alternative hypotheses concerning the possible differences between human and animal WM. Some of these can be answered, at least tentatively, from the results of existing work. However, they should also be used to frame and guide future comparative experiments.

WORKING MEMORY IN HUMANS

WM is the domain-general subsystem of the mind that enables one to activate and sustain (sometimes via active rehearsal) a set of mental representations for further manipulation and processing. The contents of working memory are generally thought to be conscious. Indeed, many identify the two constructs, maintaining that representations become conscious by gaining entry into WM (Baars, 2002). WM is generally thought to consist of an executive component that is distributed in areas of the frontal lobes working together with sensory cortical regions in any of the various sense modalities, which interact through attentional processes (Postle, 2006). It is also widely accepted that WM is quite limited in span, restricted to three or four chunks of information at any one time (Cowan, 2001). Moreover, there are significant and stable individual differences in WM abilities between people, and these have been found to predict comparative performance in many other cognitive domains (Engle, 2010). Indeed, they account for most (if not all) of the variance in fluid general intelligence, or *g* (Kane et al., 2005).

The primary mechanism of WM is thought to be executively controlled attention (Cowan et al., 2005; Postle, 2006). It is by targeting attention at representations in sensory areas that the latter gain entry into WM, and in the same manner they can be maintained there through sustained attention. Attention itself is thought to do its work by boosting the activity of targeted groups of neurons beyond a threshold at which the information they carry becomes "globally broadcast" to a wide range of conceptual and affective systems throughout the brain while also suppressing the activity of competing populations of neurons (Baars, 2002; Gazzaley et al., 2005; Knudsen, 2007). These consumer systems for WM representations can produce effects that in turn are added to the contents of WM or that influence executive processes and the direction of attention. It is through such interactions that WM can support extended sequences of processing of a domain-general sort.

It is also widely accepted that WM and long-term (especially episodic) memory are intimately related. Indeed, many claim that representations held in WM are activated long-term memories (Unsworth and Engle, 2007). This might appear inconsistent with the claim that WM representations are attended sensory ones. However, the two views in part can be reconciled by noting that most models maintain that long-term memories are not stored in a separate region of the brain [although the hippocampus does play a special role in binding together targeted representations in other regions (Squire, 1992)]. Rather, information is stored where it is produced (often in sensory areas of cortex). Moreover, although attention directed at midlevel sensory areas of the brain appears to be necessary (and perhaps sufficient) for representations to enter WM, information of a more abstract conceptual sort can be bound into those representations in the process of global broadcasting (Kosslyn, 1994). As a result, what figures in WM are often compound sensory–conceptual representations, such as the sound of a word together with its meaning or the sight of a face experienced as the face of one's mother.

A final factor to stress is that WM is also intimately related to motor processes, probably exapting mechanisms for forward modeling of action that evolved initially for online motor control (Wolpert and Ghahramani, 2000; Jeannerod, 2006). Whenever motor instructions are produced, an efferent copy of those instructions is sent to a set of emulator systems to construct so-called "forward models" of the action that should result. These models are built using multiple sensory codes (primarily proprioceptive, auditory, and visual), so that they can be aligned with afferent sensory representations produced by the action itself as it unfolds. The two sets of representations are compared, issuing in altered motor instructions if the action is failing to proceed as expected. These same systems are then used in the mental rehearsal of action, but with instructions to the muscles suppressed. The resulting sensory forward models, when targeted by attention, can gain entry into WM. Hence one can imagine oneself saying something and "hear" the result in so-called "inner speech," or one can imagine oneself doing something and "see" or "feel" the results in visual or proprioceptive imagination.

Before we proceed to consider the evidence of WM in animals, it is important to distinguish WM from two other forms of memory with which it is sometimes conflated. One is sensory short-term memory, which can retain information in sensory cortices for around 2 seconds in the absence of attention. These representations can give rise to priming effects without ever being conscious (Dehaene et al., 2006). (However, they can become conscious if attention is directed toward them before they expire. Consider the famous example of only noting the clock strike at the third chime while at the same time recalling the previous two strokes.) These sensory short-term memory representations can also be used for online guidance of action in the absence of attention (Milner and Goodale, 1995). The contents of WM, in contrast, are attention-dependent and conscious and can be held in an active state for as long as attention is directed at them.

(Note, however, that attention is quite sensitive to interference, so sustaining a representation in WM for an extended period is by no means easy.)

Some experimental results with animals that might be thought to support the existence of WM capacities are in fact best interpreted as tests of sensory short-term memory. Thus, consider the finding that chimpanzees and baboons can reliably recall a random sequence of spatial positions up to a limit of five to six items (or in the case of one animal, nine items) (Inoue and Matsuzawa, 2007; Fagot and De Lillo, 2011). The temporal delays in these experiments are of the order of fractions of a second, with the animals' responses to the entire sequence generally being executed very swiftly over a period of around 2 seconds. So although these tasks might involve WM, the data can be accounted for in terms of sensory short-term memory alone.

The other contrast is with what is sometimes called in the human literature "long-term working memory" (Ericsson and Kintsch, 1995). Long-term working memory representations are those that are no longer among the active contents of WM (having fallen out of the focus of attention for too long), but which remain readily accessible to WM processes. Sometimes these representations have been recently activated from long-term memory, but sometimes they concern stimuli that were previously encoded into WM but were forgotten within a period of minutes. Long-term WM is thought to be important in speech and text comprehension, as well as underlying such phenomena as a bus conductor's ability to know which of dozens of passengers on a bus have already paid for a ticket and which are newly arrived.

In this context it is important to note that numerous comparative studies of animals, such as those that use the radial-arm maze with rodents, use the term "working memory," when it is really a form of long-term WM that is being measured. The timescales involved, as well as the number of items that can be recalled, far exceed human WM abilities. Indeed, some writers are quite explicit that "working memory" in such studies should be defined as a memory that is used within a testing session (often lasting for minutes or hours) but not typically between testing sessions (such as the next day) (Dudchenko, 2004; Shettleworth, 2010).

Empirically, WM can be distinguished from all forms of long-term memory by its sensitivity to attentional interference. Information sustained in WM will be lost if subjects are distracted and turn their attention fully to other matters. Long-term memories, in contrast, will merely decay at the normal rate in such circumstances. The authors of the study of serial-position memory in chimpanzees described above (Inoue and Matsuzawa, 2007), for example, note that on some occasions the test subject was interrupted for a few seconds by a loud disturbance in a neighboring cage, but was nevertheless able to complete the sequence.

Although the authors suggest that this behavior manifests the operation of WM, in fact it is unlikely (Inoue and Matsuzawa, 2007). Undiminished performance following sustained and full distraction is a signature that long-term WM is involved.

WORKING MEMORY IN ANIMALS

As we have seen, there are a number of aspects or components of normal WM function in humans, including capacities to sustain, rehearse, and manipulate active representations, with a signature limit of three to four items or chunks of information. We also know that WM is attention dependent and hinges critically on capacities to resist interference from competing representations. Moreover, we know that WM plays a central role in many aspects of intelligent human life. As a result, there are a range of possible positions that one can take concerning the comparative psychology of WM. These are listed below, organized roughly in terms of how great a gulf they envisage between the WM abilities of animals and ourselves. Thereafter they will be discussed in turn and evaluated in light of the available evidence.

1. Animals lack WM abilities altogether. They (like humans) have forms of sensory short-term memory that can retain reverberating information within sensory cortices for about 2 seconds following the removal of a stimulus, but they have no capacity to further sustain or refresh those representations.
2. Animals do have the capacity to sustain a representation of an object or event beyond the 2-second window of sensory short-term memory, but it is a very limited capacity—perhaps being restricted to one or two chunks in comparison with the three- to four-limit of humans.
3. Animals, like humans, can sustain three to four chunks of information in WM, but only in the absence of interference. Their abilities collapse (or are much weaker) when required to undertake a dual task or ignore intervening distractor items.
4. Animals have capacities to sustain representations that have been activated bottom-up, but they lack the capacity to activate a representation ab initio, using top-down attention to insert it into the global workspace. Basically, they lack imagination.
5. Animals can create and sustain representations in WM, but they lack any capacity to use mental rehearsals of action to generate contents for WM. [Some researchers use the term "rehearsal" to refer to the refreshing process that sustains short-term sensory representations in WM (Jonides et al., 2008). I shall use it (as is commonly done) to refer to offline rehears-

als of action schemata that can be used to populate and sustain some of the contents of WM.]

6. Animals can create, sustain, and rehearse representations in WM, but they have limited capacities to manipulate those representations, transforming them and organizing them into effective problem-solving sequences in a controlled manner.

7. Animals have capacities to sustain, rehearse, and manipulate representations in WM much like our own. However, humans are unique in the extent to which they use their WM abilities. Specifically, humans frequently use WM in ways that are irrelevant to any current task (constituting the so-called "default network"), whereas animals' use of WM is always or generally task oriented.

8. Animals have WM abilities much like our own and may even make chronic use of them. However, they differ in the sorts of representations that they can use in WM (in particular, lacking linguistic abilities, animals cannot generate inner speech), and their more limited conceptual repertoire limits the extent to which their WM performance can benefit from chunking.

We presently lack the evidence necessary for a thorough evaluation of any of these hypotheses beyond #1 and #8 of the list. However, there are data that bear directly on some of them, and some are more plausible than others on theoretical grounds. A sustained research effort by comparative psychologists is necessary for us to resolve these questions.

No Capacity to Refresh and Sustain?

The most extreme position is to deny that animals have WM capacities at all. Animals nevertheless have forms of long-term memory as well as sensory short-term memory. But they have no capacity to refresh and sustain sensory activity in the absence of a stimulus or to keep representations active and available for longer time periods.

There are extensive data sufficient to exclude this possibility, much of it using match-to-sample or non–match-to-sample tasks. (Recall that data from animal experiments using the radial maze involve timescales too great to serve as direct tests of WM ability.) These tasks require an animal to remember the identity or location of a stimulus for more than a few seconds. By themselves these results of course cannot distinguish between the contributions of WM and long-term WM, and no doubt over extended intervals it will be long-term memory that is implicated. However, we also know from such studies that there are content-specific neurons in the prefrontal cortex that show sustained activity during retention intervals that are at least a few seconds long (Goldman-Rakic, 1995). Moreover, a great deal of what we know about the neurophysiology of human attentional and WM systems derives initially from work of this sort conducted with monkeys (Goldman-Rakic et al., 1990; Luck et al., 1997; Baluch and Itti, 2011). So we can be confident that the mechanisms underlying WM performance in match-to-sample tasks are conserved across primates, and perhaps more widely.

In addition, numerous other studies have required animals to keep a representation of a target stimulus active beyond the 2-second window of sensory short-term memory. Some have used parallel object-displacement tests with apes and human children, with very similar results across all groups (Barth and Call, 2006). Others have tested both apes and dogs to see whether they will continue to search for an item that they had seen placed in a "magic cup" after they had unexpectedly retrieved an item of a different sort with positive results (Bräuer and Call, 2011).

The suggestion that basic WM capacities are quite widespread among animals receives additional support from neurobiology, given the tight connection between the WM system and episodic memory. (This will be discussed again in *Lack of Imagination?* below, where we review behavioral evidence of episodic-like memory in animals. Note here, however, that WM is the workspace within which episodic memories are activated and sustained by top-down attentional systems. And we have already noted that attentional networks are homologous among primates at least.) This is because the brain mechanisms subserving episodic-like memory are highly conserved among mammals. In particular, all mammals share homologous hippocampal and parahippocampal structures organized into homologous subregions, which have strong reciprocal connections to areas of the frontal cortex (Allen and Fortin, Chapter 6, this volume). These structures serve to integrate and store information about what occurred, where it occurred, and when it occurred (Eichenbaum, 2013). Indeed, even birds appear to share a similar, and at least partly homologous, network (Allen and Fortin, Chapter 6, this volume).

One- or Two-Item Limit?

Some claim that nonhuman apes have a WM limit of two items, in contrast with the human WM limit of three to four chunks (Read, 2008). However, this claim is based on a questionable analysis of the WM requirements of various tasks that apes cannot solve and assumes that failure does not result from other sources, such as a lack of understanding of physical forces and their effects. In contrast, experimental work with animals suggests that their WM limits may fall within the human range. Consider, for example, a test of serial recall of position conducted with a macaque monkey, modeled on tests that have been used with humans

(Botvinick et al., 2009). The retention interval required in this test was about 4 seconds for the first item in the sequence, increasing to 11 seconds for the fourth, which places it squarely in the domain of WM. The monkey was successful in recalling the first three items in a sequence, but was at chance with the fourth. The experiment also demonstrated a very similar profile of recency, latency, and other effects commonly found with humans, suggesting that both species use a homologous WM mechanism with similar limits.

It should be stressed, however, that the work on human WM demonstrating that it has a capacity limit of three to four chunks [rather than Miller's famous 7 ± 2 (Miller, 1956)] has focused on the pure memory-sustaining function of WM. Great care has been taken to exclude other strategies for maintaining representations in WM, such as covert mental rehearsal and informational chunking, which can extend its overall capacity still further (Cowan, 2001). In the serial recall test just described, in contrast, the monkey may have used mental rehearsals of its planned movements to support its WM of the sequence of positions, thereby extending its pure memory-sustaining limits. This would be consistent with a claimed WM limit of one to two items.

Other data with animals suggesting WM limits in the human range are not so easily critiqued, however. For example, using paradigms that have previously been used with human infants, it has been shown that monkeys can track three to four items of food placed sequentially into one of two opaque containers (within which those items remain out of sight for a period of at least a few seconds). The monkeys reliably distinguish between containers that hold two versus three items, and also three versus four items, but not three versus five items (Hauser et al., 2000). One might wonder why these data do not demonstrate that monkeys have a WM limit of seven (three items in one container and four in another) rather than four. The answer is that comparisons between containers benefit from chunking and do not just reflect raw retention limits. (A similar point holds for the infancy data.)

Similar tests have been conducted with horses, showing that they can distinguish between a bucket into which two apples have been placed and one containing three apples and fail to distinguish between buckets containing four apples and six apples, respectively (Uller and Lewis, 2009). In such experiments, it seems unlikely that the animals could benefit from chunking because all of the items are of the same type. And it is likewise unclear how nonverbal forms of behavioral rehearsal could assist with the task (especially in the case of horses, whose repertoire of actions differs so widely from that of the human demonstrator). So the limit of three to four items revealed here seems most likely to reflect their pure WM retention capacity. However, until comparative psychologists use direct tests of simple WM retention abilities that can be conducted in parallel with adult humans, children, and members of various other species of animals, we will not be able to know for sure.

These results give rise to a puzzle, however. For, as noted earlier, variations in WM ability in humans are reliable predictors of fluid *g*. However, it seems that even monkeys have a WM span in the human range.[1] This might lead one to expect similar general-learning abilities across all primates, which is manifestly false. A potential solution to the puzzle emerges when we note that the simple retention component of WM is *not* a reliable predictor of fluid *g* in humans (nor is it stable within a single individual across separate occasions of testing). Rather, only complex span tasks and so-called "*n*-back" tasks lead to stable results over time and are reliable predictors of *g* (Engle, 2010). (In a complex span test, one has to undertake some other task, such as judging whether a simultaneously presented sentence makes sense or performing some simple mental arithmetic while also retaining an unrelated list in WM. In an *n*-back task, one has to keep track of the *n*th prior item in a continually presented series, which requires one to resist interference from similar memories.) Moreover, at present it appears that it is training in *n*-back tasks—and not in simple span tasks—that issues long-term improvements in fluid *g* [Jaeggi et al. (2008, 2011); but see also Chooi and Thompson (2012)].

One possible construal of this set of findings is that there are no stable differences in simple span between people or across primate species. (As a result, simple span tests only measure noise contributed by endogenous factors or the environment.) All of the stable differences between people (and among species) may lie in the flexibility with which attention is allocated and the retention strategies used, as well as in the capacity to ignore sources of interference with targeted WM representations.

---

[1] A similar puzzle arises in the context of human development as it has been shown that WM capacity increases through the childhood years (Cowan et al., 2011). In particular, 6- to 9-year-olds have a span of only two items or less in these experiments, whereas young adults have a span of three items. However, in other experiments, infants as young as 11 months seem to already have an adult-like span of three items (Feigenson and Carey, 2005). One possible explanation is that speed of presentation differs between the two paradigms. In the experiments with children, the items-to-be-remembered are presented at a rate of one per second. In the experiments with infants, in contrast, presentation of each item takes a few seconds as the experimenter draws the infant's attention to it, saying "Look at this." Another possible explanation is that the infants participated in only a single trial, whereas the children had to keep attention to task across multiple presentations. Perhaps what changes through the childhood years is the capacity to maintain focused attention, rather than WM capacity as such. However, it may be that both of these explanations really amount to the same thing because the first explanation can be described in terms of the difference between directing attention toward an event (in accordance with task requirements) and having one's attention drawn to an event.

Inability to Resist Interference?

There have been no controlled experiments comparing the abilities of humans and other animals to resist interference with WM representations. Clearly, the kinds of complex span tasks that have been used with humans are unsuitable for this purpose because most require linguistic abilities. However, there have been tests used with mice that tap into something quite similar. Some of these could be adapted for purposes of cross-species comparison.

Recent studies with mice have identified a general intelligence factor that explains about 40 percent of variance across a range of dissimilar learning tasks (Matzel et al., 2003). Moreover, although this *g* factor is not significantly correlated with measures of simple WM retention, it is strongly correlated with performance in a more complex WM task, in which the animals have to resist interference from competing memories (Kolata et al., 2005). In both cases the animals were first trained on two visually distinct radial-arm mazes located in the same room. In the test of WM retention, the animals were confined to the central compartment of one of the mazes for a fixed interval of 60 or 90 seconds, having made their first four correct choices before being allowed to complete their search. In the test of WM interference, in contrast, the animals were removed from the first maze, having made three correct choices and placed in the second maze; after three correct choices there, they were returned to the first maze until they had made another three correct choices, and so on. The fact that performance on the interference WM test but not on the retention WM test correlates with a measure of *g* in mice is suggestive of WM mechanisms homologous with those of humans.

One might question whether this and other experiments conducted in the same laboratory are genuinely measuring active WM rather than long-term WM. For how are we to know that the mice kept a representation of the arms already visited active in the focus of attention? Indeed, in experiments with rats using the eight-arm radial maze, rats typically show a near-perfect performance on the final four arms of the maze following delays of a number of hours after visiting the first four arms, enabling us to be quite confident that long-term memory is involved (Shettleworth, 2010). On reflection, however, we can be sure that active WM is also used. So although the tests might not be suitable for measuring WM span (because both short-term and long-term WM are involved), they can enable us to draw conclusions about the relationship between WM and *g*.

Why should tests using interrupted search in a radial-arm maze involve interactions between short-term and long-term WM? When commencing search following an interruption, the animal will need to access long-term representations of the four arms previously visited, holding those in active WM long enough to select a fifth. And thereafter, for the final three choices, the animal will need to use spatial retrieval cues to access a long-term memory of each of the arms initially visited while keeping active in WM the immediately previous selections and while orienting itself appropriately to make another choice. In addition, in the interference condition of the experiments described earlier (in which the mice are switched back and forth between two mazes), irrelevant memories will need to be suppressed, requiring the mice to pay careful online attention to the cues that individuate the arms of the two mazes. At the very least we can be confident that this task will place significant demands on the animals' use of selective attention, which is at the core of human WM abilities.

A subsequent study of correlations between WM abilities and *g* in mice attempted to determine the components of WM still further (Kolata et al., 2007). It involved tests of WM retention time, WM retention capacity, as well as capacities for selective attention. The first experiment measured the temporal limits of the animals' capacity to recall which of the two arms in a T maze they had previously visited. The test of WM capacity used a nonspatial version of the radial-arm maze, in which cues attached to baited cups at the end of each arm were randomly shuffled, following each choice, in such a way that the mice would need to keep in mind the cues (and which ones they had already selected) without relying on spatial position. Finally, the test of selective attention used two distinct discrimination tasks (one involving shapes and the other involving odors) that had initially been learned in separate contexts. During the test, the animals were presented with all cues of both kinds in one or the other of the two contexts, so that they would need to ignore one set of cues on which they had previously been trained in favor of the other. The results of this experiment were that retention time did not correlate with *g* at all and that WM capacity correlated moderately with *g*, whereas selective attention was strongly correlated with *g*. This, too, is what one might have predicted from what we know about human WM.

Perhaps the most impressive set of results from this series of studies with mice is the finding that WM training improves *g*, just as it appears to do in humans (Jaeggi et al., 2008; Light et al., 2010). In the first of these experiments, animals who received training using two alternating radial-arm mazes scored significantly higher than controls on subsequent tests of general learning abilities and also scored higher on a test of selective attention. The second experiment then showed that it is the attentional component of WM training specifically that leads to an improvement in *g*. This experiment used three groups of mice. One group received training in two alternating and visually similar radial-arm mazes located within the same room, which would require the mice to attend to minor differences in cues provided by spatial context to discriminate the arms of the two mazes. A second group also received training on two alternating radial-arm mazes, but this time located in separate rooms, thus placing fewer attentional demands on the animals. The third group was a control and received no WM training. The findings were that the attentionally demanding group showed the greatest increase in *g* and the second group also displayed significant improvement relative to controls.

Taken together, this series of findings with mice suggests that WM abilities in this species are heavily dependent on attentional capacities (just as they are in humans) and that mice not only have a simple capacity to retain salient information beyond the temporal window of sensory short-term memory, but also (like humans) can do so in the face of interference. It may be, then, that the basic structure of WM is at least homologous across all mammals. However, we do not know to what extent (if at all) capacities to direct and control attention and to resist interference differ between humans and other mammals. Given that such capacities are aspects of executive function, and that humans are generally supposed to excel at executive function tasks, one might predict significant differences. However, the situation cries out for direct tests of attentional abilities and complex WM capacities across species.

Lack of Imagination?

There are two basic ways in which offline representations can gain entry into WM. One is through mental rehearsals of action, which are discussed in *Inability to Mentally Rehearse Action?* below. The other is through top-down executive–attentional processes. One can search for, and activate into WM, a visual image of one's mother's face or an auditory image of the sound of her voice, for example. However, one can also search for and activate a specific episodic memory of one's graduation or one's most recent birthday dinner. It seems most likely that these two forms of ability are paired together. However, it would be possible to claim that a creature can have a capacity for generic semantic imagery without being capable of episodic memory, perhaps because representations of specific episodes are never stored in memory at all. So even if animals are incapable of mental time travel (including episodic remembering), as some have claimed (Suddendorf and Corballis, 2007), this would fail to show that they are incapable of using attentional resources to generate imagistic contents for WM in an offline manner. If animals are capable of episodic remembering, in contrast, they then will surely also be capable of generic imagery because it is hard to see what more might be required for the latter than is already present in the former.

Most tests of mental time travel in animals have focused on prospection of the future (discussed in *Inability to Mentally Rehearse Action?* below).

However, there have also been experiments with corvids showing these birds to be at least capable of recalling and reasoning appropriately from the what, where, and when components of episodic memory (Clayton et al., 2003b). Admittedly, it does not follow that the birds are experientially projecting themselves back into specific episodes of food caching. However, it does at least seem likely that they are activating into WM episodic-like representations of types of food and their locations, together with some sort of representation of elapsed time. At any rate, this is how humans would solve a problem of this sort if compelled to do so nonverbally. This consideration would provide a stronger argument, of course, if corvids were not so evolutionarily distant from us. However, despite this distance, we noted earlier that birds possess brain networks that are similar to, and at least partly homologous with, those that support episodic memory in humans and other mammals (Allen and Fortin, Chapter 6, this volume). Moreover, experiments with rats show that they, too, form tightly integrated what, where, and when representations (Ergorul and Eichenbaum, 2004; Babb and Crystal, 2005). Such data suggest that episodic-like memory representations are widespread among animals. However, in any case it seems that the animals must at least be capable of activating representations into WM using top-down attentional control.

Recall, moreover, the experiments with rodents using interrupted search of a radial-arm maze, discussed in *Inability to Resist Interference?* above. Although there is nothing in the data to suggest that in the second phase of the experiments the animals are accessing episodic memories of their earlier visits to some of the arms of the maze, they will surely at least be activating a semantic representation of some sort. For example, it might be a representation of an arm as being empty of any reward. In humans, such a memory would need to be searched for using a combination of environmental cues and top-down attentional control, resulting in that representation being activated into WM. It is therefore reasonable to assume that the same is true of rodents.

There are tentative grounds, then, for thinking that other animals are capable of top-down activation of representations for use in WM. Further grounds are discussed in *Inability to Mentally Rehearse Action?* below, because it is unlikely that the use of WM for prospection depends solely on activation of motor schemata without any enrichment from semantic or episodic memory. Indeed, we know that long-term memory systems and capacities for prospection are tightly linked, with the hippocampus being heavily implicated in each (Buckner, 2010). In fact, some have argued that the structure of long-term memory systems has been specifically adapted and shaped in the service of prospective reasoning (Schacter et al., 2007).

Moreover, one might think, on purely theoretical grounds, that any creature capable of top-down attentional selection of stimuli should also be capable of top-down activation of similar representations in an offline manner. For as we noted earlier, attention operates by boosting the neural activity of some groups of neurons while simultaneously suppressing the activity of competing populations, resulting in global broadcast of the information encoded in the former set. The same mechanisms should then be capable of operating in the presence of background levels of neural activation in the absence of an external stimulus, resulting in endogenous activation of representations in the global workspace.

Inability to Mentally Rehearse Action?

Evidence of mental rehearsal of action comes from studies of long-term planning in animals. We know that in humans such planning is conducted in large part through rehearsal of alternative actions, with people responding affectively to the WM representations that result (Damasio, 1994; Gilbert and Wilson, 2007). Although there is powerful evidence of future planning in corvids (Correia et al., 2007; Taylor et al., 2010), I shall focus on data from primates, where the argument for homologous underlying mechanisms is strongest.

One study has carefully documented the behavior of an alpha male chimpanzee in an open-plan zoo (Osvath, 2009; Osvath and Karvonen, 2012). He began to collect and store piles of stones early in the morning to throw at zoo visitors later in the day as part of an aggressive threat display. When the zookeepers responded by removing his stashes each day before zoo opening time to prevent this, he proved quite adept at concealing his stashes and at manufacturing projectiles afterward by breaking off pieces of brittle concrete from the walls in his enclosure. Note that at the times when he collected and concealed his stashes he was in a calm state, in the absence of the stimuli (human visitors) that would provoke his rage later. Such behavior in a human would likely be caused by imagining the later presence of the audience and mental rehearsal of the actions involved in grasping and throwing projectiles, issuing in a positive affective response that would in turn motivate the collection of some stones. It is reasonable to assume that similar processes took place in the mind of the chimpanzee.

Experimental data with chimpanzees point toward the same conclusion. In one experiment, chimpanzees not only selected and carried with them to their sleeping quarters a tool that they would need the next day to access a desired reward, but also remembered to bring it back with them on their return (Mulcahy and Call, 2006). In a conceptual replication of this experiment by another laboratory, chimpanzees again selected a tool needed to retrieve a later reward and remembered to bring the tool with them when returning (Osvath and Osvath, 2008). Moreover, the animals were able to resist a smaller current reward (a grape), choosing instead the tool that would get them a more valued reward later (a container of juice). In addition, when presented with a number of unfamiliar objects (while being prevented from handling them), they reliably selected and took with them the one best suited to obtain the future reward. Note that humans would solve a task of this sort by mentally rehearsing some actions directed toward the juice container involving the various objects, noting which ones could be successful.

This evidence from captive chimpanzees is fully consistent with what we know of the behavior of chimpanzees in the wild. For example, chimpanzees in the Congo regularly harvest termites from both aboveground and subterranean nests, each of which requires a distinct set of tools. The subterranean nests, in particular, require a sharp stout puncturing stick, which is always made from the branches of a particular species of tree. The chimpanzees never arrived at the site of a subterranean nest without bringing such a stick with them, unless one had previously been left at the site. And this was true even though the nearest appropriate tree was tens of meters away in the forest, from which point the nest site could not be seen (Sanz et al., 2004). Such behavior in humans would involve imagination of the target together with mental rehearsal of the actions needed to acquire it, which would both remind and motivate one to deviate from one's path to find an appropriate species of tree.

The behavioral data suggest, then, that other apes (at least) are capable of mentally rehearsing actions and that they do so for purposes of future planning, just as humans do. However, at present the argument for this conclusion is one of analogy, assuming that similar forms of behavior across closely related species should be explained in terms of similar underlying processes. Evidence of a more direct sort would be quite welcome. In particular, we need experimental paradigms that can be matched across species, whose parameters can be varied in parallel to see whether performance profiles respond similarly also. A positive outcome would provide much stronger evidence of homologous processes.

Limited Manipulative Abilities?

In one sense, the manipulative component of WM consists of an ability to organize and control sequences of representations in a task-relevant manner. The evidence of future planning in apes and corvids suggests that they are capable of doing just that. In another sense, however, manipulation involves targeting an image with a mentally rehearsed action, thereby transforming it. This has been extensively studied in humans using the visual rotation paradigm (Kosslyn, 1994). Participants are presented with two shapes of varying orientation and are asked to judge whether or not the shapes are the same. People solve these tasks by mentally rotating the image of one shape to match the orientation of the other and answering depending on whether or not the result is a fit. Among the classic findings in this literature are that participants take longer to judge shapes whose orientations are further apart from one another, suggesting that the movement of the initial image through the intervening space takes time.

What we know from brain-imaging and transcranial magnetic stimulation studies using the visual rotation paradigm is that activity in the motor or premotor cortex precedes and causes the subsequent transformation of the visual image (Ganis et al., 2000). It seems that people imagine acting on the shape represented in one of the images, initiating offline an action of twisting it with one's hand, for example, thereby causing the represented shape to change through the process of forward modeling of the action. One might wonder, then, whether animals have similar capacities. Studies conducted with baboons and sea lions suggest that they do, with the animals showing larger differences in reaction time to images that would need to be rotated through larger arcs to secure a match, just as humans do (Vauclair et al., 1993; Mauck and Dehnhardt, 1997). However, to justify claiming that the processes are homologous it would be important to know whether motor-control areas of the animals' brains are likewise involved in the process.

Similar conclusions are supported by studies of problem solving and insight in apes. For example, confronted by a peanut at the bottom of a glass container that is too deep to reach into (and which is strapped to the bars of the cage), some animals will hit upon the strategy of collecting water in their mouths and spitting it into the container until the peanut floats to the top (Mendes et al., 2008; Hanus et al., 2011). (The same task was presented to human children, with similar rates of success among 4- and 6-year-old children, but with more frequent achievement among 8-year-olds.) To arrive at the solution to this problem, one needs to mentally rehearse an action of putting water into the container, thereby transforming one's mental representation of the position of the peanut and enabling one to predict that iterated performance of the action will permit one to reach it successfully. However, once again the argument for homologous processes here is only one of analogy.

Rarity of Use?

Even if the WM capacities of animals are comparable to those of humans in all major respects, it may be that animals make use of WM only when confronted with specific practical, learning, or reasoning problems.

Humans, in contrast, make frequent use of WM in ways that are irrelevant to any current task, thereby constituting the default network (Buckner et al., 2008; Spreng et al., 2009).[2] Even when we are not confronted with a task, our minds will be occupied with fantasies, episodic memories, imagined social situations, imagined conversations, snatches of song, and so on, all of which heavily involve WM. Indeed, even when humans are engaged in a task, they are apt to slip into so-called "mind wandering," in which WM is populated with representations unrelated to the task demands (Mason et al., 2007).

There are little comparative data bearing directly on this question. However, the suggestion that humans may be unique in this respect is at least consistent with the vastly greater extent of human creativity, innovation, and long-term planning. Much of the time that humans spend mind wandering is occupied with reviewing and exploring future scenarios and anticipating future problems or successes. Moreover, there is evidence that mind wandering is significantly correlated with creativity, involving, as it does, defocused attention combined with executive control and selection (Baird et al., 2012). It has also been suggested that the uniquely human disposition to engage in pretend play in childhood is an adaptation for increased creativity in adulthood, encouraging us to use WM for purposes of creative scenario building (Picciuto and Carruthers, 2013).

Data suggesting that mind wandering may not be uniquely human come from a study comparing default network activity in humans and chimpanzees (Rilling et al., 2007). Similar regions of the brain displayed greater activity at rest in both species, including in the medial prefrontal cortex and posterior cingulate cortex, suggesting that chimpanzees, too, spend much of their time ruminating when not engaged in other tasks. These data need to be treated with caution, however, because default-mode networks overlapping those of humans have been found in both monkeys and rodents under conditions of general anesthesia (Vincent et al., 2007; Lu et al., 2012). Therefore, default-mode activity does not entail

---

[2] Brain-imaging studies of the default network rarely find activity in sensory cortices of the sort that one would expect to accompany WM use. In part, this may be an artifact of the subtraction methodology involved in these studies because the paired nondefault conditions will generally involve attention to some perceptually presented task. However, it may also be because different participants (or the same participant at different times) are using the resources of distinct sense modalities, engaging in inner speech on some occasions and visual imagery on others. What is generally agreed is that default-mode operation consists of episodic remembering, prospection of the future, and so on, which are known to make use of WM. And indeed, paired perception and imaging tasks in two distinct sense modalities (hearing and vision) show both a common core network implicated in each (which largely overlaps with the default-mode network) and modality-specific activity in midlevel sensory areas that varies by condition (Daselaar et al., 2010).

conscious mind wandering of the sort that would implicate the resources of WM. Rather, the explanation for these findings may be that the main components of the default network (especially medial regions of both the prefrontal and the parietal cortex) are important connecting hubs in the neural architecture of the brain, serving to link together other more modular regions (Sporns, 2011). As such the prefrontal and the parietal cortex will generally exhibit greater neural activity than the regions that they connect, just as airports that serve as major hubs show greater flight activity than others. In humans, we know that these default-network hubs play an important role in mind wandering. However, it does not follow that any animal with similar brain connectivity will also make use of its WM when at rest to replay the past and explore the future in the ways in which humans do.

It might be proposed that we have direct evidence of such replay activity in rats. When at rest, or during pauses in exploration of a track, place cells in the rat hippocampus fire in sequences corresponding to portions of the route already traveled or about to be traveled (Davidson et al., 2009). However, although these firing sequences take place over intervals that are linearly related to the distances represented, firing rates are very fast in comparison with the rat's normal rate of motion (corresponding to rates of about 8 m/s). In fact, the rate of "mental travel" is 15–20 times faster than actual travel. This contrasts sharply with the finding that, when humans imagine walking across a room, their imagined journey takes place at approximately the same speed as an actual journey (Decety et al., 1989). This suggests that the processes are not homologous across the two species and may serve quite different functions. Indeed, it is generally thought that rapid place-cell firing probably plays a role in the consolidation of memory (and, as such, is likely to take place in humans as well as in rodents).

It seems, then, that at present there is no real evidence to counter the suggestion that humans are unique in making frequent use of WM for purposes of rumination and mind wandering. However, this suggestion is supported (albeit quite weakly) by a theoretical inference from differences in long-term planning and creativity.

More Limited Behavioral and Conceptual Resources

Even if animals have WM capacities that are in all respects like our own, and likewise make chronic use of them, we can be confident that they are systematically different from us in the contents that figure in their WM. The primary reason for this is that only humans are capable of speech. This means that there is an entire range of actions (namely, speech actions) that only humans can mentally rehearse. In addition, the vastly greater conceptual repertoire possessed by humans (in part resulting from previous speech communication) will mean that humans have available many more ways in which to chunk information in WM, thereby extending the latter's scope and flexibility.

It is in these terms that we can characterize the unique character of so-called "system 2" reasoning and decision making in humans. Psychologists who study human reasoning have increasingly converged on the hypothesis that we use two distinct sets of processes when doing so (Evans and Frankish, 2009; Evans, 2010; Kahneman, 2011). System 1 is swift, unconscious, and intuitive and is thought to be largely shared with other animals. System 2 is reflective, serial, and slow, and its operations are largely conscious, using the limited resources of WM. Many (but by no means all) system 2 processes use mental rehearsals of sentences and phrases in inner speech, so in this respect system 2 is uniquely human. Moreover, given that WM and fluid *g* largely coincide, differences in WM capacities explain a significant portion of the variance between people in tests of their reasoning abilities, with the remainder of the variance being accounted for by differences in people's disposition to stop and reflect before answering and in their knowledge of norms of reasoning, or their "mindware" (Stanovich, 2009).

If the animal studies reviewed above have been correctly interpreted, then system 2 as such will not be uniquely human. For any animal engaged in prospection, envisaging and responding affectively to the consequences of the various actions open to it (which are mentally rehearsed in sequence) will qualify as engaging in system 2 processing. What is unique to humans is our ability to vastly extend the topics and forms of reflective thinking in which we can engage by virtue of our capacity for mental rehearsal of speech.

CONCLUSION

We can be confident that other primates, at any rate, have WM systems in many respects homologous with our own. We can be just as confident that humans are unique in some of the uses that they make of WM, specifically of inner speech. However, between these two items of knowledge there is a large space of possibilities about which little is known for sure. It seems likely, on current evidence, that other primates (and perhaps all mammals) have pure retention abilities whose limits are similar to those of humans. Moreover, whereas humans are by no means unique in having a capacity for prospection and future planning using WM, it seems likely that humans excel in their abilities to withstand interference and to deploy attention and rehearsal in flexible ways to maintain and manipulate representations in WM. In addition, there is some reason to suspect that humans may be unique in making frequent task-independent use of their WM abilities. However, until there is a sustained effort by comparative psychologists to devise and carry out matching tests of WM ability involving humans and various other species of animal, many of these claims must remain at least partly speculative.

6

The Evolution of Episodic Memory

TIMOTHY A. ALLEN* AND NORBERT J. FORTIN*†

One prominent view holds that episodic memory emerged recently in humans and lacks a "(neo)Darwinian evolution." Here, we review evidence supporting the alternative perspective that episodic memory has a long evolutionary history. We show that fundamental features of episodic memory capacity are present in mammals and birds and that the major brain regions responsible for episodic memory in humans have anatomical and functional homologs in other species. We propose that episodic memory capacity depends on a fundamental neural circuit that is similar across mammalian and avian species, suggesting that protoepisodic memory systems exist across amniotes and, possibly, all vertebrates. The implication is that episodic memory in diverse species may primarily be due to a shared underlying neural ancestry, rather than the result of evolutionary convergence. We also discuss potential advantages that episodic memory may offer, as well as species-specific divergences that have developed on top of the fundamental episodic memory architecture. We conclude by identifying possible time points for the emergence of episodic memory in evolution, to help guide further research in this area.

---

*Center for the Neurobiology of Learning and Memory, Department of Neurobiology and Behavior, University of California, Irvine, CA 92697. †To whom correspondence should be addressed. E-mail: norbert.fortin@uci.edu.

In humans, episodic memory has been defined as the capacity to recall specific experiences, as if one were to "mentally time travel" to reexperience individual events (Tulving, 1972, 2002). Although a prominent view holds that episodic memory is unique to humans (Tulving and Markowitsch, 1998; Tulving, 2002), accumulating evidence indicates that birds and rodents can demonstrate a memory capacity that satisfies behavioral criteria for episodic memory (Clayton et al., 2003a; Eichenbaum et al., 2005; Crystal, 2010). Does this evidence imply that episodic memory capacity is fundamentally conserved across avian and mammalian species? Or does it suggest "episodic-like" memory capacity evolved separately in a few species and thus is the result of convergent evolution? Notably, these important questions cannot be answered by focusing on behavior alone because it is difficult, perhaps impossible, to distinguish between homologous and analogous memory capacities. Here, our objective is to shed light on the potential evolution of episodic memory. We go beyond previous efforts by integrating the behavioral evidence across species with a comparative analysis of the neurobiology and neural mechanisms underlying episodic memory capacity. We also discuss the potential functions of episodic memory in an evolutionary context, as well as species-specific divergences.

EPISODIC MEMORY CAPACITY ACROSS SPECIES

Episodic memory refers to the memory for specific personal experiences. Although accurate, this definition does not capture the considerable challenge associated with distinguishing episodic memory from other memory capacities. A common mistake is to assume that one-trial learning is a sufficient criterion for episodic memory capacity. This is clearly not the case, as nonepisodic memories can be formed after a single exposure [e.g., conditioned taste aversion or familiarity (Morris, 2001; Clayton et al., 2003a; Eichenbaum et al., 2007)]. In this section, we consider the main approaches used to define and demonstrate episodic memory capacity across species.

Subjective Measures of Episodic Recall

Because the concept of episodic memory was first studied in cognitive psychology, one approach is to define it in terms of the subjective experience associated with episodic recall. Specifically, Tulving (2002) proposed that episodic recall involves the ability to "mentally time travel" to reexperience specific events, a capacity that requires a sense of self, subjective time, and autonoetic awareness (conscious awareness that the experience occurred in the past). Although this definition may capture the phenomenological aspects associated with episodic memory in humans, it relies entirely on verbal reports of subjective mental experiences. Because this definition of episodic memory precludes its investigation in animals, the hypothesis that this capacity is unique to humans lacks falsifiability. The absence of objective measures for episodic memory is also not conducive to rigorous scientific investigation in human studies. A more productive approach to defining episodic memory is to identify fundamental features that can be measured experimentally.

Receiver Operating Characteristics

The main objective of the receiver operating characteristics (ROC) approach is to use signal detection analyses to characterize recognition memory performance. More specifically, this method can be used to objectively quantify the relative contributions of episodic recollection versus familiarity in a recognition memory task. Although this approach was originally developed for human studies, it was successfully adapted to rodents and provided strong evidence that rodents have recollective and familiarity processes similar to those of humans (Fortin et al., 2004). However, considerable effort is required to adjust the experimental parameters (e.g., response biases) for each species. Therefore, although this approach has distinct advantages [for a comprehensive review, see Eichenbaum et al. (2007, 2010)], it is unlikely to become widely used across species.

Memory for "Events in Context"

The events-in-context approach capitalizes on the fact that, in the episodic memory system, information about specific events is tied to the spatial, temporal, and other situational contexts in which they occurred (Tulving, 1972; Mishkin et al., 1997; Clayton and Dickinson, 1998). Based on this operational definition, demonstrations that animals can remember events in context (Clayton and Dickinson, 1998; Fortin et al., 2002; Babb and Crystal, 2006) provided compelling evidence that core properties of episodic memory are present in nonhumans. This capacity is often termed episodic-like to emphasize that, whereas it does not address the phenomenological aspects associated with episodic memory in humans, it satisfies three key behavioral criteria (Clayton et al., 2003a):

(*i*) Content: The individual remembers information about the event ("what") and its context of occurrence (e.g., "where" or "when" it happened).

(*ii*) Structure: The information about the event and its context is integrated in a single representation.

(*iii*) Flexibility: The memory can be expressed to support adaptive behavior in novel situations.

These criteria have provided a solid theoretical framework for behavioral tests of episodic memory. It is important to note that the criteria are usually satisfied using converging evidence from multiple studies, as it is impractical to address them all in every experiment. Here, we examine the three main approaches used to study the memory for events in context: (*i*) "what-where-when," (*ii*) "what-where," and (*iii*) "what-when." The distinct content requirements of these models provide an opportunity to investigate different aspects of episodic memory capacity.

Memory for What-Where-When

An influential animal model of episodic memory took advantage of the natural caching behavior of scrub jays. In an ingenious paradigm, Clayton and Dickinson (1998) demonstrated that scrub jays could remember what food they stored (worms or peanuts), as well as where (the location in the cage) and when (4 hours or 124 hours ago) it was cached, thus fully satisfying the content criterion. Similar evidence of what-where-when memory has also been reported in other bird species, including other corvids [magpies (Zinkivskay et al., 2009)] and noncorvids [black-capped chickadees (Feeney et al., 2009)]. This approach has also been adapted to many mammalian species, including rats (Ergorul and Eichenbaum, 2004; Eacott et al., 2005; Babb and Crystal, 2006; Kart-Teke et al., 2006), mice (Dere et al., 2005), meadow voles (Ferkin et al., 2008), pigs (Kouwenberg et al., 2009), nonhuman primates (Hoffman et al., 2009; Martin-Ordas et al., 2010), and humans (Hayne and Imuta, 2011; Holland and Smulders, 2011). It is important to note that the structure and flexibility criteria have been much less investigated than the content criterion, so it remains to be determined whether all these species will meet all three behavioral criteria. As of now, there is evidence for what-where-when integration (structure criterion) in birds (Clayton et al., 2001), rodents (Ergorul and Eichenbaum, 2004), and primates (Hoffman et al., 2009). Evidence for the flexibility criterion comes from the demonstration that the what-where-when memory can be updated with new information [birds (Clayton and Dickinson, 1999; Clayton et al., 2003b); rodents (Babb and Crystal, 2006)], and that it can be expressed spontaneously [i.e., without training or in response to an unexpected test; birds (Singer and Zentall, 2007); rodents (Dere et al., 2005; Kart-Teke et al., 2006)]. Although this approach has been momentous, leading to the development of a number of animal models of episodic memory, it also has limitations. In particular, the content criterion is very stringent, requiring memory for what, where, and when. On one hand, this is a positive aspect of the model as it established a very high threshold for the first convincing behavioral demonstration of episodic memory in animals. On the other hand, this criterion may be overly restrictive. In fact, there is no clear evidence that all episodic memories contain all three types of information. Therefore, other forms of memory for events in context should also be considered episodic, such as memories involving a subset of the two (e.g., what-where), other types of contextual information [e.g., internal context (Kennedy and Shapiro, 2004)], or possibly where-when associations [no "what" component (Mankin et al., 2012)].

Memory for What-Where

This approach focuses on the memory for the spatial context of episodic memory, the ability to remember where specific events occurred. It is important to note that this capacity does not simply correspond to spatial memory (memory for "where"), as it requires animals to remember specific what-where associations (i.e., specific items in specific places). In these paradigms, the "what" component refers to the presentation of a specific item (e.g., odor, object). The "where" component varies depending on the species, typically referring to a specific place in an environment in rodent studies, or to a specific location on a screen (or complex visual scene) in primate studies. Tasks involving item-place associations have been used extensively in rats (e.g., Gilbert and Kesner, 2002, 2003; Day et al., 2003; Rajji et al., 2006) and nonhuman primates [e.g., item-scene associations (Gaffan, 1994)], particularly to study the neural basis of episodic memory. Paradigms relying on spontaneous preference, which require no training, have also been developed [e.g., Dix and Aggleton (1999)]. A more detailed review of what-where approaches, including their use as preclinical tests for assessment of cognitive function in animal models of aging and Alzheimer's disease, is available elsewhere (Snigdha et al., 2013).

Memory for What-When

This approach requires subjects to remember the temporal context in which specific events occurred, a defining feature of episodic memory (Tulving, 1972, 2002). There are different forms of memory for when events occurred, including memory for the order of events in a sequence, for how long ago events happened, and for the time of day at which they took place (Friedman, 1993; Roberts, 2002; Eichenbaum and Fortin, 2003; Crystal, 2010; Eacott and Easton, 2010; Jacobs et al., 2013). The vast majority of studies have focused on memory for the order of events, which reflects the capacity of episodic memory to preserve the "flow of events" as they occurred in experience (Tulving, 1972, 2002). The typical paradigm involves the presentation of a sequence of items (e.g., odors, objects), followed by a choice between two of the presented items. Memory for order is expressed by selecting [e.g., Fortin et al. (2002) and Kesner et al. (2002)], or preferentially exploring [e.g., Hannesson et al. (2004)], the item that appeared earlier in the sequence. Importantly, information about the spatial context is irrelevant to performance. This basic approach has been used in rodents (Fortin et al., 2002; Kesner et al., 2002), and similar approaches have been developed in nonhuman primates (Petrides, 1995; Naya and Suzuki, 2011; Templer and Hampton, 2013) and humans (Kumaran and Maguire, 2006; Lehn et al., 2009; Ross et al., 2009). Notably, the NIH Toolbox Cognition Battery proposes a what-when paradigm, which requires memory for sequences of pictured events, as the new standard measure for episodic memory capacity in humans [for a review, see Snigdha et al. (2013) and Weintraub et al. (2013)].

Section Summary

The evidence reviewed strongly suggests that core properties of episodic memory are present across mammals, as well as in a number of bird species. Although the ROC method has distinct advantages, the memory for the events-in-context approach is more practical and widely used. Therefore, the latter is more appropriate to examine episodic memory capacity across species and shed light on its evolution. What-where-when paradigms have the strictest behavioral criteria and thus are better suited for determining whether a given species has the capacity for episodic memory. In contrast, paradigms that focus on isolating a specific form of contextual information (e.g., what-where, what-when) are promising for investigating the types of contextual information fundamental to episodic memories, as well as elucidating its critical neurobiological substrate (see below). Although no single definition or approach is likely to capture all features of episodic memory, converging evidence from these operational approaches has greatly furthered our understanding of episodic memory across phylogeny.

BRAIN STRUCTURES IMPORTANT FOR EPISODIC MEMORY

Studies of neurological patients and functional neuroimaging in humans have shown that episodic memory critically depends on the integrity of the hippocampus (Vargha-Khadem et al., 1997; Tulving and Markowitsch, 1998; Eichenbaum and Fortin, 2005) but also involves a large network of cortical areas that includes the adjacent parahippocampal region and the prefrontal cortex (Cabeza and St. Jacques, 2007; Schacter et al., 2007). In this section, we review basic anatomical and functional evidence to determine the extent to which these structures are conserved in mammals and birds.

Hippocampus

The hippocampus has been identified in many species, including a large breadth of mammals (Insausti, 1993; Manns and Eichenbaum, 2006), birds (Székely, 1999; Atoji and Wild, 2006), reptiles [medial cortex (Rodríguez et al., 2002)], and teleost fish [dorsolateral telencephalon (Rodríguez et al., 2002; Broglio et al., 2005)]. The neurobiological and functional evidence strongly suggests that the hippocampus is a homologous structure across species.

In mammals, the hippocampus is remarkably conserved across species, including humans, nonhuman primates, pigs, rodents, and bats (Insausti, 1993; Manns and Eichenbaum, 2006). The cytoarchitecture can be easily identified by the dense layers of folded cell bodies that make up hippocampal subregions, including the subiculum, dentate gyrus, and cornu ammonis (CA) fields (Amaral and Witter, 1989; Manns and Eichenbaum, 2006; van Strien et al., 2009) (Fig. 6.1). Major inputs to the hippocampus originate from the entorhinal cortex and synapse on all subfields. Within the hippocampus, the dentate gyrus projects to CA3 through mossy fiber connections. CA3 projects to itself, through recurrent connections, as well as to CA1, through the Schaffer collaterals. The major outputs of the hippocampus originate from CA1 and the subiculum, and terminate in the entorhinal cortex [for a comprehensive account of the hippocampal circuitry, see van Strien et al. (2009)]. Additionally, a major anatomical characteristic of the mammalian hippocampus is a connection with the septum, which is conserved across all mammals. The function of the hippocampus is also well conserved across mammalian species. In fact, the hippocampus is critical for spatial memory in rats [reviewed in O'Keefe and Nadel (1978)], nonhuman primates (Banta Lavenex and Lavenex, 2009), and humans (Burgess et al., 2002). Moreover, neurophysiological studies have identified hippocampal neurons that encode specific places in an environment (place cells) in rodents (O'Keefe and Dostrovsky, 1971; Wilson and McNaughton, 1993; Knierim et al., 2006), nonhuman primates (Nishijo et al., 1997; Matsumura et al., 1999), and humans (Ekstrom et al., 2003), as well as in bats (Yartsev et al., 2011).

Birds also have a hippocampus, which arises from the same developmental origin as in mammals (Székely, 1999; Atoji and Wild, 2006; Rattenborg and Martinez-Gonzalez, 2011). As in mammals, a hippocampal–septal pathway is a major feature of the avian hippocampus (Atoji and Wild, 2004; Rattenborg and Martinez-Gonzalez, 2011). The avian hippo-

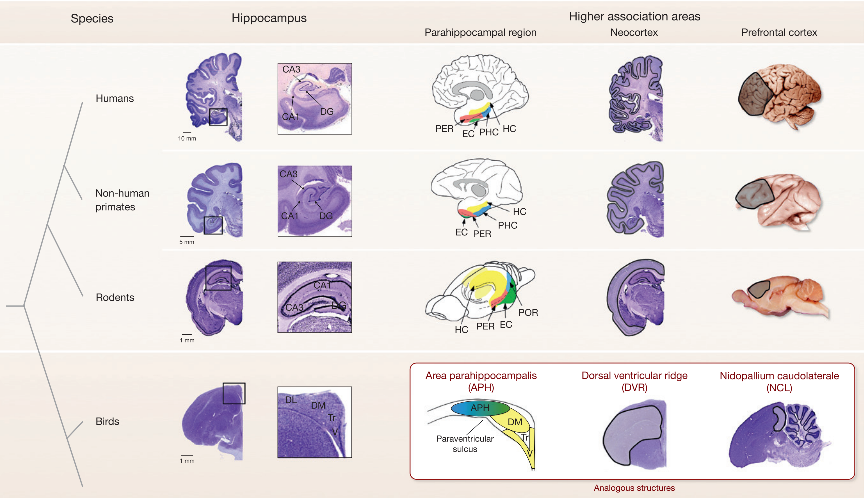


FIGURE 6.1 Brain regions important for episodic memory. Anatomical comparison of the hippocampus (avian hippocampus), parahippocampal region (avian area parahippocampalis), associational neocortex (avian dorsal ventricular ridge), and prefrontal cortex (avian nidopallium caudolaterale). The mammalian hippocampus shows distinct subregions, which are less evident in the avian hippocampus. The mammalian parahippocampal region is shown in diagrams [adapted with permission from Furtak et al. (2007), copyright Wiley-Liss, Inc.] to highlight the conserved relative spatial locations among species, with similar adjacent locations of area parahippocampalis and hippocampus in birds. Neocortical areas in mammals and associational areas of the dorsal ventricular ridge are outlined. The prefrontal cortex is shown in whole brains in mammals (medial surface in rat) and in a sagittal section in the bird. Human, nonhuman primate (*Macaca mulatta*), and rodent (*Rattus norvegicus*) sections were adapted with permission from http://www.brains.rad.msu.edu, and www.brainmuseum.org supported by the U.S. National Science Foundation, and bird (*Taeniopygia guttata*) sections from http://zebrafinch.brainarchitecture.org. DG, dentate gyrus; DL, dorsolateral region; DM, dorsomedial region; EC, entorhinal cortex, HC, hippocampus; PER, perirhinal cortex; PHC, parahippocampal cortex; POR, postrhinal cortex; Tr, triangular region; V, V-shaped layer.

campal subregions are not as visually obvious (Fig. 6.1) but nonetheless show homologies to those in mammals. Based on anatomical connectivity, Atoji and Wild (2006) noted that the dorsomedial area of the hippocampus is similar to the mammalian subiculum and CA regions, whereas the V-shaped layer in the ventromedial portion is similar to the mammalian dentate gyrus. However, a consensus on the exact homologies of hippocampal subregions is lacking (Székely, 1999; Atoji and Wild, 2006;

Rattenborg and Martinez-Gonzalez, 2011). Functionally, the avian hippocampus is similar to the mammalian hippocampus. Neurons in the avian hippocampus also show distinct place fields [reviewed in Bingman and Sharp (2006)], and lesions to the avian hippocampus specifically disrupt spatial memories (Hampton and Shettleworth, 1996; Colombo et al., 1997; Gagliardo et al., 1999). Notably, hippocampal lesions similarly impair spatial memories in turtles and goldfish (Rodríguez et al., 2002), further evidence that these functional similarities result from a long neurobiological ancestry.

Parahippocampal Region

In mammals, the hallmark of cortical–hippocampal connectivity is the existence of associative cortical structures that serve as an interface between the hippocampus and the rest of the neocortex. These associative regions include the entorhinal cortex, perirhinal cortex, and parahippocampal cortex [postrhinal cortex in rodents (Furtak et al., 2007)], which are collectively referred to as the parahippocampal region (Fig. 6.1). There are two main information processing pathways within the parahippocampal region (Fig. 6.2*A*). The "what" pathway, composed of the perirhinal and lateral entorhinal cortex, is important for processing and representing features of specific objects or items. In rodents and primates, this system receives information from all sensory modalities (Lavenex and Amaral, 2000; Suzuki and Amaral, 2004; Furtak et al., 2007), is critical for object memory (Brown and Aggleton, 2001; Squire et al., 2004; Feinberg et al., 2012), and contains neurons that respond to specific objects (Fried et al., 2002; Allen et al., 2007; Naya and Suzuki, 2011; Deshmukh et al., 2012). The second pathway processes "where" information and is composed of the parahippocampal/postrhinal cortex and medial entorhinal cortex. This system primarily receives visuospatial information (Suzuki and Amaral, 2004; Furtak et al., 2007). Consistent with a role in processing "where" information, neurons in a subregion of the medial entorhinal cortex fire in a triangular grid pattern as animals explore an environment [grid cells (Fyhn et al., 2004)]. Evidence for grid cells has been reported in rodents (Fyhn et al., 2004), nonhuman primates (Killian et al., 2012), and humans (Doeller et al., 2010), as well as in bats (Yartsev et al., 2011). Although species differences exist in the information processed by these pathways, the distinct informational segregation is conserved across rats, nonhuman primates, and humans (Burwell, 2000; Suzuki and Amaral, 2004; Eichenbaum et al., 2007).

In birds, the primary inputs and outputs of the hippocampus originate in the area parahippocampalis (Atoji and Wild, 2006) (Figs. 6.1 and 6.2*B*). Afferents to area parahippocampalis arise from several locations, includ-

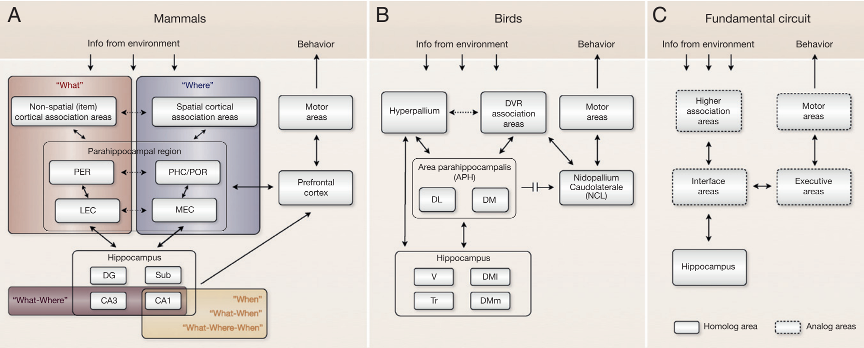


FIGURE 6.2 Neural circuits underlying episodic memory capacity in mammalian and avian species. (*A*) Schematic diagram of neural mechanisms supporting episodic memory encoding and expression in mammals. After information from the environment reaches the neocortex, the processing of "what" and "where" information is divided in parallel streams of cortical association areas. This functional segregation is maintained in the parahippocampal region, where the information is further processed before it reaches the hippocampus. Episodic memories are formed when the hippocampus integrates information about a specific event (what happened) with the context in which it occurred (e.g., where and/or when it happened). Although what-where coding has been shown in regions CA3 and CA1, lesion studies suggest that this type of integration depends specifically on region CA3. Recent evidence suggests that region CA1 provides an internal representation of elapsed time (when), which could support the formation of what-when and what-where-when associations. Episodic recall is thought to occur when the integrated event-in-context representation is reactivated in the hippocampal network, which leads to the reactivation of the associated representations in parahippocampal and neocortical association areas. The process by which the retrieved memories can guide behavior depends on the prefrontal cortex. (*B*) Comparable circuit in the avian brain. Note that connectivity between the area parahippocampalis and the nidopallium caudolaterale is indirect, as depicted with a broken arrow. (*C*) Fundamental circuit hypothesized to support episodic memory across species. Anatomical, behavioral, and physiological evidence demonstrates that this system involves homologous and analogous structures. DG, dentate gyrus; DL, dorsolateral region; DM, dorsomedial region (lateral and medial); DVR, dorsal ventricular ridge; LEC, lateral entorhinal cortex; MEC, medial entorhinal cortex; PER, perirhinal cortex; PHC, parahippocampal cortex; POR, postrhinal cortex; Sub, subiculum; Tr, triangular region; V, V-shaped layer.

ing the dorsal ventricular ridge and hyperpallium. Its efferents project back to the same structures and to the V-shaped layer and triangular region of the avian hippocampus. Therefore, the avian hippocampus has access to information from all modalities through the area parahippocampalis (Atoji and Wild, 2006), much like the mammalian system. However, it is unknown whether the dorsolateral and dorsomedial subregions of area parahippocampalis are involved in segregated informational streams. As in the medial entorhinal cortex in mammals, grid-like cells have been observed near the avian hippocampus, although their exact location remains unclear (Bingman and Sharp, 2006).

To summarize, the extent to which the mammalian parahippocampal region and the avian area parahippocampalis are homologous remains to be determined. However, it is clear that there are similarities in the circuit organization and functions of these regions across mammals and birds, and especially within mammals.

Prefrontal Cortex

The size of the prefrontal cortex varies greatly across mammals, especially between primates and rodents (Fig. 6.1), but there is strong evidence of anatomical and functional correspondence across species (Kesner, 1998; Brown and Bowman, 2002; Uylings et al., 2003). The prefrontal cortex receives information from most cortical association areas and strongly projects to cortical and subcortical motor regions, suggesting that it plays a key role in the representation and execution of actions (Goldman-Rakic, 1996; Fuster, 2001) (Fig. 6.2*A*). The prefrontal cortex is also connected to the hippocampus by a direct pathway from CA1 (Verwer et al., 1997) and indirect connections through the parahippocampal region (Lavenex and Amaral, 2000; Furtak et al., 2007). Importantly, individual prefrontal neurons exhibit delay-related activity in nonhuman primates [reviewed in Goldman-Rakic (1996) and Fuster (2001)] and rodents (Jung et al., 1998), activity that may contribute to working memory, inferential reasoning, and decision-making abilities. These findings are consistent with the view that the prefrontal cortex is the primary executive region of the brain, a structure particularly important for bridging perception, memory, and action (Goldman-Rakic, 1996; Fuster, 2001).

Birds also have an executive region thought to be similar to the mammalian prefrontal cortex, called the nidopallium caudolaterale (Güntürkün, 2005; Herold et al., 2011). Importantly, the nidopallium caudolaterale directly projects to motor regions and has indirect access to the hippocampus and the area parahippocampalis [Güntürkün (2005); see also Allen and Fortin (2013)] (Fig. 6.2*B*). Delay-related neuronal activity has also been observed in individual nidopallium caudolaterale neurons (Rose and Colombo, 2005). However, it is important to note that, despite these similarities to the mammalian prefrontal cortex, the nidopallium caudolaterale is not homologous to its mammalian counterpart [i.e., the similarities are due to convergent evolution (Rose and Colombo, 2005)].

Section Summary

In sum, the hippocampus, parahippocampal region, and prefrontal cortex form a neural system that is thought to underlie episodic memory capacities in humans, but this basic neurobiology is not unique to humans. Considerable evidence shows that this circuit is present across mammals and that a comparable circuit exists in the avian brain. Interestingly, regions that are homologous to the hippocampus also exist in reptiles and bony (teleost) fish. Considering the long evolutionary history and structure–function similarities, it seems reasonable to hypothesize that the human episodic memory circuit shares an ancestral protoepisodic memory system with other mammals and possibly birds.

NEURAL MECHANISMS UNDERLYING EPISODIC MEMORY

Episodic memory in mammals depends on the hippocampus, the parahippocampal region, and the prefrontal cortex. However, until recently, it was unclear how this network of structures could give rise to episodic memory. In fact, considerable progress has been made in recent years toward understanding the specific contribution of each structure, as well as the nature of their functional relationships. Here, we describe a model, derived primarily from rodent and primate studies, summarizing the neural mechanisms thought to support the encoding and expression of episodic memories in mammals (Fig. 6.2*A*).

Processing Information About Events and Elements of Context

After being processed by sensory receptors and thalamic nuclei, information from the external world reaches primary sensory areas of the neocortex. A hierarchy of association cortical areas then processes this information at increasing levels of complexity and abstraction, culminating in multimodal representations. This information is funneled into the parahippocampal region, which mediates communications between the neocortex and the hippocampus (McClelland and Goddard, 1996).

The processing of "what" (e.g., stimuli, items) and "where" information is generally segregated into parallel streams. This functional segregation is maintained in the parahippocampal region (Burwell, 2000; Lavenex and Amaral, 2000; Eichenbaum et al., 2007): the perirhinal and lateral entorhinal areas play a critical role in item memory (what) whereas the postrhinal and medial entorhinal areas are important for the memory of contextual information (where). In contrast, the neural basis of the memory for "when" is much less understood. Although the hippocampus may play a critical role in processing "when" information under specific conditions (Meck et al., 1984; Jacobs et al., 2013), this capacity is generally thought to depend on other cortical and subcortical structures [e.g., striatum (Buhusi and Meck, 2005)].

Integrating Event and Context Information

Before reaching the hippocampus, information about the "what," "where," or "when" of individual events is not yet integrated into a single representation and thus does not satisfy the structure criterion for episodic memory. Episodic memory requires the integration of the representation of a single event with its distinctive contextual information, and it is this process that critically depends on the hippocampus [for potential mechanisms, see Buzsáki and Moser (2013)].

What-Where Integration

Studies in rodents (Gilbert and Kesner, 2002, 2003; Day et al., 2003; Rajji et al., 2006) and primates (Gaffan, 1994) show that the hippocampus plays a critical role in forming specific item–place associations. It is important to note that the spatial layout is already well learned in these paradigms, so deficits after hippocampus lesions cannot be solely attributed to an impairment in processing "where" information. Similarly, the deficits cannot be attributed to a deficiency in processing "what" information, as this capacity is normal in animals with hippocampal damage (Fortin et al., 2002; Gilbert and Kesner, 2002; Feinberg et al., 2012). The integration of what-where information can also be demonstrated in the coding properties of individual hippocampal neurons. A study by Wood et al. (1999) showed that different subsets of neurons selectively coded for "what" (e.g., a specific odor) and "where" (e.g., a specific location) information, whereas others coded for specific what-where conjunctions (a specific odor in a particular place). More recent studies have shown that the emergence of what-where coding parallels the learning of item-place associations (Komorowski et al., 2009; Kim et al., 2011). Although lesion studies suggest what-where integration depends on subregion CA3 but not CA1 (Gilbert and Kesner, 2003), what-where neural coding has been reported in both subregions with no significant differences reported (Wood et al., 1999; Komorowski et al., 2009).

What-When Integration

Accumulating evidence suggests that the hippocampus also plays a critical role in forming what-when associations, including memory for the order in which specific events occurred. For instance, in sequence memory paradigms, rats with hippocampal damage were shown to have normal memory for the individual items presented (what) but consistently failed to remember the temporal relationships among events [what-when (Fortin et al., 2002; Kesner et al., 2002)]. Functional neuroimaging studies have shown that the hippocampus is strongly engaged during performance of similar tasks in humans as well (Kumaran and Maguire, 2006; Lehn et al., 2009; Ross et al., 2009). Furthermore, recent electrophysiological evidence suggests that a fundamental role of the hippocampus is to provide an internal representation of elapsed time, which could support the formation of what-when memories (MacDonald et al., 2011; Naya and Suzuki, 2011; Shapiro, 2011). In fact, recent studies have shown that individual hippocampal neurons exhibit robust timing signals during stimulus-free intervals ["time cells" (Pastalkova et al., 2008; MacDonald et al., 2011)] and during the presentation of sequences of events (Naya and Suzuki, 2011). In addition, the pattern of activity in hippocampal ensembles has been shown to gradually change over time, a form of population coding that could serve as a timing signal (Manns et al., 2007; Mankin et al., 2012). The above lesion and electrophysiological studies provide converging evidence that this capacity primarily depends on subregion CA1 of the hippocampus.

Episodic Recall and Response Selection

Episodic recall is thought to occur when the integrated event-in-context representation is reactivated, involving a pattern completion process that can be initiated by cueing the hippocampal network with elements of the event or context. This hippocampal reactivation leads to the reactivation of the corresponding representations in the parahippocampal region and other cortical association areas (McClelland and Goddard, 1996; Eichenbaum et al., 2007). The process by which the retrieved information can guide behavior is thought to critically depend on the prefrontal cortex (Goldman-Rakic, 1996; Fuster, 2001; Ninokura et al., 2003; Eichenbaum and Fortin, 2009). First, the episode-specific patterns of activity retrieved in the hippocampus are thought to reach the prefrontal cortex, either directly or through the parahippocampal region. The prefrontal cortex then evaluates the retrieved information and plans the appropriate course of action, which is then conveyed to motor regions (Goldman-Rakic, 1996; Fuster, 2001; Ninokura et al., 2003; Eichenbaum and Fortin, 2009).

Section Summary

Significant progress has been made in our understanding of the neural circuits underlying episodic memory capacity in mammals. In its essence, the circuit requires higher association areas to process the sensory information (neocortex), interface areas to communicate with the hippocampus (parahippocampal region), the hippocampus to integrate and retrieve information about the episode, and executive areas to produce the appropriate behavior (prefrontal cortex). Although little is known about the neural mechanisms underlying episodic memory in birds, it is important to note that they have a similar circuit that could perform the same fundamental operations. The corresponding system in birds involves a combination of homologous (the hippocampus and, to some degree, the area parahippocampalis) and analogous (dorsal ventricular ridge, nidopallium caudolaterale) structures (Fig. 6.2*B*). Therefore, we hypothesize that a fundamental circuit may be shared between species that demonstrate episodic memory abilities (Fig. 6.2*C*).

FUNCTIONS OF EPISODIC MEMORY ACROSS SPECIES

As we examine the evolution of episodic memory, it is important to consider its potential functions across species. What are its potential contributions to the fitness of an individual? What advantage could it provide? Episodic memory is not necessary for animals to find food, shelter, mates, or to avoid dangerous situations. However, given the dynamic nature of the environment, the ability to remember unique experiences could certainly help animals be more successful. This advantage may be especially beneficial under conditions of limited resources, when incremental gains in the likelihood of success can amount to large effects on long-term survival. As mentioned earlier, our central argument is that fundamental properties of episodic memory, as well as their underlying neural circuits, are shared across mammals and birds. Therefore, some basic functions of episodic memory should be common across species.

Memory-Based Predictions

The purpose of memory is not to reminisce about the past, but to allow us to think, reason, and plan for the future (McGaugh, Chapter 9, this volume). Along these lines, we propose that the main function of episodic memory is to provide memory-based predictions to support adaptive behavior in the present or immediate future (Eichenbaum and Fortin, 2009). There are two ways in which episodic memory could contribute to this capacity. First, episodic memory is the only memory system to provide spatially and temporally specific information about single experiences. For instance, when faced with a specific need (e.g., a tool), an individual could use episodic memory to make predictions as to how to satisfy this need (e.g., look where the tool was last seen). This unparalleled specificity allows animals to take into account unique events in guiding their behavior and to quickly adapt to changing circumstances. Second, episodic memory could contribute to memory-based predictions by supporting the capacity to make novel inferences. In fact, it has been proposed that a fundamental role of the hippocampus is to integrate episodic and semantic memories into a relational (declarative) memory network (Eichenbaum et al., 1999; Eichenbaum and Fortin, 2009). Because many of our memories overlap in information content, the network is thought to represent relationships among memories by linking them using their common elements. This network structure could support the flexible expression of inferred relationships between elements that were never experienced together, such as deducing a novel trajectory between two locations or the social hierarchy among a group of individuals. It should be noted that nondeclarative memory abilities also extract regularities from the environment to support the ability to generalize to other situations, but the process requires multiple exposures and lacks flexibility of expression (i.e., is tied to specific cues).

Planning for the Distant Future

Future planning involves making predictions about the distant future (many hours ahead) to anticipate future needs, an extension of the capacity for memory-based predictions described above. In humans, future planning involves “episodic future thought,” the ability to simulate plausible future events or scenarios [e.g., imagining future activities to determine what to pack for an upcoming trip (Addis et al., 2007; Hassabis et al., 2007; Szpunar et al., 2007)]. Interestingly, there is considerable overlap between the neural circuits involved in retrieving episodic memories and those involved in simulating future events, suggesting that the two capacities are intrinsically linked (Addis et al., 2007; Hassabis et al., 2007; Szpunar et al., 2007). Does this capacity for future planning extend beyond humans? Any attempt to examine future planning in animals must address the Bischof-Köhler hypothesis, which states that only humans can dissociate themselves from their current motivational state and take action for future needs (Suddendorf and Corballis, 2007). The criteria for demonstrating future planning in animals are as follows: (*i*) the behavior involved should be a novel action or combination of actions, (*ii*) the action should be appropriate for the future motivational state, and (*iii*) the anticipatory action should not have been extensively reinforced (Clayton et al., 2003a; Raby et al., 2007; Shettleworth, 2007; Suddendorf and Corballis, 2007). The first study satisfying all criteria has been conducted in scrub jays. In this study, the birds demonstrated the ability to make provisions for a future need, thus showing that they could dissociate themselves from their current motivational state and spontaneously plan for the next day (Raby et al., 2007). Accumulating evidence suggests that apes are also capable of future planning, as they can save tools for future use (Mulcahy and Call, 2006) and can override immediate drives in favor of future needs (Naqshbandi and Roberts, 2006; Osvath and Osvath, 2008). Although it is clear that the behavior of other animals can be future oriented or based on future consequences [e.g., selecting an item to receive a reward (Roberts, 2002)], it remains to be determined whether animals other than humans, apes, and scrub jays are capable of future planning.

Building Social Relationships and Networks

Episodic memory could be particularly useful for processing and using social information. Although some aspects of social information are static (e.g., who is related to whom?), others can change over time (e.g., who has been cooperative? who has been aggressive?) and thus could depend on the capacity to remember specific experiences. Interestingly, the species in which episodic memory capacity has been most convincingly demonstrated (primates, rodents, and scrub jays) are highly social (Emery and Clayton, 2004; Brennan and Kendrick, 2006). Recent evidence suggests that humans with episodic memory impairments have social circles that are limited compared with controls, suggesting that episodic memory may be crucial for establishing and/or maintaining social bonds (Davidson et al., 2012). Thus, there may be a relationship between episodic memory capacity and social interactions.

Species-Specific Uses of Episodic Memory

Although we have so far emphasized the commonalities in episodic memory capacity, there are also clear differences across species. These divergences include unique uses of episodic memory, as well as species-specific attributes. For instance, in humans, episodic memory is thought to be intrinsically tied to other mental capacities such as language, a sense of self, empathy, and theory of mind (Tulving, 2002; Schacter et al., 2007; Duff and Brown-Schmidt, 2012). Although such characteristics were initially used as evidence that episodic memory is unique to humans, according to the present conceptual framework, they represent species-specific attributes (or modules) associated with the expansion of neocortical (particularly prefrontal) areas in humans. Other species-specific uses of episodic memory may include meadow voles predicting when and where sexually receptive females will be located (Ferkin et al., 2008) and hummingbirds keeping track of the location, quality, and renewal rate of different sources of nectar (González-Gómez et al., 2011). Episodic memory may be of particular importance in hummingbirds because of the enormous energy cost in gathering nectar, which makes repeat visits or poor planning highly detrimental (González-Gómez et al., 2011).

Section Summary

Given that several species demonstrate episodic memory capacity, it is reasonable to assume that it offers significant advantages. Some of these benefits could be common across species; others may be species-specific. However, further research is needed before we can understand the specific nature of these advantages or establish that they are causally linked with an increase in fitness.

CONCLUSIONS

Episodic memory is the remarkable capacity to remember specific personal experiences. Although it was originally thought that this capacity was particular to humans, the ample evidence reviewed here indicates that core properties of episodic memory are present across mammals, as well as in birds. This cross-species approach to episodic memory research is made possible by the use of operational definitions that can be applied across species, a method we strongly suggest should be used in animal and human studies. The most common approach to investigate episodic memory capacity across species is to determine whether animals can remember events within the context in which they occurred (e.g., memory for what-where-when, what-where, or what-when). Using this conceptual framework, we showed that episodic memory in mammals depends on a functional relationship between the hippocampus, parahippocampal region, neocortical association areas, and prefrontal cortex. Importantly, we described a comparable neural circuit in birds, which includes homologous (hippocampus, and to some degree, parahippocampal region) and analogous (dorsal ventricular ridge association areas, nidopallium caudolaterale "prefrontal" area) structures. Finally, we submit that this fundamental circuit underlies episodic memory capacity across species but that species-specific divergences have also evolved around this central architecture.

When did episodic memory emerge? Unfortunately, the available evidence cannot support a definitive answer at this time. We speculate that it evolved at a stage when the hippocampus was already present because the hippocampus is known to be a critical substrate. However, we are not implying a one-to-one relationship between the hippocampus and episodic memory (e.g., if the hippocampus is present, the animal has episodic memory capacity). Because the hippocampus is essential for spatial memory across species, ranging from humans to teleost fish, it is likely that its role was limited to the processing of "where" information when it first emerged (Fig. 6.3). We propose that episodic memory capacity emerged at a later time, when the hippocampus began supporting the integration of information about events in context (e.g., "what," "where," and/or "when" information). As the neural architecture of the hippocampus indicates, the content of its associations is determined by its inputs. Thus, the change to supporting episodic memory likely occurred when the hippocampus began receiving highly processed event and contextual information from higher association areas. In light of the cross-species behavioral and neurobiological similarities reviewed here, it is tempting to conclude that episodic memory capacity emerged before mammals and reptiles diverged (possibility **1** in Fig. 6.3). However, because of the limited data available in nonavian reptiles, the hypothesis that it resulted from convergent evolution (e.g., possibilities **2** and **3** in Fig. 6.3) cannot be rejected at this time. Addressing this important issue will require converg-

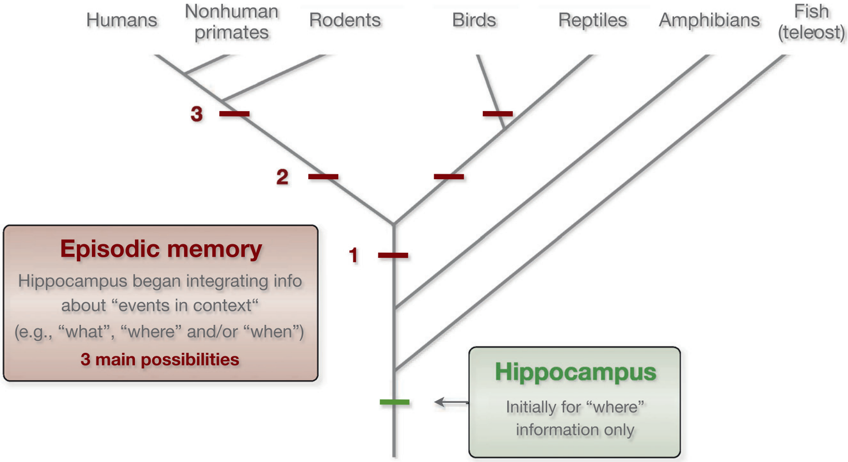


FIGURE 6.3 Possible time points for the emergence of episodic memory in evolution. Initially, the role of hippocampus was likely limited to the processing of spatial information ("where"). We hypothesize that episodic memory capacity emerged later on, when the hippocampus began supporting the integration of information about events in context (e.g., "what," "where," and/or "when" information). The striking behavioral and neurobiological similarities reviewed in this chapter suggest that episodic memory capacity emerged before mammals and reptiles diverged (possibility **1**). However, additional evidence from birds and reptiles is needed before the alternative hypothesis that episodic memory is the result of convergent evolution (e.g., possibilities **2** and **3**) can be safely rejected.

ing evidence from anatomical, behavioral, and neurobiological studies in different avian and reptilian species.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation CAREER award IOS-1150292, The Feinberg Foundation, and the University of California, Irvine.

7

Neuroethology of Primate Social Behavior

STEVE W. C. CHANG,[*†] LAUREN J. N. BRENT,[*†]
GEOFFREY K. ADAMS,[*†] JEFFREY T. KLEIN,[‡]
JOHN M. PEARSON,[*†§] KARLI K. WATSON,[*†] AND
MICHAEL L. PLATT[*†‖#**]

A neuroethological approach to human and nonhuman primate behavior and cognition predicts biological specializations for social life. Evidence reviewed here indicates that ancestral mechanisms are often duplicated, repurposed, and differentially regulated to support social behavior. Focusing on recent research from nonhuman primates, we describe how the primate brain might implement social functions by co-opting and extending preexisting mechanisms that previously supported nonsocial functions. This approach reveals that highly specialized mechanisms have evolved to decipher the immediate social context, and parallel circuits have evolved to translate social perceptual signals and nonsocial perceptual signals into partially integrated social and nonsocial motivational signals, which together inform general-purpose mechanisms that command behavior. Differences in social behavior between species, as well as between individuals within a species, result in part from neuromodulatory regulation of these neural circuits, which itself appears to be under partial genetic control. Ultimately, intraspecific variation in social behavior has differential fitness consequences, providing fundamental building blocks of natural selection. Our review suggests that the neu-

---

Departments of [*]Neurobiology and [§]Neurosurgery, Duke University School of Medicine, Durham, NC 27710; [†]Duke Institute for Brain Sciences, Center for Cognitive Neuroscience and Departments of [‖]Psychology and Neurosciences and [#]Evolutionary Anthropology, Duke University, Durham, NC 27708; and [‡]Bowles Center for Alcohol Studies, University of North Carolina, Chapel Hill, NC 27599. [**]To whom correspondence should be addressed. E-mail: platt@neuro.duke.edu.

roethological approach to primate behavior may provide unique insights into human psychopathology.

Sensitivity and responsiveness to information about others is critical for human health (Berkman, 2000; Cohen, 2004), survival (Barefoot et al., 2005), and even financial success (Baron and Markman, 2003). To navigate our social worlds, we track the behavior of others and form models of their intentions and emotional states, we actively seek out and exchange information about others, and we flexibly alter our behavior in response to what we know about others. These faculties are so important to human behavior that their disruption constitutes psychopathology (Adolphs, 2003; Meyer-Lindenberg et al., 2011). These specializations for social behavior reflect a rich evolutionary heritage of adaptation to group life (Byrne and Whiten, 1989; Dunbar, 1998; Allman, 1999). Like humans, many nonhuman primates also live in large groups characterized by patterns of social behaviors like grooming, imitative and cooperative foraging, differentiated affiliative relationships, ritualized courtship and mating behavior, and competitive interactions structured by social dominance (Wilson, 1975; Smuts et al., 1987). Not surprisingly, the ability to deftly navigate the social environment has observable consequences for reproductive success in some nonhuman primates (Silk et al., 2003).

EVOLUTIONARY PERSPECTIVE ON SOCIAL BEHAVIOR

Social behavior places strong and unique demands on the nervous system. Across primate species, group size (a potential proxy of social complexity) is correlated with forebrain volume, after correcting for body size (Dunbar, 1998). Additional brain tissue beyond that required to maintain a body of a particular size is costly, in both developmental complexity and metabolic demands (Aiello and Wheeler, 1995; Allman, 1999; Lennie, 2003; Leonard et al., 2003). Indeed, social complexity and the elaboration of neural mechanisms to support it are associated with diets high in dependable calorie-rich foods (Harvey et al., 1980; Harding, 1981; Milton, 1981). Major expansion of the hominine brain during human evolution appears to have coincided with the development of new behaviors that added more calories to the diet, such as eating meat (*Homo habilis*, ~2.3 Mya) (Leakey et al., 1964) and cooking (*Homo erectus*, ~1.5 Mya) (Wrangham, 2009).

Social behavior seems likely to depend on homologous neural mechanisms in humans and nonhuman primates (Rushworth et al., 2013). Novel behaviors can evolve by connecting, repurposing (i.e., shifted to serve a new function), or elaborating upon ancestral mechanisms that originally served a different function (Katz and Harris-Warrick, 1999), and the evolution of social behaviors seems likely to follow this pattern. A striking example of such elaboration and repurposing is the electrocommunication system of mormyrid fish. These fish have electrosensory receptors that are part of their lateral line system, which originally evolved to aid orienting and the detection of motion (Montgomery, 1991; Katz, 2006). In mormyrids, the cerebellum, where sensations from the lateral line system are processed, is greatly enlarged and serves an important role in electrocommunication, a social function absent in the ancestral state (Montgomery, 1991; Katz, 2006). The evolution of the neuropeptide oxytocin (OT) is another excellent example of repurposing for social functions. The ancestral anxiolytic (Neumann et al., 2000; Yoshida et al., 2009), approach- and tolerance-enhancing (Young, 2002; Averbeck, 2010; Kemp and Guastella, 2010) roles of OT in early vertebrates may have been co-opted to support parental behavior and social bonding in mammals.

In this review, we discuss recent evidence supporting the idea that social behavior can be constructed from the basic building blocks of nonsocial behaviors. In some cases, sociality is supported by general-purpose mechanisms whereas others may require special-purpose mechanisms. By "general purpose," we mean that a given mechanism is used generally across both social and nonsocial domains, whereas, by "special purpose," we mean that a given mechanism has a privileged role in the social domain. Specialized mechanisms, such as the electrosensory receptor organ of mormyrid fish tuned for species communication and face identification cells in the temporal lobes of primates (Perrett et al., 1982; Desimone et al., 1984; Desimone, 1991; Tsao et al., 2003) and ungulates (Kendrick, 1994), are more frequently found near the input stages of social processing (i.e., receiving social information) whereas generalized mechanisms are more common near the output stages of effector control (Klein et al., 2008). By contrast, a mixture of specialized and generalized mechanisms appear to characterize intermediate computational stages of processing that translate socially specific inputs into motivational signals that guide learning and decision making, ultimately resulting in motor commands that generate behavior (Watson and Platt, 2012; Chang et al., 2013; Klein and Platt, 2013). Our review focuses on recent behavioral, neurobiological, and genetic findings supporting these general principles. Selected examples used in this review to support our claim are summarized in Table 7.1.

PARALLELS BETWEEN SOCIAL AND NONSOCIAL BEHAVIORS

Many of our behaviors are driven by reinforcement, and we and other animals seek a variety of rewards by foraging. Foraging is one of the most primitive and basic behavioral states, being a feature of essentially all motile, heterotrophic life. It is therefore unsurprising that foraging strate-

TABLE 7.1 Summary List of Selected Examples from the Current Paper on How Nonsocial Functions Are Repurposed to Serve Social Functions Throughout Evolution

Biological Units	Type/ Region	Nonsocial Functions	Social Functions
Behaviors	Foraging	Reward seeking, information seeking (Charnov, 1976; Stephens and Krebs, 1986; Miller and Remington, 2004; Pirolli, 2007; Lawrance et al., 2013)	Social information seeking (Keating and Keating, 1982; Johnson et al., 1991; Emery, 2000; Deaner et al., 2005; Hayden et al., 2007; Adams et al., 2012)
	Imminent threat response	Reflexive, escape behavior (Fanselow and Lester, 1988)	Gaze aversion (Deaner et al., 2005; Watson and Platt, 2012)
	Distant threat response	Cautious exploratory behavior (Dielenberg et al., 2001)	Social exploration (Deaner et al., 2005; Watson and Platt, 2012)
Neural circuits	Posterior superior sulcus (pSTS)	Multisensory integration, perceiving intention from animacy (Bruce et al., 1981; Gao et al., 2012)	Gaze perception, gaze following (Hoffman and Haxby, 2000; Roy et al., 2014)
	Lateral intraparietal area (LIP)	Spatial orienting, motor planning (Snyder et al., 2000; Bisley and Goldberg, 2010)	Gaze direction, social value associated with space (Klein et al., 2008; Roy and Platt, 2009; Shepherd et al., 2009)
	Striatum (medial)	Reward and learning (Moll et al., 2006; Izuma et al., 2008)	Social image category, reward donation (Izuma et al., 2008; Klein and Platt, 2013)
	Orbitofrontal cortex (OFC)		Social image category, received reward during social interactions, social network size (Dunbar, 1995; Lewis et al., 2011; Watson and Platt, 2012; Chang et al., 2013)

TABLE 7.1 Continued

Biological Units	Type/ Region	Nonsocial Functions	Social Functions
	Anterior cingulate sulcus (ACCs)	Foraging decisions, performance monitoring (Hayden et al., 2011)	Foregone reward during social interactions (Chang et al., 2013)
	Anterior cingulate gyrus (ACCg)	Reward and learning (Amemori and Graybiel, 2012)	Shared and donated reward during social interactions, social evaluation, other-regard, mentalizing about others' states of mind (Singer et al., 2004; Rudebeck et al., 2006; Saxe, 2006; Mobbs et al., 2009; Waytz et al., 2012; Chang et al., 2013)
Neuromodulators	Oxytocin/ vasopressin	Water regulation, reproduction, anxiolysis (Belin and Moos, 1986; Neumann et al., 2000; Donaldson and Young, 2008; Yoshida et al., 2009)	Pair-bonding, parental care, selective aggression, social salience, generosity, trust (Pedersen et al., 1982; Winslow et al., 1993; Cho et al., 1999; Young, 2002; Kosfeld et al., 2005; Zak et al., 2007; Heinrichs et al., 2009; Averbeck, 2010; Kemp and Guastella, 2010; Bartz et al., 2011; Chang et al., 2012; Crockford et al., 2013)
	HPA axis	Physical stress	Psychosocial stress (social status) (Abbott et al., 2003; Blumstein et al., 2006; Tung et al., 2012)
	HPG axis	Reproduction	Social regulation/ control, social opportunity (social status) (Wingfield et al., 1990; Burmeister et al., 2005; Hirschenhauser and Oliveira, 2006; Fernald, 2012; Higham et al., 2013)

TABLE 7.1 Continued

Biological Units	Type/ Region	Nonsocial Functions	Social Functions
	Serotonin	Cardiac and gastrointestinal functions, mood, memory, reward and learning (Sirviö et al., 1994; Hayes and Greenshaw, 2011)	Social network integration, social structure, social information processing (Wendland et al., 2006; Watson et al., 2009; Brent et al., 2013)

gies are under strong selective pressure for maximizing returns on investment. Animals often forage for foods sparsely distributed in locally dense patches (Charnov, 1976). As an animal forages in a patch, resources are depleted and the rate of energy intake slows. However, traveling to a new patch may be costly and accompanied by uncertain outcomes, leading to a decision to abandon a patch to maximize its overall rate of consumption. The same principle applies to many everyday decisions made by people. Because resources are often patchily distributed, this model has broad applicability. The optimal solution, known as Charnov's Marginal Value Theorem, is that a patch should be abandoned when the current rate of consumption falls to the average for the overall environment (Charnov, 1976). This model has been remarkably successful at describing the foraging behavior of a wide variety of organisms (Stephens and Krebs, 1986) and recently has been applied to understand neural correlates of foraging decisions (Hayden et al., 2011; Kolling et al., 2012). In fact, foraging theory has also been applied to problems far afield from its original purpose, including the efficient design of websites (Miller and Remington, 2004) and a description of how computer programmers search for errors in code (Lawrance et al., 2013).

Organisms searching for information can be said to be "information foraging" (Pirolli, 2007). Like foraging for primary rewards, information foraging presents opportunities as well as costs. Costs come in the form of missed opportunities to eat, drink, or sleep because information-seeking behaviors often demand certain postures or behavioral states incompatible with attentive orienting, as well as social costs, such as aggression from conspecifics and missed opportunities to interact with partners. Because social information has reinforcement value (either positive or negative), the basic problems studied by foraging theory may apply to the acquisition of social information. A wealth of behavioral data indicates that both humans and nonhuman primates actively seek social information. Humans and nonhuman primates find social stimuli to be intrinsically rewarding, and certain types of social stimuli are more interesting and reinforcing than others (Emery, 2000; Deaner et al., 2005; Hayden et al., 2007). For instance, even shortly after birth, human infants look longer at faces than at similar nonface stimuli (Johnson et al., 1991). Likewise, nonhuman primates spend more time looking at pictures of faces directed toward them compared with pictures of faces with averted gaze (Keating and Keating, 1982), and direct their gaze more often toward higher-ranking than lower-ranking animals (McNelis and Boatright-Horowitz, 1998). Furthermore, active social interactions such as cooperative transactions (Rilling et al., 2002; Rand et al., 2012) or the opportunity to punish a traitor (de Quervain et al., 2004), which can be understood using a game theoretic framework (Lee, 2008), can be as motivating as primary rewards in humans. These observations support the hypothesis that the brains of many animals, especially those of primates, have evolved mechanisms that find social information rewarding and worth foraging.

We propose that, because a major function of the brain is to seek resources, it is likely that mechanisms that evolved to support foraging are readily repurposed to solve other, formally similar computational problems. With respect to social behavior, if information about others is a valuable resource, then the biological mechanisms underlying foraging decisions will be used to support social information seeking (Adams et al., 2012). For example, opportunities and costs associated with social information foraging are likely to engage fundamental biological mechanisms for computing opportunities and costs. Foraging mechanisms seem likely to have become further specialized to cope with the unique demands of interindividual dynamics that arise as a consequence of group living.

Another potential example of similarities between social and nonsocial behaviors arises from the comparison of behavioral responses to predators and social threats. In both cases, an imminent threat evokes fast, reflexive behaviors, such as freezing, defensive aggression, or escape behavior (Fanselow and Lester, 1988). A distant threat, however, elicits cautious exploratory behavior of the threatening object (Dielenberg et al., 2001). Rhesus macaques, when given the opportunity, will opt to view pictures of dominant monkeys, a potentially threatening social stimulus, over pictures of subordinates (Deaner et al., 2005; Watson and Platt, 2012). Despite this interest, low-status monkeys typically avert their gaze from high-status monkey faces when confronted (Deaner et al., 2005) and look quickly away from dominant male pictures after choosing to see them (Deaner et al., 2005). This behavior is reminiscent of the exploratory behavior of rodents confronted with cat odor (Dielenberg et al., 2001) and the avoidance behavior in the presence of an actual predator. Indeed, many fundamental behavioral strategies designed for nonsocial settings seem to resonate across behavioral strategies used in social settings.

NEURAL CIRCUITS GUIDING SOCIAL DECISIONS

The neural mechanisms supporting social behaviors are broadly distributed throughout the primate forebrain, overlapping with areas involved in more general-purpose functions (Fig. 7.1*A*). Current evidence suggests that most neural circuits involved in social behavior are not dedicated exclusively to "social" functions. Rather, such circuitry is also typically engaged in related nonsocial behaviors, regardless of whether social information is processed in a privileged manner (i.e., special purpose) or not (i.e., general purpose). This evidence supports the hypothesis that the evolution of novel social behaviors has occurred by co-opting existing neural hardware for the purpose of interacting with others.

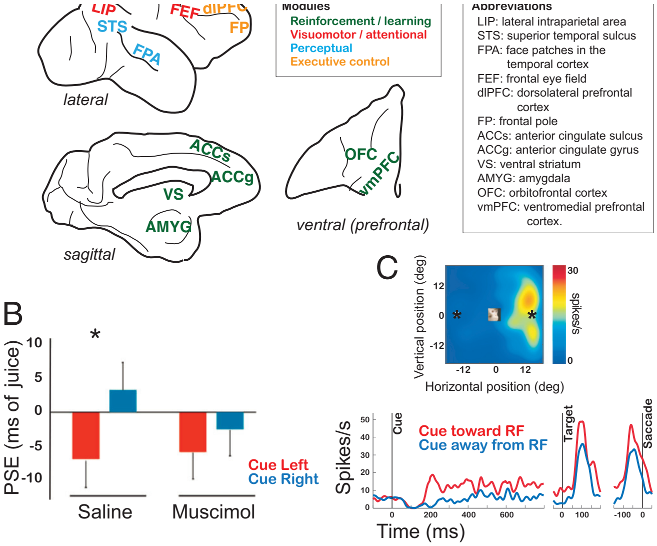


FIGURE 7.1 Example neural circuits co-opted to serve social functions. (*A*) Representative brain regions in rhesus macaques whose preexisting functions encompass reward, attention, perception, and executive control. (*B*) Point of subjective equality (PSE), bias for socially cued target in terms of foregone juice, after saline or muscimol injections in pSTS. Reproduced from Roy et al. (2014) with permission from Oxford University Press. (*C*) LIP neuron showing firing rate enhancement by observed gaze directed toward the receptive field (RF). (*Upper*) RF map. (*Lower*) Neuronal activity as a function of time. Reproduced with permission from Shepherd et al. (2009). [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

Broadly speaking, these circuits can be thought of as organized into input, integrative, and output stages of social processing. The input stage of social processing comprises specialized sensory channels that transduce socially important information, including face-selective (Tsao et al., 2006) and identity-specific cells (Quiroga et al., 2005) in primates, pheromone-sensing systems like the vomeronasal organ in rodents (Keverne, 1999), and specialized regions for species-specific vocalizations in birds (Doupe and Konishi, 1991) and mammals (Ghazanfar and Hauser, 2001; Eliades and Wang, 2008), and language in humans (Damasio and Geschwind, 1984). The output stage of social processing comprises socially specific motor patterns, including highly stereotyped behaviors like allogrooming (Schino et al., 1988), ritualized play (Grant and Mackintosh, 1963), and threat and submission gestures (Deag, 1977). In the integrative stages of social information processing, studies in humans have shown that phenomena such as opprobrium and moral disgust rely in large part on circuits involved in nociception and interoception, particularly those linking the amygdala, periaqueductal gray, insular cortex, and anterior cingulate cortex (ACC) (Moll et al., 2005). Experiments in both humans and other animals have shown that information about socially relevant stimuli such as attractive faces, bodies, and rewards delivered to others activate regions likewise implicated in nonsocial reward (Moll et al., 2006; Izuma et al., 2008; Klein et al., 2008; Mobbs et al., 2009; Smith, 2010; Azzi et al., 2012; Watson and Platt, 2012; Chang et al., 2013). These results are consistent with the idea that social processing is largely built upon and extended from other nonsocial computations by these neural circuits.

The demands of dynamic social interactions are likely to have further shaped the functions of neural circuits involved in social behavior (i.e., selection on a mechanism for a specific function). Humans and other primates clearly elaborate upon the aforementioned basic, relatively stereotyped patterns of social behavior. For example, both human and nonhuman primates can covertly attend to a specific location in space without looking at it directly (Eriksen and Yeh, 1985; Herrington and Assad, 2010), a behavior that seems likely to have evolved to support monitoring of others in social groups (Moore et al., 2003; Hunnius, 2007). Watching another individual shift gaze to an object or location in space typically evokes a gaze shift, as well as a shift in covert attention, in the same direction, in humans and other nonhuman primates (Shepherd, 2010). This gaze-following response depends upon neural circuits involved in decoding where another individual is looking, and circuits that orient attention and plan gaze shifts. Neurons in the primate superior temporal sulcus (STS) are involved in the integration of converging inputs from multiple sensory modalities (Bruce et al., 1981). A posterior portion of STS (pSTS) seems to have evolved the specialized function of perceiving the gaze of other individuals (Hoffman and Haxby, 2000) as well as intention implied from animacy (Gao et al., 2012). Consistent with its role in gaze perception, inactivating pSTS with muscimol abolishes gaze following in rhesus macaques (Roy et al., 2014) (Fig. 7.1*B*). Neurons in the primate lateral intraparietal area (LIP), an area important for spatial attention and the oculomotor planning (Snyder et al., 2000; Bisley and Goldberg, 2010), are activated by the mere observation of a monkey looking toward the region of space covered by the neurons' receptive fields (Shepherd et al., 2009) (Fig. 7.1*C*). Unlike pSTS, however, inactivating LIP has no specific impact on gaze following (Roy and Platt, 2009), consistent with a more generalized role in visuomotor behavior.

As mentioned previously, both human and nonhuman primates are highly motivated by social information. Social information activates key reward areas in humans and nonhuman primates, including the ACC, orbitofrontal cortex (OFC), nucleus accumbens, and caudate nucleus (Moll et al., 2006; Izuma et al., 2008; Mobbs et al., 2009; Smith, 2010; Azzi et al., 2012; Watson and Platt, 2012; Chang et al., 2013; Klein and Platt, 2013). These observations suggest the possibility that social information and information about primary motivators like food are translated into a common framework or currency that drives both learning and decision making (Levy and Glimcher, 2012). When monkeys choose between fluid rewards and information about others (Deaner et al., 2005; Watson and Platt, 2012), neurons in area LIP simultaneously encode the social value and fluid value associated with a target in space, consistent with a common currency of target/action value (Klein et al., 2008). By contrast, neurons in the primate striatum, particularly the medial aspect, appear to be more specialized for signaling social information (Klein and Platt, 2013). In monkeys choosing between fluid rewards and information about others, similar proportions of neurons (~30–35 percent) carried information about fluid outcomes and social image outcomes, but these populations were largely nonoverlapping. Thus, multiple, unique, small ensembles of striatal neurons appear to convey idiosyncratic yet highly specific information about motor responses, contexts, cues, outcomes, or combinations thereof, and this organization extends to social behavior.

The OFC also encodes the value of rewards like food and money (Padoa-Schioppa and Assad, 2006). Like the striatum, OFC also contains neurons specialized for social interaction. We found that even when monkeys' choices were dominated by the value of fluid rewards, the responses of ~50 percent of neurons encoded social information, but only ~20 percent encoded information about fluid rewards (Fig. 7.2*A*) (Watson and Platt, 2012). As in striatum, these populations of neurons were largely distinct, but, unlike striatum, they were anatomically intermingled. Notably, individual OFC neurons also signaled categorical information with respect

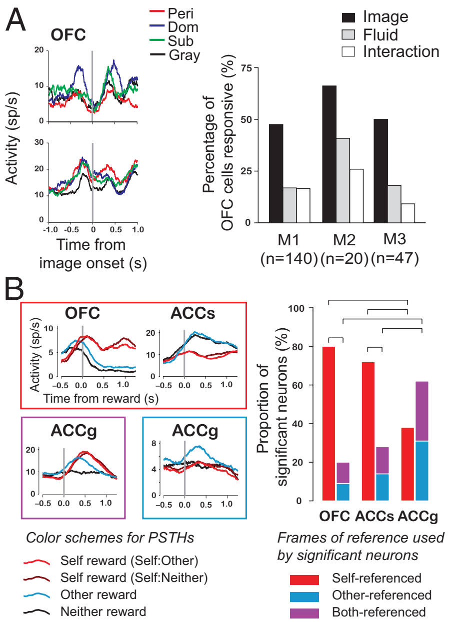


FIGURE 7.2 Reward circuits co-opted to serve social functions. (*A, Left*) Firing rates aligned to social image onset for OFC neurons in a social choice task. (*Right*) Percentage of OFC neurons with activity significantly modulated by social image category (black bar), fluid amount (gray bar), or their interaction (white bar) for three monkeys (M1–M3). Reproduced from Watson and Platt (2012) with permission from Elsevier. (*B, Left*) Firing rates of example neurons from each area, aligned to reward delivery. Box color signifies the category to which these neurons belong in the bar graphs. (*Right*) Proportion of significant neurons from OFC, ACCs, and ACCg using self, other, and shared frames of reference to encode reward outcomes during a reward-allocation task. Horizontal lines indicate significant differences ($P < 0.05$, χ^2 test). Reproduced from Chang et al. (2013) with permission. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

to images of other monkeys (Fig. 7.2*A*). On the basis of its connections to gustatory, olfactory, interoceptive, and limbic systems, OFC has been proposed to function as a feeding circuit (Carmichael and Price, 1995a,b, 1996). Thus, the observation that more neurons responded to social information than to fluid reward supports the idea that ancestral neural adaptations are repurposed to serve social functions. These findings, along with the observed relationship of OFC size to social network size in humans (Lewis et al., 2011) and group size across primates (Dunbar, 1995), suggest that OFC is part of a specialized neural circuit that evolved concomitantly with increasing sophistication of social behavior.

Highly specialized neural mechanisms may be required to support complex social interactions that depend on the behavior and intentions of other individuals. This process may require the brain to encode sensory, motor (Rizzolatti and Fabbri-Destro, 2008), and even reward information in multiple frames of reference (Chang et al., 2011). We recently investigated how neurons in three frontal cortical areas—anterior cingulate gyrus (ACCg), anterior cingulate sulcus (ACCs), and OFC—encoded reward information while monkeys decided to deliver juice to themselves, to a recipient monkey, or to no one (Chang et al., 2013). In this social reward-allocation task, monkeys tend to prefer to reward someone over no one, and this prosocial preference is magnified by familiarity and dominance status (Chang et al., 2011) and significantly modulated by neuropeptide OT (Chang et al., 2012). We found remarkable specializations in the way neurons in these three areas encoded reward information in this social task. OFC neurons predominantly signaled rewards directly received by the donor monkey, revealing its egocentric encoding scheme; ACCs neurons predominantly signaled rewards foregone by the donor monkey, a process critical for monitoring outcomes and learning; and ACCg neurons signaled rewards delivered to the recipient or mirrored rewards delivered to either the donor or the recipient, indicating specialized functions for other-regarding social behaviors (Chang et al., 2013) (Fig. 7.2*B*). These findings resonate with previous work showing that lesions in ACCg, but not ACCs or OFC, lead to deficits in understanding the meaning of social cues in monkeys (Rudebeck et al., 2006) and the activation of medial prefrontal and gyral portions of ACC in humans by observing events occurring to others or thinking about others' states of mind (Singer et al., 2004; Saxe, 2006; Mobbs et al., 2009; Waytz et al., 2012). Together, these observations suggest that ACCg is a key structure supporting shared experience and social reward and may be specialized in human and nonhuman primates to support complex social interactions.

NEUROMODULATORY INFLUENCES ON SOCIAL BEHAVIOR

Differences between species or between individuals within a species may reflect neuromodulatory influences on the development and function of neural circuits mediating social and nonsocial behaviors. Hormones strongly influence brain development (Keverne, 2004; McEwen, 2007) and shape the expression of fundamental behaviors like feeding, fleeing, fighting, and mating (Adkins-Regan, 2005). Neuropeptides (peptides used by neurons to communicate with one another) set the tone for state-specific neuronal signaling by altering chemical transmission within individual neurons as well as across networks of neurons (Adkins-Regan, 2005). For example, OT cells in the paraventricular and supraoptic nuclei synchronize their activity to achieve coordinated neurosecretory bursts required for milk ejection during lactation (Belin and Moos, 1986).

Neuropeptides involved in these primary functions are often recruited to mediate social behavior. The nonapeptides OT and arginine vasopressin (AVP) nicely illustrate this principle. Both OT and AVP are involved in basic reproductive functions in mammals, including parturition and lactation in females and erection and ejaculation in males (Donaldson and Young, 2008). Building on pioneering work demonstrating a role for OT in maternal behavior in rats (Pedersen et al., 1982), a series of elegant studies in voles has revealed that OT and AVP also regulate social behaviors like pair bonding (Cho et al., 1999) and selective aggression (Winslow et al., 1993). More recently, it has been shown that exogenous application of OT can promote emotions like trust (Kosfeld et al., 2005) and encourage generosity (Zak et al., 2007), in a context-dependent and sometimes idiosyncratic fashion (Bartz et al., 2011).

Recently, we demonstrated that OT inhaled via a nebulizer effectively penetrates the central nervous system in rhesus macaques (Chang et al., 2012) (Fig. 7.3*A*), endorsing the potential promise of OT inhalation therapy in individuals with neuropsychiatric disorders marked by social deficits (Meyer-Lindenberg et al., 2011). Increasing OT levels in the brain via inhalation also promotes prosocial decisions in monkeys as well as their attention to a social partner (Fig. 7.3*B* and *C*). Surprisingly, OT also promotes selfish decisions in the same task when there is a perceived cost (Chang et al., 2012) (Fig. 7.3*B*). Furthermore, a recent study in chimpanzees has shown that a rise in OT levels following grooming depends on whether the two animals have strong bonds (Crockford et al., 2013), suggesting that the OT system has been further specialized to process partner-specific affiliative interactions. Together, these observations endorse the idea that neuropeptides like OT, which serves basic sexual and parenting functions, can be co-opted to regulate more complex social behaviors in species that live in large, complex groups, like humans and rhesus macaques.

Ultimately, neuropeptides like OT may impact even complex social behavior via a basic set of mechanisms. The anxiolytic effects (Neumann et al., 2000; Yoshida et al., 2009) of OT may have served as a preadaptation for the prolonged interaction necessary for high-intensity parental care in mammals by promoting approach behavior and enhancing tolerance (Young, 2002; Averbeck, 2010; Kemp and Guastella, 2010). These basal functions could then serve as building blocks for more complex social behaviors. Suppressing vigilance and increasing tolerance to non-offspring may permit extended interactions with others. Ultimately, complex emotions like trust may arise via reduced social apprehension and

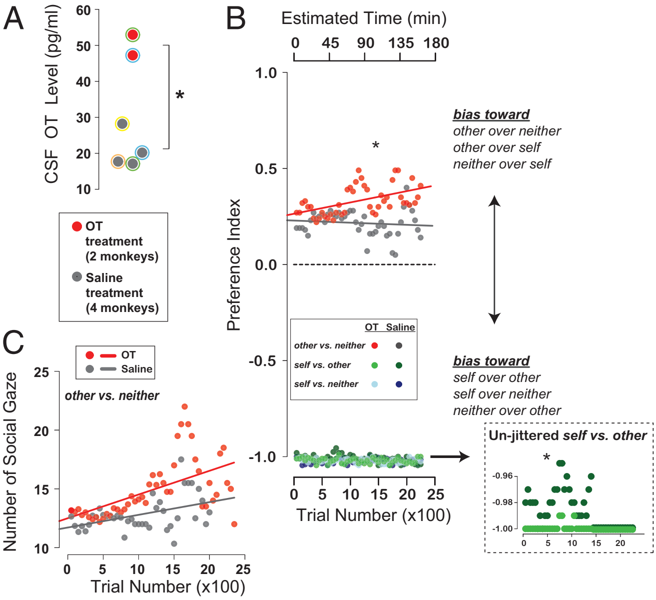


FIGURE 7.3 Social functions of neuropeptide OT. (*A*) OT concentration in cerebrospinal fluid (CSF) after inhaling OT (red) or saline (dark gray; $*P < 0.05$, Welch two-sample t test). Colored outlines on data points indicate animal IDs. (*B*) Choice preference index for OT (red) and saline (gray) for rewards delivered to: other (recipient) vs. neither, self (actor) vs. other, and self vs. neither in the social reward-allocation task. Data points from self vs. other and self vs. neither are jittered for visibility. *Inset* shows unjittered data from self vs. other trials. (*C*) Number of gaze shifts to recipient after reward delivery over the course of each session for other vs. neither choice trials. Reproduced from Chang et al. (2012) with permission. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

enhanced tolerance, under the regulatory influence of neuropeptides like OT (Heinrichs et al., 2009).

Other neuromodulatory systems also contribute to variation in social behavior. For example, the hypothalamic–pituitary–adrenal (HPA) axis has long been associated with social status in primates (Abbott et al., 2003; Tung et al., 2012) and may play a critical role in the production of behavior. Yellow-bellied marmots were shown to be more likely to emit alarm calls during periods in which their HPA axis activity (measured by fecal cortisol concentrations) was high compared with periods during which it was low (Blumstein et al., 2006). The hypothalamic–pituitary–gonadal

(HPG) axis also shapes social behavior in vertebrates. According to the "challenge hypothesis," males' androgen levels are modulated according to context-dependent requirements for aggressive behavior (Wingfield et al., 1990), and this prediction has been substantiated broadly among vertebrates (Hirschenhauser and Oliveira, 2006). In rhesus macaques, modulations of testosterone levels in response to social challenge are also dependent on social rank (Higham et al., 2013). Male social status in African cichlid fish is regulated by gonadotropin-releasing hormone 1, a hormone critical for reproduction, at various levels of neuronal processing (Burmeister et al., 2005; Fernald, 2012). These findings resonate with the idea that preexisting signaling pathways, in this case pathways that regulate stress and mating behaviors, are repurposed to shape the development and function of neural circuits mediating social behavior. Through duplication, repurposing, and dynamic regulation of elements, a relatively limited toolkit of basic hormonal mechanisms can be used to generate a wide array of social behavior.

GENETIC REGULATION OF SOCIAL BEHAVIOR

The influence of genes on social behavior is undeniable because genes shape the neural circuits that produce behavior (Plomin, 2001). The adoption of preexisting biological mechanisms for social purposes, and indeed the evolution of social behavior in general, must, therefore, have roots in genetic change, or, in more Darwinian terms, must be based on modification through descent of inherited material. One hint that social behavior influences change in gene pools over time is a handful of studies linking sociality with fitness. In species such as baboons and rhesus macaques, engaging in social interactions is correlated with reproductive output; the offspring of individuals that spend a greater amount of time grooming and associating with others are more likely to survive to 1 year of age (Silk et al., 2003; Brent et al., 2013). This correlation, in female baboons at least, seems to be driven by the quality of social relationships as individuals with the strongest, most enduring social bonds have higher offspring survival (Silk et al., 2009) and greater longevity (Silk et al., 2010) than others. These findings suggest that there are adaptive benefits to interacting with others and that social behavior is shaped by natural selection.

However, such findings beg confirmation that social tendencies actually have a genetic basis and ask that we explore the roles of environment and experience in shaping the impact of genes on behavior. Quantitative genetic analysis is a tool that allows researchers to determine the amount of variance in a trait that can be attributed to genes, otherwise known as the amount of additive genetic variance or heritability. Using this technique, dimensions of human personality, including sociability, have been shown to be heritable (Johnson et al., 2008). Similar findings show that the behavioral tendencies of a number of vertebrate species, including some nonhuman primates (Weiss et al., 2000; Williamson et al., 2003; Fairbanks et al., 2004), are heritable, thus pointing to a (partly) genetic basis for primate social behavior. Not only are social components of personality heritable, but so too is the extent to which individuals are integrated into their social networks in both humans (Fowler et al., 2009) and rhesus macaques (Brent et al., 2013). This integration includes social network connections mediated by multiagent relationships, such as friend-of-a-friend relationships. Such indirect social connections might be emergent properties of a social network or reflect meaningful aspects of the way individuals navigate large groups. Nevertheless, humans exploit these connections, and our actions (consciously or not) are influenced by them via reputation, one of the primary mechanisms believed to underlie the evolution of cooperation in humans (Nowak, 2006b).

Genetic information also shapes the specific proximate mechanisms that underlie the processing of social information and expression of social behavior. An excellent example is the serotonin pathway. Serotonin is involved in a host of peripheral functions, including cardiac and gastrointestinal functions (Hayes and Greenshaw, 2011). Centrally, serotonin regulates mood, memory, and reward (Sirviö et al., 1994; Hayes and Greenshaw, 2011). The serotonin pathway is also involved in the expression of social behavior. Genetic studies have tied this neuromodulatory pathway to social behavior in humans and other primates, with variants of two serotonergic genes having been examined in particular depth: a variable insertion in the gene encoding tryptophan hydroxylase (*TPH2*), the rate-limiting enzyme in serotonin synthesis, and the 5HTTLPR (serotonin-transporter-linked polymorphic region) polymorphism within the promoter region of the serotonin transporter gene (*SLC6A4*, solute carrier family 6 member 4). Both variants have orthologs in humans and rhesus macaques, have been associated with altered development of several brain regions (Hariri and Holmes, 2006; Jedema et al., 2010), and may influence the intensity and duration of signaling at serotonergic synapses (Hariri and Holmes, 2006; Chen et al., 2006).

Both *TPH2* and *SLC6A4* have been associated with social behavior phenotypes and endophenotypes, many of which are likely to have strong ties to serotonin's central functions, such as the regulation of reward. For example, both genes have been implicated in neuropsychiatric diseases, such as autism and depression (Caspi et al., 2003; Coon et al., 2005), which are partly characterized by disruptions in social attention and interaction, and are accompanied by differences in brain response to social stimuli (Canli et al., 2008). The 5-HTTLPR polymorphism predicts social avoidance in rhesus macaques in response to familiar dominant face images across many contexts. Specifically, rhesus macaques with a copy of the "short" allele spend less time looking at the eyes of other monkeys, show greater pupil dilation—a peripheral index of arousal—when viewing dominant faces, shy away from risk after being primed with dominant faces, and typically avoid dominant faces during a reward-guided decision-making task (Watson et al., 2009) (Fig. 7.4*A*).

Across the genus *Macaca*, the 5-HTTLPR polymorphism has been related to social structure, with more despotic species, such as the rhesus macaque, possessing both long and short numbers of repeats, whereas purportedly less despotic macaque species are monomorphic for the long allele (Wendland et al., 2006). This finding may suggest that this polymor-

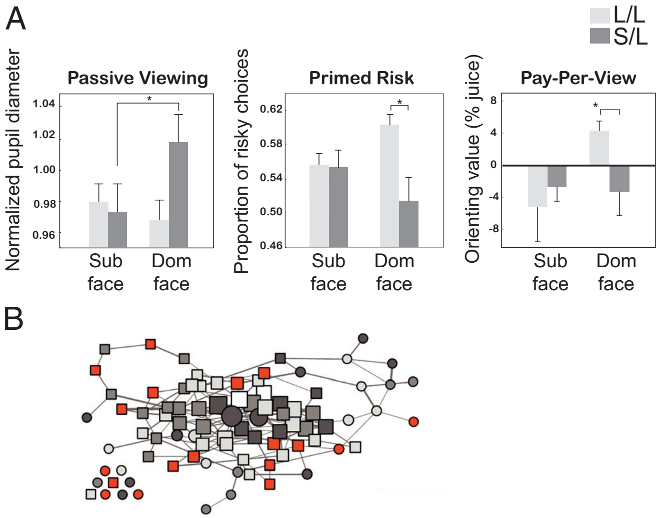


FIGURE 7.4 Genetic variations in the serotonergic system predict social behavior. (*A*) Monkeys with a "short" copy of the 5-HTTLPR polymorphism (S/L) show increased pupil dilation to a dominant face (*Left*), suppressed risk following a dominant face flash (*Center*), and do not forego juice to view a dominant face (*Right*). (*B*) Serotonergic gene profiles predict social network position in free-ranging rhesus macaques. Squares, females; circles, males; lines, presence of a grooming interaction between monkeys. Increasing line thickness indicates frequency of interaction. Node size and position reflect social centrality; largest nodes are the most socially central. Monkeys most central in the network were less likely to carry the minor allele for both the 5-HTTLPR or *TPH2*-length polymorphisms (gray nodes). *A* was reproduced from Watson et al. (2009), and *B* was reproduced from Brent et al. (2013) with permission. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

phism confers resilience to psychosocio challenges (Suomi, 2006) but may also point to the interplay between serotonin, social behavior, reward, and risk aversion. Heightened social vigilance may confer particular advantages in the competitive situations that occur more frequently in despotic societies (Homberg and Lesch, 2011). The 5-HTTLPR polymorphism is associated with differential activation of a number of brain regions associated with affiliative behavior (e.g., ACC, insular cortex) (Canli and Lesch, 2007), leading to speculation that serotonergic gene profiles play a role not only in competition, but also in positive social interactions (Canli and Lesch, 2007).

We recently found preliminary evidence supporting this hypothesis in a study of rhesus macaques living in a free-ranging colony on Cayo Santiago Island, Puerto Rico. An individual monkey's position in the social (grooming) network was predicted by the interaction between the 5-HTTLPR and *TPH2*-length polymorphisms. Either mutation alone had no effect on network position, but monkeys with the rare allele of both genes were less well integrated socially (Brent et al., 2013) (Fig. 7.4*B*). Overall, these results suggest that genetic factors that influence the development and functioning of the serotonin system shape primate social behavior. Serotonin-related genes therefore may be viewed as a valuable example of "candidate genes" that provide tractability to empirical questions about the interaction of genes, neural circuits, and social behavior. These tantalizing findings require further study to understand the specific genetic contributions of this system and other neuromodulatory systems to various aspects of social behavior and cognition.

It is fitting to end a survey of the neuroethology of social behavior on a genetic note, as in doing so we return to the very roots of evolutionary change. Genetic information not only represents a powerful tool to investigate the proximate bases of social behavior, but also allows us to establish direct links between sociality and evolutionary fitness, the ultimate driving force behind natural selection. Genetic information exposes the dynamic contingencies upon which sociality is based, where the interactions between genes that lay the foundations of neural architecture and the social, physical, and biochemical environments in which those genes exist are brought to light, and wherein lie some of the greatest challenges facing future researchers hoping to understand this complex and enigmatic trait.

CONCLUDING REMARKS

Social information is clearly valuable—it is worth foraging, often receives privileged attention over other types of information, and is inherently rewarding. The social environment is rife with information and tinged with uncertainty, and as a result much of our mental machinery is applied to reducing the cognitive load of social interaction. Social behaviors impact evolutionary fitness (Silk et al., 2003; Brent et al., 2013), suggesting they are critical for survival and reproduction. Biological mechanisms that primarily functioned to mediate nonsocial behaviors in the ancestral state have been repurposed in some species, like humans and rhesus macaques, to mediate social behavior. Biological mechanisms are rededicated and further modified for social functions at multiple levels of organization, from neurons and circuits, to hormones and genes. It is important to note, however, that social behavior also feeds back upon these mechanisms to shape their structure and function. Manipulations of social network size in rhesus macaques alter cortical thickness and functional coupling across brain areas that support social functions (Sallet et al., 2011). Epigenetics and gene regulation are also essential to guiding changes in neural development and social behavior (Curley et al., 2011; Fernald, 2012; Tung et al., 2012). Epigenetic changes that are related to reinforcement and learning might be particularly powerful and are important directions for future research.

A neuroethological approach to the study of human and nonhuman primate social behavior is powerful in the extent to which it is encompassing and holistic. By presenting the evolution of social behavior through a lens of nonsocial functions, we have provided evolutionarily parsimonious lines of reasoning and evidence, along with tractable avenues for future research. For many human psychopathologies, the interactions between social and nonsocial deficits are poorly understood. Greater comprehension of the general-purpose mechanisms that generate social action and translate social signals may therefore improve disease diagnosis and treatment.

ACKNOWLEDGMENTS

We thank Monica L. Carlson for general technical assistance. This work was collectively supported by National Institute of Mental Health Grants K99-MH099093 (to S.W.C.C.), R01-MH095894 (to M.L.P. and S.W.C.C.), R01-MH086712 (to M.L.P., K.K.W., and G.K.A.), R01-MH096875 and R01-MH089484 (to M.L.P. and L.J.N.B.), and F31-MH081443 (to J.T.K.); Department of Defense CDMRP Grant W81XWH-11-1-0584 (to M.L.P. and S.W.C.C.); National Eye Institute Grant R01-EY019303 (to J.M.P.); Cure Autism Now (K.K.W.); The Davis Foundation (K.K.W.); a Duke Institute for Brain Sciences Incubator Award (to M.L.P.); and a Duke Center for Interdisciplinary Decision Sciences Fellowship (to L.J.N.B.).

8

Synaptogenesis and Development of Pyramidal Neuron Dendritic Morphology in the Chimpanzee Neocortex Resembles Humans

SERENA BIANCHI,[*‖‖##] CHERYL D. STIMPSON,[*‖‖]
TETYANA DUKA,[*] MICHAEL D. LARSEN,[†]
WILLIAM G. M. JANSSEN,[‡] ZACHARY COLLINS,[*]
AMY L. BAUERNFEIND,[*] STEVEN J. SCHAPIRO,[§]
WALLACE B. BAZE,[§] MARK J. MCARTHUR,[§] WILLIAM
D. HOPKINS,[‖#] DEREK E. WILDMAN,[**] LEONARD
LIPOVICH,[**] CHRISTOPHER W. KUZAWA,[††] BOB JACOBS,[‡‡]
PATRICK R. HOF,[‡§§] AND CHET C. SHERWOOD[*#]

Neocortical development in humans is characterized by an extended period of synaptic proliferation that peaks in mid-childhood, with subsequent pruning through early adulthood, as well as relatively delayed maturation of neuronal arborization in the prefrontal cortex compared with sensorimotor areas. In macaque monkeys, cortical synaptogenesis peaks during early infancy and developmental changes in synapse density and dendritic spines occur synchronously across cortical regions. Thus, relatively prolonged synapse and neuronal maturation in humans might contribute to enhancement of social learning during development and transmission of cultural practices, including language. However,

---

[*] Department of Anthropology, The George Washington University, Washington, DC 20052; [†] Department of Statistics and Biostatistics Center, The George Washington University, Rockville, MD 20852; [‡] Fishberg Department of Neuroscience and Friedman Brain Institute, Icahn School of Medicine at Mount Sinai, New York, NY 10029; [§] Department of Veterinary Sciences, The University of Texas MD Anderson Cancer Center, Bastrop, TX 78602; [‖] Neuroscience Institute and Language Research Center, Georgia State University, Atlanta, GA 30302; [#] Division of Developmental and Cognitive Neuroscience, Yerkes National Primate Research Center, Atlanta, GA 30322; [**] Center for Molecular Medicine and Genetics, Wayne State University, Detroit, MI 48201; [††] Department of Anthropology, Northwestern University, Evanston, IL 60208; [‡‡] Department of Psychology, Colorado College, Colorado Springs, CO 80903; and [§§] New York Consortium in Evolutionary Primatology, New York, NY 10024. [‖‖] Contributed equally to this work. [##] To whom correspondence may be addressed. E-mail: sbianchi@gwmail.gwu.edu or sherwood@gwu.edu.

because macaques, which share a last common ancestor with humans ~25 million years ago, have served as the predominant comparative primate model in neurodevelopmental research, the paucity of data from more closely related great apes leaves unresolved when these evolutionary changes in the timing of cortical development became established in the human lineage. To address this question, we used immunohistochemistry, electron microscopy, and Golgi staining to characterize synaptic density and dendritic morphology of pyramidal neurons in primary somatosensory (area 3b), primary motor (area 4), prestriate visual (area 18), and prefrontal (area 10) cortices of developing chimpanzees (*Pan troglodytes*). We found that synaptogenesis occurs synchronously across cortical areas, with a peak of synapse density during the juvenile period (3–5 years). Moreover, similar to findings in humans, dendrites of prefrontal pyramidal neurons developed later than sensorimotor areas. These results suggest that evolutionary changes to neocortical development promoting greater neuronal plasticity early in postnatal life preceded the divergence of the human and chimpanzee lineages.

Among primates, humans are characterized by an especially prolonged period of postnatal brain development during which cultural traditions and practices, including language, are acquired. Because culture plays a fundamental role in the human adaptive complex (Boyd et al., 2011), the comparative examination of neural development is important to understand the origins of human sociocognitive specializations. Compared with other primates, in humans a relatively large proportion of brain size growth takes place postnatally, allowing for social and environmental factors to powerfully impact the establishment of neural connectivity (Sacher and Staffeldt, 1974; Leigh, 2004; DeSilva and Lesnik, 2008; Barton and Capellini, 2011; McFarlin et al., 2012). Whereas macaque monkeys, the primate species that has been studied most extensively as a comparative model of neurodevelopment, are born with brains that are already ~70 percent of adult mass and neonatal brain mass in great apes ranges from 36 percent to 56 percent of adult size (DeSilva, 2011; McFarlin et al., 2012), in humans only ~25 percent of adult mass is achieved at birth (Robson and Wood, 2008). Concomitantly, the postnatal refinement of cortical microstructure in humans progresses along a more protracted schedule relative to macaques. In macaques, the process of synaptogenesis, whereby new synapses are formed, peaks during infancy at around 3 months of age, and pruning of excess synapses is completed by the end of adolescence (Rakic et al., 1986; Liu et al., 2012). In contrast, in humans, peak synapse density occurs in mid-childhood around 5 years of age (Huttenlocher and Dabholkar, 1997; Liu et al., 2012), with pruning of synapses extending into the third decade of life (Petanjek et al., 2011).

Interspecific differences between macaque and human neural development have also been reported in the timing of maturation among different cortical regions. Whereas synaptogenesis occurs synchronously across the entire cerebral cortex in macaques (Rakic et al., 1986), it appears delayed in the prefrontal region in humans (Huttenlocher and Dabholkar, 1997). In macaques, moreover, densities of spines located on the dendrites of prefrontal pyramidal neurons are higher than other areas from the time of birth and throughout postnatal development (Elston et al., 2009). In humans, however, dendritic arbors of prefrontal cortex pyramidal neurons reach adult-like morphological complexity and spine density later in development than dendritic arbors in sensory and motor cortices (Travis et al., 2005). A temporally staggered, or heterochronous development of the human cerebral cortex, with association regions maturing later than sensorimotor cortices, has also been documented through imaging techniques assessing longitudinal changes in metabolic activity (Chugani et al., 1987), gray matter growth (Gogtay et al., 2004), and cortical thickness (Shaw et al., 2008).

Relatively slow development of neocortical connectivity might contribute to the emergence of uniquely human cognitive abilities. This interpretation is supported by evidence that the cortical regions that develop later in human ontogeny also underwent the greatest expansion during human brain evolution (Hill et al., 2010; Sherwood et al., 2012), suggesting that evolutionary selection to enlarge these regions was accompanied by a prolongation of their development. Among these regions, the prefrontal cortex, which shows particularly extended maturation in humans relative to macaques, has also been reported to exhibit uniquely human neuroanatomical and molecular specializations (Deacon, 1997; Elston et al., 2001; Semendeferi et al., 2001; Cáceres et al., 2007; Fu et al., 2011; Spocter et al., 2012). However, because macaques and humans shared a last common ancestor ~25 million years ago, it is currently unclear whether features that distinguish human cortical development (i.e., extended period of synaptogenesis and maturational delay of prefrontal pyramidal neurons) are unique to our lineage, or if they evolved before the divergence of modern humans and more closely related great ape species, such as chimpanzees.

Relative to macaques, chimpanzees display greater behavioral similarities with humans, including slow postnatal development during which socially learned and “culturally” transmitted behaviors, such as tool use, are acquired (Lonsdorf, 2006; Lonsdorf and Bonnie, 2010). Although chimpanzees provide one of the best animal models for comparison with which to investigate human-unique specializations, studies of cortical development in this species are lacking because of ethical and practical barriers and the rare availability of postmortem brain tissue from infants and juveniles. To date, only a few comparative studies of brain development have included data from chimpanzees. By examining ontogenetic changes through longitudinal MRI, it has been shown that, similar to humans, the maturation of white matter volume in chimpanzees is not complete at early puberty (6 years), but in macaques it reaches adult values during earlier juvenile development (Sakai et al., 2011). Relative to chimpanzees, however, human brain development is marked by more rapid addition of white matter volume during the first year of life (Sakai et al., 2011, 2013). That white matter growth differs between humans and chimpanzees has been further demonstrated by recent histological analyses demonstrating that myelination within the cerebral cortex continues past adolescence in humans, whereas it is completed by sexual maturity in chimpanzees (Miller et al., 2012).

With regard to synaptogenesis, current data from chimpanzees are extremely limited (Liu et al., 2012). Therefore, the present study examined two developmental markers in chimpanzees, synaptogenesis and dendritic growth of pyramidal neurons, in four regions, including prestriate visual (area 18), primary motor (area 4), primary somatosensory (area 3b), and prefrontal (area 10) cortices. Previous studies of neuron morphology in adult primates have shown that these areas form a functional hierarchy whereby association cortices (i.e., area 10) that integrate input from other areas display greater potential for corticocortical connectivity than unimodal, sensory and motor regions (areas 4, 3b, and 18) (Elston et al., 2001; Jacobs et al., 2001; Bianchi et al., 2012). We predicted that, if chimpanzee cortical development is more similar to humans than to macaques, synaptogenesis and maturation of dendritic arbors of pyramidal neurons would be extended into the juvenile period, and show a more prolonged trajectory in the prefrontal cortex relative to other regions.

RESULTS

Synaptogenesis

We used immunohistochemistry against synaptophysin, a protein localized in presynaptic vesicles, to label the density of synapses in chimpanzee neocortical samples (Fig. 8.1). To assess the effect of age on synapse density during postnatal development, a cubic regression model was fitted to synaptophysin-immunoreactive puncta densities from each of the four neocortical regions. Individual cubic polynomial regression curves were significant for most cortical areas (Table 8.1), indicating the presence of developmental changes in synapse density. A steep rise was observed in early postnatal life across all regions followed by a peak at approximately 3 years, which was sustained until the age of 5 years. Synapse densities

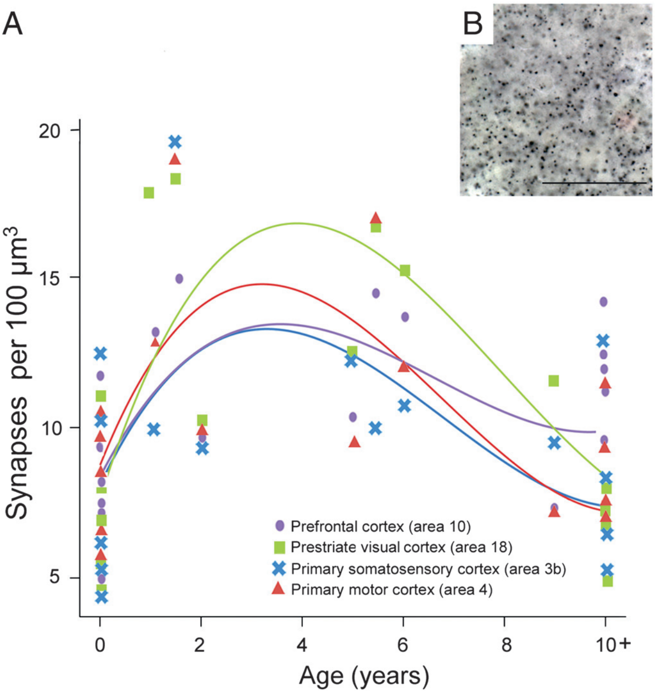


FIGURE 8.1 (*A*) Individual cubic polynomial regression curves fit to counts of synaptophysin-immunoreactive puncta densities for areas 3b, 4, 18, and 10. (*B*) Photomicrograph of synaptophysin-immunoreactive puncta from the prefrontal cortex of an 11-year-old chimpanzee. (Scale bar, 25 µm.) [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

then declined gradually through late juvenile life and approached adult-like levels around puberty (~10 years of age) (Fig. 8.1).

To test for similarities in the cubic polynomial fit among the different cortical regions, we used a generalized least-squares model. This model confirmed a significant cubic polynomial regression based only on age, and showed a better Akaike information criterion value than a model including the cubic polynomial based on both age and a term for cortical region differences. The model with differences by cortical region did not fit significantly better according to a likelihood ratio test; *P* values were 0.55 and 0.48 for either an unstructured or a compound symmetry model, respectively. These results suggest that there is a similar developmental trajectory of synaptogenesis across cortical regions, and were further

TABLE 8.1 Regression Models for Primary Somatosensory (Area 3b), Primary Motor (Area 4), Prestriate Visual (Area 18), and Prefrontal (Area 10) Cortex

Region	Intercept	Age	Age^2	Age^3	r^2	Root MSE	Overall Regression *P* Value
Area 3b	94.3	−11.5	−56.5	48.7	0.26	33.6	0.22
Area 4	100.5	−25.6	66.2*	59.7+	0.42	29.3	0.05
Area 18	99.5	−30.0	−135.4***	53.0	0.62	30.9	0.003
Area 10	106.3	41.1	−41.7	44.3+	0.38	24.6	0.07

NOTE: Linear (Age), quadratic (Age^2), and cubic (Age^3) effects of age are shown. ***$P < 0.001$, *$P < 0.05$, $^+P < 0.10$.

confirmed by using a cubic model including age with random effects by subjects.

Although the patterns of synaptic development were similar across cortical areas, we found regional differences in synapse density to emerge between newborns and adults (Fig. 8.1). A repeated-measures ANOVA of synapse density indicated that there were no significant differences across cortical areas in neonates ($n = 6$, 0- to 1-month-old; $F_{3,\,15} = 0.580$, $P = 0.637$). However, by adulthood, regional differences in synapse density emerged ($n = 5$, 10+ years old; $F_{3,\,12} = 5.974$, $P = 0.010$; after correcting for sphericity that was not assumed: $P = 0.061$), with the prefrontal cortex showing greater synapse density than prestriate visual cortex ($P = 0.022$).

Examination of synaptogenesis by electron microscopy (EM) (Fig. 8.2*A*) in the same regions of four of the chimpanzee brains that had also been processed for synaptophysin immunohistochemistry corroborated these findings. Agreement between counts of synaptophysin-immunoreactive puncta and synapse density by EM was demonstrated by a significant, positive relationship between both measures (Fig. 8.2*B*) ($r = 0.63$, $P = 0.009$, $n = 16$). Results from EM synapse density counts showed a pronounced developmental increase in the prefrontal cortex, which can be attributed mostly to postnatal changes in the density of excitatory asymmetric synapse subtypes.

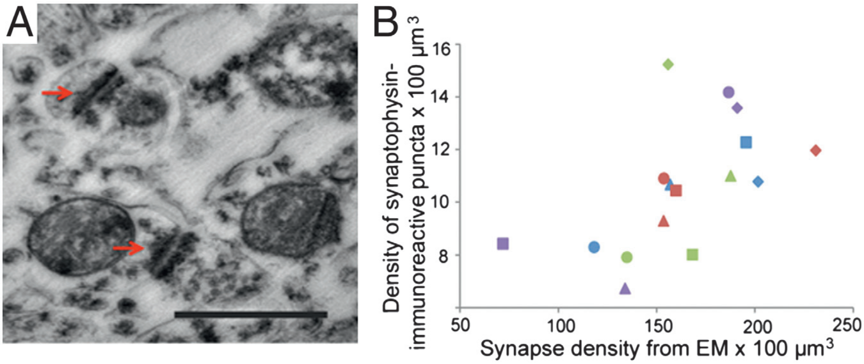


FIGURE 8.2 (*A*) Photomicrograph of synapses as observed under EM. Arrows indicate synaptic junctions. (Scale bar, 0.5 µm.) (*B*) Bivariate plot between synaptophysin-immunoreactive puncta densities and synaptic densities from EM data. Squares represent age 0, triangles age 2, diamonds age 6, and circles age 11. Color scheme for areas as in Fig. 8.1. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

Development of Pyramidal Neuron Dendritic Morphology

We analyzed the morphology of pyramidal neurons from seven infant and juvenile chimpanzee brains that were used in the immunohistochemistry and EM studies of synapse densities described above. Results indicated significant regional differences in the dendritic structure of pyramidal neurons across areas of the infant chimpanzee neocortex ($n = 4$, 0- to 24-month-old), as assessed by six measures of morphological complexity, including cell body size: $F_{12,\,144} = 1.86$, $P = 0.04$; total dendritic length (TDL): $F_{12,\,144} = 3.64$, $P < 0.001$; mean segment length (MSL): $F_{12,\,144} = 5.34$, $P < 0.001$; dendritic segment count (DSC): $F_{12,\,144} = 2.09$, $P = 0.021$; dendritic spine number (DSN): $F_{12,\,144} = 10.65$, $P < 0.001$; and dendritic spine density (DSD): $F_{12,\,144} = 21.373$, $P < 0.001$ (Table 8.2). Pairwise comparisons revealed that dendrites in prefrontal cortex (area 10) were significantly shorter than those in areas 3b ($P = 0.022$) and area 4 ($P = 0.037$). Pyramidal neurons in prefrontal area 10 also had shorter mean segment length than area 3b ($P < 0.001$) and area 4 ($P = 0.002$), as well as fewer spines (area 3b, $P < 0.001$; area 4, $P = 0.005$; area 18, $P = 0.005$) and lower spine density (area 3b, $P < 0.001$; area 4, $P < 0.001$; area 18, $P < 0.001$) than in other regions. On average, prefrontal neurons in infant chimpanzees had dendrites that were 22 percent shorter, had 44 percent fewer spines, and 30 percent lower spine density than the mean for neurons from areas 3b, 4, and 18. No differences were found in the number of dendritic segments ($P = 1.000$) across cortical areas (see, e.g., Fig. 8.4).

Because pyramidal neuron morphology in infant chimpanzees was analyzed with the same methodology used in a previous study of adult chimpanzees (Bianchi et al., 2012), we could compare regional variation in dendritic complexity in these two age groups (Figs. 8.3 and 8.4, and Table 8.2). It should be noted that, similar to reports in human infants (Travis et al., 2005), in the young chimpanzees, the rapid Golgi technique stained neurons predominantly in layer V, whereas neurons in layer III were typically best impregnated in adults. For this reason, only the pattern of relative differences in dendritic complexity across regions between infant and adult chimpanzees can be interpreted. Illustrations of regional variation by age are provided in Fig. 8.4. Pyramidal neurons of the prefrontal cortex continued to be the least elaborate among the cortical areas examined according to most measures of dendritic complexity through infancy and juvenile development (ages 5–6) and only began to increase in the later juvenile period (age 9), ultimately becoming the most complex neurons in adulthood (Bianchi et al., 2012).

TABLE 8.2 Measures of Pyramidal Neuron Morphological Complexity and Position (Depth from Pial Surface) in Somatosensory (Area 3b), Primary Motor (Area 4), Prestriate Visual (Area 18), and Prefrontal (Area 10) Cortex (Mean ± SD)

Morphological Measure	Area 3b	Area 4	Area 18	Area 10
Newborns and infants (*n* = 4)				
Cell soma area (μm^2)	185 ± 88	176 ± 45	152 ± 68	189 ± 46
Cell soma depth (μm)	1,314 ± 733	1,040 ± 548	1,062 ± 468	1,151 ± 603
TDL (μm)	879 ± 361	866 ± 376	805 ± 516	655 ± 293
MSL (μm)	47 ± 15	38 ± 12	37 ± 12	30 ± 8
DSC (μm)	20 ± 8	22 ± 8	21 ± 7	22 ± 8
DSN (μm)	179 ± 105	139 ± 91	138 ± 132	84 ± 68
DSD (μm)	0.20 ± 0.07	0.15 ± 0.05	0.16 ± 0.07	0.12 ± 0.06
Adults (*n* = 7)				
Cell soma area (μm^2)	183 ± 88	185 ± 62	167 ± 75	190 ± 63
Cell soma depth (μm)	796 ± 209	707 ± 247	692 ± 241	733 ± 224
TDL (μm)	894 ± 429	966 ± 377	851 ± 406	1,329 ± 705
MSL (μm)	27 ± 8	47 ± 11	40 ± 11	49 ± 16
DSC (μm)	21 ± 8	21 ± 6	21 ± 7	27 ± 10
DSN (μm)	148 ± 78	166 ± 101	169 ± 84	401 ± 203
DSD (μm)	0.16 ± 0.04	0.17 ± 0.07	0.19 ± 0.04	0.33 ± 0.22

NOTE: TDL, total dendritic length; MSL, mean segment length; DSC, dendritic segment count; DSN, dendritic spine number; DSD, dendritic spine density.

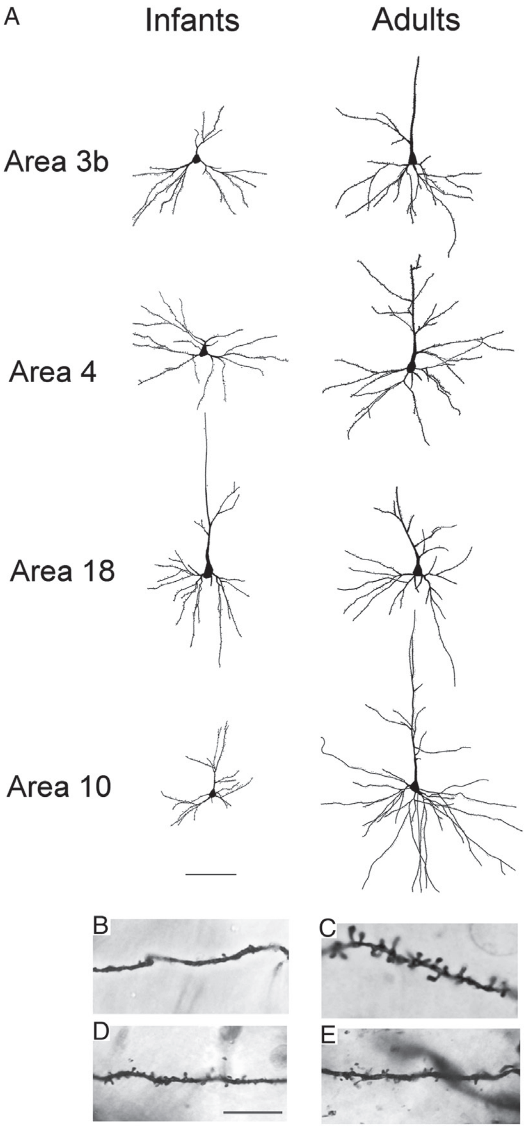


FIGURE 8.3 (*A*) Tracings of Golgi-stained pyramidal neurons in cortical areas 3b, 4, 18, and 10 in infant and adult chimpanzees. (Scale bar, 100 μm.) Below the tracing, closeup photomicrographs depict dendritic shafts of pyramidal neurons in (*B*) area 10 of a 1-year-old chimpanzee, (*C*) area 10 of an adult chimpanzee, (*D*) area 3b of a 1-year-old chimpanzee, and (*E*) area 3b of an adult chimpanzee. (Scale bar, 25 μm.)

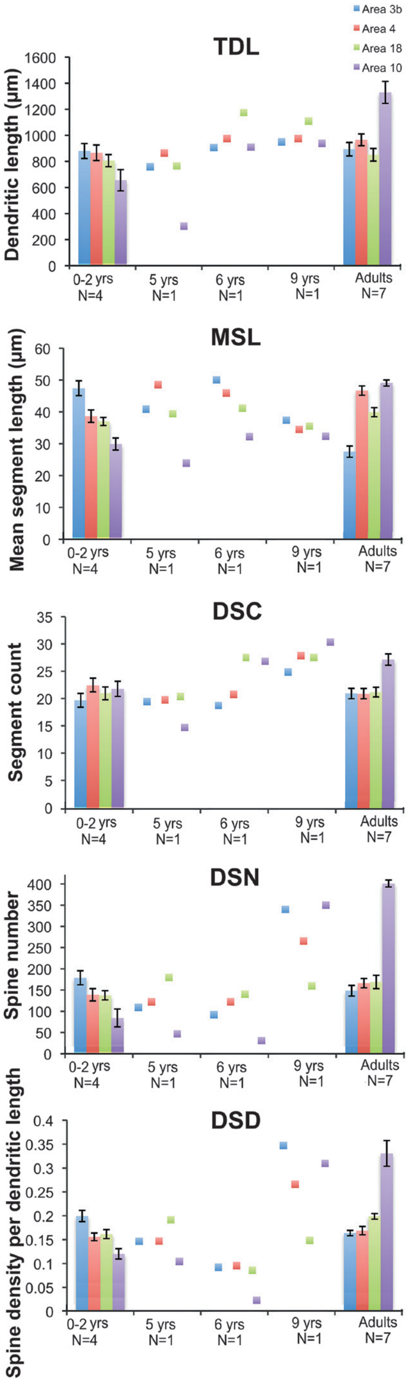


FIGURE 8.4 Regional differences in morphological measures of complexity of basilar dendrites for all cortical regions of interest between adult and infant chimpanzees, including TDL, MSL, DSC, DSN, and DSD. Data from juveniles (5–9 years), for which one individual per age group was available, are illustrated as individual data points. Error bars represent SEM. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

DISCUSSION

Similar to humans, chimpanzees have a relatively long lifespan and prolonged period of dependency during which "cultural traditions" (e.g., tool use, grooming postures) are acquired from conspecifics (Lonsdorf, 2006; Lonsdorf and Bonnie, 2010). As postnatal experience shapes cognitive and social development, changes in the timing of cortical maturation may be important for understanding the evolution of species differences in behavior. Indeed, many genetic differences between humans and other primates affect processes involved in cerebral development (Pollard et al., 2006; Dennis et al., 2012; Derrien et al., 2012). Until recently, however, little was known about the nature of microstructural changes during neural ontogeny in the cerebral cortex of nonhuman primates other than macaques, making it difficult to assess how the developmental trajectory of the human brain might be unique (Miller et al., 2012). Our current analyses demonstrate that similar to humans, synaptic proliferation in chimpanzees is prolonged through the mid-juvenile period, and development of pyramidal neurons in the prefrontal cortex is delayed relative to other cortical areas.

Prolonged Synaptogenesis

Like humans (Huttenlocher and Dabholkar, 1997; Petanjek et al., 2011), chimpanzees exhibit a substantially later peak in synapse density (between 3 and 5 years) than macaques (3 months) (Rakic et al., 1986), and a prolonged phase of synapse pruning, which extends into the late juvenile period (around 10 years). Evidence for an extended period of synaptic refinement in chimpanzees is consistent with previous findings indicating that prefrontal white matter development is prolonged until at least the mid-juvenile period in this species (Sakai et al., 2011). This finding contrasts, however, with a recent report by Liu et al. (2012), suggesting that relatively increased synapse-associated gene expression in the prefrontal cortex continues until 5 years of age in humans only, but in chimpanzees and macaques synaptic gene expression peaks within the first year of life. Because the analysis by Liu et al. (2012) included only three chimpanzee brains between 1 year of age and adulthood, however, differences in the sample sizes represented in these two studies could contribute to the divergent findings, especially because interindividual variation is pronounced. Additionally, little is still known regarding how gene expression regulates anatomical changes in synapse densities during development (Goyal and Raichle, 2013).

Prolonged synaptogenesis in chimpanzees is consistent with behavioral evidence indicating that the juvenile period is critical for social learning of group-specific behaviors acquired from conspecifics. Tool use in chimpanzees displays regional variation to an extent that exceeds other nonhuman animals, including such varied techniques as stone hammering to access nuts, dipping or digging for ants or termites with sticks, and stabbing small vertebrates with spears (Whiten et al., 1999). Young chimpanzees require at least 5 years of postnatal development before they are able to master tool use, and the acquisition of competence in these skills depends on environmental variables, such as the time spent with the mother and her proficiency (Lonsdorf, 2006). Thus, an extended period of synaptogenesis in chimpanzees through juvenile life may be important to enhance neuronal plasticity for the experience-dependent behaviors that emerge following social exposure and learning from conspecifics.

We found no differences in the timing of peak synapse density across different regions of the chimpanzee neocortex. These findings appear to contrast with reports in humans indicating that the prefrontal cortex matures later than other cortical areas, as reflected by metabolic rate, cortical thickness, and peak synapse density (Chugani et al., 1987; Huttenlocher and Dabholkar, 1997; Giedd et al., 1999; Shaw et al., 2008; Liu et al., 2012). It should be noted, however, that prior data suggesting a relative delay of synaptogenesis in the human prefrontal cortex are based on a single study of a modest sample that lacked statistical analysis (Huttenlocher and Dabholkar, 1997). Thus, evidence of heterochronous development within the human neocortex as measured by metabolic activity and cortical thickness may reflect the combined effect of multiple microstructural changes, including neuronal dendritic branching growth (Travis et al., 2005), synapse density, glial cell numbers, and other factors.

Delayed Dendritic Growth in the Prefrontal Cortex

In addition to synaptogenesis, we examined regional changes in the development of dendritic branching of pyramidal neurons. In adult primates, remarkable variation in the morphology and complexity of pyramidal neurons has been reported (Giedd et al., 1999; Elston et al., 2001; Jacobs et al., 2001; Bianchi et al., 2012). Specifically, it has been shown that pyramidal neurons of the prefrontal cortex are characterized by more elaborate dendritic trees than other cortical areas, to support increased connectivity from integrating diverse corticocortical inputs and to orchestrate cognitively complex behaviors (Elston et al., 2001; Jacobs et al., 2001; Semendeferi et al., 2011; Bianchi et al., 2012). Although dendritic arbors are more extensive in the prefrontal cortex relative to other cortical regions in adult humans (Jacobs et al., 2001), chimpanzees (Bianchi et al., 2012), and macaques (Elston et al., 2001), the timing of development of these neuronal specializations appears to be species specific (Travis et al., 2005; Elston et al., 2009).

By demonstrating that dendritic arborization and spine density in the prefrontal cortex of infant chimpanzees is not as extensive as other cortical areas, our data indicate a delay in the maturation of pyramidal neurons in this region, a pattern that shares greater similarities with dendritic development in humans (Travis et al., 2005) than with macaques (Elston et al., 2009). Dendrites regulate the integration of inputs and provide sites for synapses on spines (Yuste and Tank, 1996; Spruston, 2008). As such, they are extremely plastic structures that undergo changes in response to experience, which is especially evident during development (Diamond and Connor, 1982; Jacobs and Scheibel, 1993; Moser et al., 1994; Anderson et al., 1995; Koenderink and Uylings, 1995; Jacobs et al., 1997; van Praag et al., 2000; Grutzendler et al., 2002; Sin et al., 2002; Radley et al., 2006; Kabaso et al., 2009; Yang et al., 2009; Bose et al., 2010; Bloss et al., 2011; Petanjek et al., 2011; Yadav et al., 2012). For this reason, a delay in the formation of dendritic trees in the prefrontal cortex may be important for processing and integrating the extensive load of information that both humans and chimpanzees acquire during development and for maintaining plasticity of executive functions. Although the present study focused on the rostral prefrontal cortex to be consistent with previous research in adult chimpanzees and humans, it is possible that delayed maturation of pyramidal neurons also characterizes association cortices in other frontal, parietal, and temporal regions.

Despite sharing these neurodevelopmental similarities, it is important to note that cognitive ontogeny in chimpanzees differs from humans in several respects. Behavioral studies suggest that the different social and environmental contexts in which humans and chimpanzee develop may have also been important in the evolution of human-specific sociocognitive abilities (Burkart et al., 2009). For example, whereas young chimpanzees do not fully wean until 4–5 years of age and remain closely attached to their mothers during the early years of development, human infants often interact with multiple caregivers and engage in joint attention (Carpenter and Tomasello, 2006). Experiments with enculturated great apes demonstrate the modulating effect of social environment on cognition; being reared in close human contact in an enriched environment is associated with improved performance on sociocognitive tasks and tool use (Buttelmann et al., 2007; Furlong et al., 2008; Lyn et al., 2010; Russell et al., 2011).

Future studies investigating whether the progression of cortical development in chimpanzees also characterizes other great apes (bonobos, gorillas, and orangutans) would help identify more precisely the evolutionary emergence of these traits. In this regard, genome sequences and brain transcriptome datasets from multiple great apes may be helpful in identifying the specific gene sequence or regulatory changes that contribute to phylogenetic variation in the timing of neocortical development.

The study of other large-brained and long-lived species, such as cetaceans and elephants, may also shed light on the evolutionary mechanisms and constraints of developing a plastic, "cultural" brain.

Altogether, our findings indicate that brain development in humans and chimpanzees are both characterized by an extended period of cortical synaptogenesis and a delay in the maturation of dendritic arbors in pyramidal neurons of the prefrontal cortex. These results suggest that several key features of human brain ontogeny for enhanced developmental plasticity emerged before the divergence of the chimpanzee and human lineages. In addition to these shared similarities of early postnatal development, later phases of human neocortical maturation appear to be more evolutionarily modified and distinct from chimpanzees, involving prolonged myelination that continues into early adulthood (Miller et al., 2012). When combined with changes to human social organization, the prolonged developmental plasticity and shift toward delayed development of the prefrontal cortex present in hominin ancestors may have increased learning potential for higher-order sociocognitive functions.

MATERIALS AND METHODS

Specimens

Formalin-fixed brain samples were obtained from the left hemisphere of 17 common chimpanzees (*Pan troglodytes*) (age range: 0–41 years) and one case where only the right hemisphere was available (5.3-year-old). Chimpanzees were housed according to each institution's Animal Care and Use Committee guidelines, and died for reasons unrelated to the present study. Within 14 hours of each individual's death, the brain was removed and immersed in 10 percent (vol/vol) formalin. After a variable period of fixation, brains were then transferred to 0.1 M PBS with 0.1 percent sodium azide solution and stored at 4°C. Blocks of tissue containing prefrontal (area 10), primary motor (area 4), primary somatosensory (area 3b), and the lateral surface of the prestriate cortex (area 18) were dissected and used for immunohistochemistry against synaptophysin protein, rapid Golgi impregnation, and quantification of synapses using electron microscopy. These regions were chosen to be consistent with previous studies in adult chimpanzees and humans. Because chimpanzees reach sexual maturity around 10–13 years (females), and 12–15 years (males), individuals up to the age of 10 years were considered subadults, age 5–9 years as juveniles, and 0–2 years as infants.

Immunohistochemistry for Synaptophysin and Stereologic Quantification

All 18 individuals were used for immunohistochemistry analyses (age range: 0–41 years). Free-floating sections of the regions of interest were stained with rabbit polyclonal IgG_1 antibodies against synaptophysin, which is an acidic, homo-oligomeric integral membrane glycoprotein isolated from presynaptic vesicles (1:100 dilution, A0010; DakoCytomation). Before immunostaining, sections were rinsed thoroughly in PBS and pretreated for antigen retrieval by incubation in 10 mM sodium citrate buffer (pH 3.5) at 37°C in an oven for 30 min. Sections were rinsed and immersed in a solution of 0.75 percent hydrogen peroxide in 75 percent methanol to eliminate endogenous peroxidase activity, then incubated in the primary antiserum diluted in PBS with 2 percent normal goat serum and 0.1 percent Triton X-100 for ~24 hours on a rotator at 4°C. After rinsing in PBS, sections were incubated in biotinylated anti-rabbit IgG (1:200 dilution, BA-2000; Vector Laboratories) and processed with the avidin-biotin-peroxidase method using a Vectastain Elite ABC kit (pk-6100; Vector Laboratories). Sections were rinsed again in PBS, followed by a rinse in sodium acetate buffer. Immunoreactivity was revealed using 3,3′-diaminobenzidine and nickel enhancement according to a modification of methods described previously (Shu et al., 1988; Van der Gucht et al., 2001). Specificity of the reaction was confirmed by processing negative control sections as described, excluding the primary antibody. No immunostaining was observed in the control sections.

Quantification of the numerical density of synaptophysin-immunoreactive puncta was performed using StereoInvestigator software (v9; MBF Bioscience). Beginning at a random starting point, three equidistantly spaced sections were chosen for stereologic analysis. To quantify the density of synaptophysin-immunoreactive puncta, the area comprising the cortex, spanning layers I to VI, of each region of interest was outlined at low magnification and segmented through a set of optical disector frames (3 × 3 μm) with a square scan grid size ranging between 400 × 400 μm and 700 × 700 μm. Disector analysis was performed under Koehler illumination using a 100× oil objective (Zeiss Plan-Apochromat, N.A. 1.4). The thickness of optical disectors was set to 1 μm, with a 1-μm guard zone at the top of the section. All numerical densities of synaptic puncta derived from these optical disector counts were corrected by the number-weighted mean section thickness as described previously (Sherwood et al., 2007). All synapse counting was performed blind to the region of interest and age of the specimen. Data were analyzed by fitting cubic regression models to synapse counts from each of the four regions separately using standardized polynomials in R software (R Development Core Team, 2010). Testing for similarities in cubic polynomial fit to the regions of interest was accomplished by using a generalized least-squares model and a linear mixed model. Results were plotted against age (0–10 years), where individuals older than 11 years were grouped together with adults to emphasize changes during growth (Fig. 8.1).

EM Counts of Synaptic Density

Sections from four individuals (age 0 year, $n = 1$; age 2 years, $n = 1$; age 6 years, $n = 1$; age 11 years, $n = 1$) that contained the regions of interest were postfixed (1 percent OsO_4), and stained with 1 percent uranyl acetate. After embedding in Epon, ultrathin sections were collected on mesh copper grids. Quantification of synapse density was then measured on digital images obtained from a JEOL JEM 1200EX transmission EM at a magnification of 40,000×. Sampling fields were chosen by using the random sampling method and the number of synapses per unit volume was calculated through the following formula: $N_V = N_A/d$, where N_V is the number of synapses per unit volume, N_A is the number of synaptic junctions per unit area of an electron micrograph, and d is the mean length of densities associated with the synaptic junctions (Colonnier and Beaulieu, 1985). One hundred images from each cortical area were analyzed. Measures of synapse length were also obtained from 50 to 130 randomly chosen synapses in each set of micrographs for an individual cortical region. Criteria for identification of synapses included the presence of a postsynaptic density, synaptic vesicles at the presynaptic terminal, and opposing membranes between the pre- and the postsynaptic terminals. A synapse was only marked if the synaptic junction was apparent, and if at least two synaptic vesicles were seen in the presynaptic component of the synapse.

Rapid Golgi Staining

Adjacent blocks (3–5 mm in thickness) from 14 individuals were stained with a modified rapid Golgi technique (Scheibel and Scheibel, 1978) for neuronal morphology quantification. However, only seven (age range 0–9 years) yielded complete neuron staining that met criteria for tracing and quantification (see below). Blocks were sectioned on a Vibratome at 120 µm, mounted, coverslipped, and stored at 4°C. Morphological analyses of dendritic complexity were conducted on 10 neurons per region ($n = 280$). Criteria for neuron selection required that neurons be relatively isolated and unobstructed, located within the center of the section, and as complete as possible (Jacobs et al., 2001). Neurons were sampled from layer V, at a similar depth across regions: area 3b, 1,314 ± 733 µm; area 4, 1,040 ± 548 µm; area 18, 1,062 ± 468 µm; and area 10, 1,151 ± 603 µm.

Neurons meeting criteria were traced using a Zeiss Axioplan 2 photomicroscope equipped with a Ludl XY motorized stage (Ludl Electronics), Heidenhain *z*-axis encoder, and an Optronics MicroFire color videocamera coupled to a Dell PC workstation running Neurolucida software (MBF Bioscience). Tracings were performed under Koehler illumination using a 40× dry objective (Zeiss Plan-Apochromat, N.A. 0.75), and involved following dendrites along their entire length across the *z*-plane and manually marking all visible spines. Once tracing was complete, neuronal morphology was quantified in NeuroExplorer (MBF Bioscience), according to the following measurements of dendritic morphology, derived from Jacobs et al. (2001): (*i*) TDL, the sum of the individual lengths of all dendritic segments; (*ii*) DSC, the number of all dendritic segments; (*iii*) MSL, which is essentially TDL/DSC; (*iv*) DSN, the number of all spines marked on the dendritic arbor; and (*v*) DSD, the number of spines per micrometer of dendritic length. The cell body cross-sectional area was also recorded. For each variable of dendritic morphology, measurements were taken for both basilar and apical dendrites. However, because apical dendrites were often incomplete because of sectioning, quantitative comparisons of dendritic length and spine number across cortical regions were limited to basilar dendrites. All tracings were performed blind to the regions of interest by C.D.S. and S.B., who were normed with another rater (A.L.B.), and checked by C.C.S. Intra- and interrater reliability of measures were determined to be in good concordance.

Because of the small size in the juvenile and subadult category, statistical analyses were conducted only on the group including newborns and infants; data from the juveniles and subadults are illustrated as individual points (Fig. 8.4). To analyze regional differences in dendritic complexity, we used a nested ANOVA design (IBM SPSS 18.0), in which each neuron was nested within region (areas 3b, 4, 10, 18), which was nested within individual brains. Data for each variable of interest (soma area, TDL, DSC, MSL, DSN, DSD) were analyzed separately. Pairwise contrasts were then performed using a Bonferroni correction for multiple comparisons. Data for comparisons with adult chimpanzees, as shown in Fig. 8.4, were taken from a previous study that used the same methodological procedure (Bianchi et al., 2012), and included seven individuals, age 35+ years.

ACKNOWLEDGMENTS

We thank Dr. Anastas Popratiloff, director of the Center for Microscopy and Image Analysis at The George Washington University, for his advice and support in the data collection. This work was supported by National Science Foundation Grants BCS-0515484, BCS-0549117, BCS-0824531, and DGE-0801634; National Institutes of Health Grant NS-42867; and James S. McDonnell Foundation Grants 22002078 and 220020293.

Part III

THE HUMAN DIFFERENCE: FROM ETHICS TO AESTHETICS

As stated in earlier chapters, our species and other primates share different memory systems. However, James McGaugh argues in Chapter 9 that, although forgetting is the common fate of most of our experiences, mechanisms exist that somehow permit us to create lasting memories of our more important experiences. The author explores such mechanisms. Several neurobiological systems link this selective capacity to emotional arousal, giving clues about how humans and other animals reach memory-enhancement episodes by means of an activation of brain regions such as the amygdala. The fact that some subjects are able to keep highly superior autobiographical memory raises the question of how this capacity might be associated with genetic and brain particularities.

Self-awareness and the capacity to evaluate others' acts and their consequences are among the main components of altruistic behavior. Three chapters in these proceedings deal with different aspects of altruism and its more extreme related behaviors. In Chapter 10, Barbara Oakley examines the mechanistic bases of biased altruism, in which attempts to promote the welfare of others result in unanticipated harm. She defends the need for quantitative models of altruistic behavior along a spectrum ranging from strong benefit to extreme harm. These models might help to scientifically distinguish between beneficial and harmful egoistic behavior, as well as clarify the relationships between egoism, altruism, and pathological altruism.

Next, in Chapter 11, Sarah Brosnan begins her contribution with a question: What leads us to care about justice? She proposes a comparative approach to clarify why justice, which is a highly important component of our values, is so difficult to achieve. By means of experiments on primates' answers to perceived inequities in social interactions, Brosnan concludes that humans are not alone in responding negatively to differential treatment. Although nonhuman primates do not show a sense of justice in the same sense that humans do, understanding their responses may help to anticipate, prevent, and perhaps solve problems arising from the human perception of inequity.

Beyond direct perception of equality/inequality in social relationships, altruism and, more generally, human cooperation can be related to indirect reciprocity based on reputation. Since social reputation is directly observed, but widely spread by communication, indirect reciprocity can reach highly sophisticated patterns. In Chapter 12, Erez Yoeli et al. offer experimental results on large-scale (a total of 2,413 participants) cooperation between small groups under laboratory conditions. Since subjects were California residents of 15 homeowners' associations that voluntarily participated in an energy-saving program, the experiment matched real-world conditions of cooperation. Yoeli and coworkers' results provide evidence that observable participation in favor of public goods promotes cooperative behavior. The authors hold that reputational concerns were the driving force to reach such a high level of indirect cooperation, suggesting easy and practical ways to improve future public policy initiatives.

Next, Robert Zatorre and Valorie Salimpoor review empirical evidence for the neural substrates of several aspects of musical perception. First, the authors identify the auditory cortical circuits that are responsible for encoding and storage of tonal patterns. Then, they study the functional role of brain areas, such as the nucleus accumbens, codifying the reward value of music. The authors suggest that the cortical system, highly evolved, decodes tonal or rhythmic relationships present in music, thereby generating expectations about upcoming events based on the subjects' former events. In turn, the striatal dopaminergic system would add the emotional arousal associated with these predictions.

Experimental approaches to visual issues constitute the next contribution to this colloquium. In Chapter 14, Leanne Chukoskie and coworkers study how subjects search a novel scene for a target whose location was stochastically drawn on each trial from a fixed prior distribution. Participants rapidly learn where to search, looking near previously rewarded locations and avoiding previously unrewarded sites. A reinforcement-learning model, similar to that used previously to examine both foraging animal behavior and neuronal firing of dopaminergic cells, can describe the resulting search performance. In addition, this search performance approaches the theoretical optimum on this task. Thus, the authors offer a framework for considering how prior experience guides saccade choice during natural vision.

A complementary phenomenon provides the focus for Oshin Vartanian and coworkers, who in Chapter 15 provide clues on how variation in contour impacts aesthetic judgments and approach decisions about the places in which we live and work, thereby influencing how we feel and act. Subjects are more likely to judge spaces as beautiful if they are curvilinear than rectilinear. Curvilinear spaces activate the medial orbitofrontal cortex, a region strongly implicated in reward and that is particularly activated among architects compared to nonarchitects when assessing the aesthetic value of buildings. In contrast, contour has no impact on approach decisions. Contemplating curvilinear spaces activates the precentral gyrus—a region engaged in motor imagery and the planning of voluntary motor movement. Although curvilinear spaces did not result in a greater likelihood of deciding to enter such areas, they might facilitate the production of visual and motor imagery consistent with movement planning in that context. The authors conclude that their research sheds light on a fundamental question—why is it that we have come to prefer the places that we do?

Finally, by analyzing the dynamics of brain functional connectivity, Camilo Cela-Conde and coworkers in Chapter 16 offer the first identification of brain networks engaged within distinct time frames during the appreciation of beauty. A fast aesthetic perception of the beautiful/not-beautiful condition of each visual stimulus appears within 250–750 ms, whereas further aesthetic appreciation processes are subsequently performed in the 1,000- to 1,500-ms range. The delayed processes activate a brain network matching the default mode network, present during subjects' resting state.

9

Making Lasting Memories: Remembering the Significant

JAMES L. MCGAUGH

Although forgetting is the common fate of most of our experiences, much evidence indicates that emotional arousal enhances the storage of memories, thus serving to create, selectively, lasting memories of our more important experiences. The neurobiological systems mediating emotional arousal and memory are very closely linked. The adrenal stress hormones epinephrine and corticosterone released by emotional arousal regulate the consolidation of long-term memory. The amygdala plays a critical role in mediating these stress hormone influences. The release of norepinephrine in the amygdala and the activation of noradrenergic receptors are essential for stress hormone–induced memory enhancement. The findings of both animal and human studies provide compelling evidence that stress-induced activation of the amygdala and its interactions with other brain regions involved in processing memory play a critical role in ensuring that emotionally significant experiences are well remembered. Recent research has determined that some human subjects have highly superior autobiographic memory of their daily experiences and that there are structural differences in the brains of these subjects compared with the brains of subjects who do not have such memory. Understanding of neurobiological bases of such exceptional memory may provide additional insights into the processes underlying the selectivity of memory.

Department of Neurobiology and Behavior, Center for the Neurobiology of Learning and Memory, University of California, Irvine, CA 92697-3800. E-mail: jlmcgaug@uci.edu.

> Our brains, remarkable as they are, could not begin to contain and give equal weight to our every moment of life.
>
> Glore (1987)

The ability to learn and remember is essential for our survival. Remembering what has happened enables us to predict what is likely to happen and alter our behavior accordingly. As noted by Bernecker (2010, p. 1), "[r]emembering is a fundamental cognitive process, subserving virtually all other important cognitive functions . . . . Since without memory one couldn't think, some philosophers go as far as to claim that memory is the mark of being human." This latter claim is, of course, off of the mark, because most, if not all, animals display memory of their experiences. However, the many moments of their lives and our lives are not given equal weight in memory: we do not remember equally well all of our experiences. As James (1890, p. 643) commented, "[o]f some [experiences] no memory survives the instance of their passage. . . . Others . . . may be recalled as long as life endures. How can we explain these differences?" There are many possible explanations. Experiences that we attend to are, of course, more likely to be remembered. Some new experiences become lasting, because they fit well with and can be readily processed and integrated with existing memories (Craik and Lockhart, 1972). Additionally, beginning with the pioneering studies of Ebbinghaus (1885), we learned that memories are strengthened by repetition or retrieval (Roediger and Butler, 2011).

EMOTIONAL AROUSAL AND LASTING MEMORY

There is also extensive evidence that experiences that are emotionally arousing are well remembered (Brown and Kulik, 1977; Conway, 1995; McGaugh, 2003; Reisberg and Hertel, 2003). Experiences of unpleasant occasions, such as an automobile accident, a mugging, or learning about the death of a loved one, are remembered better than those experiences of a routine day (Stratton, 1919; Pillemer, 1984; Bohannon, 1988; Christianson, 1992; Conway et al., 1994; Conway, 1995; Neisser et al., 1996; Schmolck et al., 2000; Sharot et al., 2007). Memories of pleasant occasions, such as birthdays, holidays, and weddings, are also well retained. The strength of memories of events varies with the emotional significance of the events. Individuals who were close to San Francisco at the time of the 1989 San Francisco earthquake had better memories of the earthquake months later compared with individuals in Atlanta, Georgia (Neisser et al., 1996). Three years after the terrorist attack on September 11, 2001, individuals who were in downtown Manhattan at the time of the attack had more detailed memories of the attack compared with individuals who were in midtown Manhattan, several miles from the attack (Sharot et al., 2007).

MODULATION OF MEMORY CONSOLIDATION

These findings clearly support Bacon's (2000) assertion that "[m]emory is assisted by anything that makes an impression on a powerful passion, inspiring fear, for example or wonder, shame or joy." However, such evidence provides only the beginnings of an answer to William James' wondering about why some memories are lasting. A more comprehensive answer requires an understanding of the effects of emotional arousal that regulate the strength of memories.

Lasting memories are not created at the time of an experience. There is considerable evidence supporting the hypothesis of Mueller and Pilzecker (1900) that experiences initiate neural processes that perseverate and induce, over time, the consolidation of memory. Subsequently, Hebb (1949) proposed a dual-trace hypothesis of memory formation. According to this hypothesis, memories are initially based on the reverberation of neural circuits, and long-term memory results from synaptic changes induced by the neural reverberation. Thus, for both the consolidation hypothesis and the dual-trace hypothesis, lasting memory is formed after an experience.

The time-dependent process of memory consolidation thus provides an opportunity for conditions occurring after learning (i.e., during the consolidation of memory) to regulate the strength of memory. Studies of the effects of electroconvulsive shock (Duncan, 1949) were the first studies to provide experimental evidence supporting the consolidation hypothesis. Electroconvulsive shock treatments impaired memory when administered to rats immediately after training. These findings were replicated and extended in extensive research with rats and mice in experiments using many kinds of treatments that disrupt brain functioning (McGaugh and Herz, 1972; McGaugh, 2000). The common finding was that the treatments affected memory when administered shortly after training and were less effective when administered several hours or longer after training. These early findings of retrograde amnesia induced by disrupting brain functioning after learning suggested the possibility that mild stimulation of the brain shortly after an experience might enhance memory (McGaugh, 1966). The finding of many studies that memory is enhanced by administration of low doses of CNS stimulants to rats and mice shortly after training but not after a delay provided strong support for this implication (Breen and McGaugh, 1961; Westbrook and McGaugh, 1964; McGaugh and Petrinovich, 1965; McGaugh, 1966, 1968, 1973; Krivanek and McGaugh, 1968; McGaugh and Roozendaal, 2009). Also, importantly, comparable findings were obtained in studies using human subjects (Soetens et al., 1993).

ENDOGENOUS MODULATION OF MEMORY CONSOLIDATION

The findings of experimentally induced retrograde amnesia and memory enhancement also suggest a hypothesis that might provide an answer to the question of why, as Francis Bacon asserted, memory is assisted by passion. Emotional arousal induces the release of the adrenal stress hormones epinephrine and cortisol (corticosterone in rats). Thus, the levels of the hormones activated by arousing training experiences are increased while memories are undergoing consolidation. Gerard (1961, p. 30) noted that "as epinephrine is released in vivid emotional experiences, such an intense adventure should be highly memorable." Much subsequent evidence supports this suggestion. As found with stimulant drugs, posttraining administration of epinephrine as well as corticosterone enhances memory for many kinds of training experiences (Micheau et al., 1984; Sandi and Rose, 1994; Zorawski and Killcross, 2002; Berlau and McGaugh, 2006; Roozendaal et al., 2006a). Furthermore, adrenoreceptor antagonists (e.g., propranolol) and glucococorticoid receptor antagonists block the effects of emotional arousal and adrenal stress hormones on memory consolidation (Gold and Van Buskirk, 1975; Gold and McGaugh, 1977; McGaugh, 1983; McGaugh and Gold, 1989; Roozendaal, 2000; Krugers et al., 2011; Roozendaal and McGaugh, 2011; Parfitt et al., 2012). Although most experiments investigating stress hormone influences have used memory of stressful training, such as stress induced by mild footshocks, posttraining administration of stress hormones enhances memory for many kinds of less stressful experiences, including memory for rewards (Dornelles et al., 2007).

AMYGDALA ACTIVATION AND MEMORY MODULATION

Thus, the experimental evidence provides strong support for the hypothesis that adrenal stress hormones enhance the consolidation of memory of experiences that induce their release. Additionally, the findings provide an initial step to providing an answer to William James' question of why some memories endure. A next essential step requires understanding of how adrenal stress hormones act to influence brain processes involved in memory consolidation. When released into the blood, epinephrine passes poorly, if at all, into the brain (Arai et al., 1981). Considerable evidence indicates that epinephrine influences on brain function are mediated by activating adrenoreceptors located on the ascending vagus nerve that projects to brainstem nuclei (to the locus coeruleus through the nucleus of the solitary tract) responsible for noradrenergic activation of other brain regions (Miyashita and Williams, 2006; McIntyre et al., 2012). Moreover, direct electrical stimulation of the ascending vagus after learning enhances memory in human subjects as well as rats (Clark et al., 1998, 1999; Clayton and Williams, 2000; Hassert et al., 2004). Cortisol passes freely into the brain, where it can activate glucocorticoid receptors throughout the brain.

Several findings suggested the amygdala, a collection of nuclei located in the medial temporal lobe, as a possible critical brain region involved in mediating stress hormone influences on memory consolidation. Findings of several early (Gold et al., 1975; McGaugh and Gold, 1976) as well as more recent studies (Bergado et al., 2006; Bass et al., 2012) indicated that, in rats, memory is enhanced by brief low-intensity posttraining electrical stimulation of the amygdala. Other early findings indicated that, in rats, β-adrenoreceptor antagonists infused into the amygdala after training impaired memory consolidation and that concurrent infusions of norepinephrine blocked the impairment (Gallagher et al., 1981; Kesner and Ellis, 1983). Other studies reported that systemically administered epinephrine induces the release of norepinephrine in the brain (Gold and van Buskirk, 1978) and that epinephrine enhancement of memory consolidation is blocked by intra-amygdala infusions of propranolol (Liang et al., 1986). There is now substantial evidence that norepinephrine or other noradrenergic agonists administered into the amygdala or selectively into the basolateral region of the amygdala (BLA) after training enhance memory for many kinds of training experiences (Hatfield and McGaugh, 1999; LaLumiere et al., 2003; McGaugh, 2004; Huff et al., 2005; Roozendaal et al., 2008). Also, posttraining intra-amygdala infusions of β-adrenoreceptor antagonists impair memory and block the memory-enhancing effects of both corticosterone and epinephrine administered systemically (Liang et al., 1986; Quirarte et al., 1997; Roozendaal et al., 2002, 2006b). Such findings strongly suggest that glucocorticoid-induced enhancement of memory consolidation requires noradrenergic activation of the amygdala. Noradrenergic activation induced by emotional arousal seems to enable glucocorticoid modulation of memory consolidation (Okuda et al., 2004).

The extensive evidence that memory is influenced by noradrenergic agonists and antagonists infused into the amygdala after training suggests that emotionally arousing training experiences should increase norepinephrine release within the amygdala. The findings of experiments using microdialysis and HPLC to assess norepinephrine release provide strong support for this implication. Footshock training increases the release of norepinephrine within the amygdala (Galvez et al., 1996; Quirarte et al., 1998), and rats that have greater increases in release subsequently display better retention (McIntyre et al., 2002). Additionally, several drugs that enhance memory consolidation, including GABAergic and opioid peptidergic antagonists, increase the release of norepinephrine in the amygdala (Quirarte et al., 1998; Hatfield et al., 1999).

AMYGDALA INFLUENCES ON OTHER BRAIN SYSTEMS

Decades before initiation of the research discussed above investigating the involvement of the amygdala in memory consolidation, Gerard (1961, p. 30) noted that, "[because] the amygdala [acts] directly on cortical neurons to alter . . . their responsiveness to the discrete impulses that reach the cortex . . . these deep nuclei could easily modify the ease and completeness of experience fixation." The amygdala is richly interconnected with other brain regions, including the cortex, known to be involved in processing different aspects of memory. Additionally, there is now considerable evidence supporting the prescient suggestion by Gerard (1961) that the amygdala influences memory consolidation through projections to other brain regions (McGaugh, 2000, 2002, 2004; Paré et al., 2002; Pelletier et al., 2005; Popescu et al., 2009; Stefanik et al., 2013). However, the interactions are not restricted to the cortex.

The findings of many studies using rats indicate that the hippocampus is involved in spatial learning (O'Keefe and Dostrovsky, 1971; Olton et al., 1979; Eichenbaum et al., 1990), whereas the caudate nucleus is involved in the learning of specific cues associated with responses (Packard and White, 1991; Packard and McGaugh, 1996; Packard and Goodman, 2012). Packard et al. (1994) found that posttraining activation of the amygdala (using microinfusions of D-amphetamine) enhanced memory for both place learning and cued response learning in a water maze. In contrast, hippocampal infusions selectively enhanced spatial memory, and caudate infusions selectively enhanced cued response memory. Posttraining, intra-BLA drug infusions enhance rats' memory of a context as well as the memory of a brief footshock subsequently received in that context (Malin and McGaugh, 2006). Additionally and importantly, McIntyre et al. (2005) found that, in rats, noradrenergic activation of the BLA that enhanced memory consolidation increased the expression of activity-regulated cytoskeletal (Arc) protein in the hippocampus. Furthermore, posttraining inactivation of the BLA impairs memory consolidation and decreases hippocampal Arc protein expression. These findings are of interest in view of evidence indicating that Arc is involved in regulating synaptic plasticity and memory consolidation (Guzowski et al., 2000). Additionally, electrical stimulation of the BLA enhances the development of hippocampal plasticity as assessed by induction of long-term potentiation (Ikegaya et al., 1995; Akirav and Richter-Levin, 1999).

As noted by Gerard (1961), the amygdala also projects to the cortex. Electrical stimulation of the BLA activates the cortex, which is indicated by EEG desynchronization (Dringenberg and Vanderwolf, 1996; Dringenberg et al., 2001), and enhances cortical long-term potentiation (Dringenberg et al., 2004). Additionally, electrical stimulation of the amygdala enhances the development of plasticity in the auditory cortex (Chavez et al., 2012). It is well established that pairing of a tone stimulus with a reinforcing stimulus (e.g., footshock) alters the representation of the tone in the auditory cortex (Weinberger, 2004, 2007). The frequency-receptive fields shift to the frequency of the tone stimulus, inducing an increased representation of significant sounds. Pairing of a tone with BLA stimulation, which is neither rewarding nor punishing, induces a shift of the auditory tuning curve to that tone of the conditioning tone frequency. Moreover, the tuning curve continues to shift to the conditioning tone frequency over a period of 45 min after the training (Chavez et al., 2009). Importantly, the learning-induced shifts in responsiveness of the auditory cortex are maintained for several weeks (Chavez et al., 2013).

EMOTIONAL AROUSAL, ADRENAL STRESS HORMONES, AND HUMAN MEMORY

The findings of studies of the influence of arousal on human memory are consistent with the findings of studies using animal subjects: emotional arousal during or after learning enhances long-term memory, and the modulation involves epinephrine and cortisol. However, experiences do not have to be intensely emotional to influence memory strength. Many studies have reported that subjects presented with pictures or words judged to be only mildly emotional, whether positive or negative in effect, subsequently have stronger memories of those stimuli than pictures and words judged not to be emotional (Anderson et al., 2006; Liu et al., 2008; Henckens et al., 2009; Nielson and Lorber, 2009; Kensinger et al., 2011). Viewing of emotionally arousing pictures also enhances memory of a cognitive skill (Steidl et al., 2011).

In support of the view that emotional arousal modulates memory consolidation, several studies have reported that inducing arousal after subjects learn material enhances memory tested after a retention interval of 1 day or longer (Nielson et al., 1996; Anderson et al., 2006; Liu et al., 2008; Nielson and Lorber, 2009; Kensinger et al., 2011). In one study, subjects learned a word list and then watched an emotionally arousing pleasant (comedy) or unpleasant (surgery) brief video either immediately or after delays of up to 45 min. When viewed within 30 min, both the pleasant and unpleasant postlearning videos enhanced memory as assessed 1 week later (Nielson and Powless, 2007). Furthermore, the effect of postlearning arousal is not restricted to laboratory experiments. College students who watched an arousing video clip after a lecture compared with students who did not watch the clip performed significantly better on a midterm examination 2 weeks later (Nielson and Arentsen, 2012).

There is also extensive evidence that arousal influences on memory consolidation involve both epinephrine and cortisol. Administration of the adrenoreceptor antagonist propranolol before subjects' viewing of a series of pictures accompanied by an emotionally arousing story blocked the enhancing effects of emotional arousal on memory assessed at 1 week later (Cahill et al., 1994). Administration of epinephrine or cold pressor stress (induced by holding an arm in ice water), which induces the release of epinephrine and cortisol, immediately after presentation of emotionally arousing pictures enhances subjects' memory of the pictures (Cahill and Alkire, 2003; Cahill et al., 2003). Furthermore, Hupbach and Fieman (2012) reported that arousal induced by exposure to cold pressor stress after a memory retrieval test increased salivary cortisol and enhanced memory of the test material when tested several days later.

Other studies have reported evidence that adrenergic activation selectively influences memory for emotionally arousing stimulation (Maheu et al., 2004). Cold pressor stress induced after listening to neutral and emotional words selectively enhanced memory of the emotional words on a test the next day. Furthermore, levels of cortisol and salivary α-amylase, a biomarker for noradrenergic activity, assessed immediately after the cold pressor stress correlated highly with subsequent memory performance (Smeets et al., 2008). Additionally, Segal and Cahill (2009) found that levels of salivary α-amylase assessed shortly after subjects viewed a series of emotional and neutral pictures correlated significantly and selectively with memory of the emotional pictures on a 1-week retention test (Segal and Cahill, 2009). Salivary α-amylase measured after exposure to emotionally arousing pictures also correlated highly with subsequent memory assessed by successful discrimination of pictures seen from other similar pictures (i.e., pattern separation) (Segal et al., 2012). Such discrimination is known to involve the hippocampus (Yassa and Stark, 2011).

Findings of human studies provide additional evidence that emotional arousal influences on memory involve activation of the amygdala. In an initial study using PET imaging, Cahill et al. (1996) found that amygdala activation induced by watching emotionally arousing films correlated highly with memory of the films as tested 3 weeks later. Subsequent studies using PET imaging reported similar findings (Hamann et al., 1999, 2002). Furthermore, studies using functional MRI imaging found that the relationship between amygdala activity during learning and subsequent memory varied directly with the intensity of emotional arousal and that the valence—positive or negative—is not critical (Canli et al., 2000, 2002; Kensinger and Corkin, 2004).

Imaging studies have also provided evidence, consistent with evidence obtained with animal studies, that emotional arousal influences on consolidation of long-term memory involve interactions of the amygdala with other brain regions, including the hippocampus, during learning (Kilpatrick and Cahill, 2003; Dolcos et al., 2004; Kensinger et al., 2006; LaBar and Cabeza, 2006; Ritchey et al., 2008, 2011; Schwarze et al., 2012). Findings of human brain imaging studies using functional MRI provide additional evidence that emotional arousal influences on memory involve noradrenergic activation of the amygdala. Propranolol blocks amygdala activation induced by emotionally arousing stimuli as well as subsequent memory of the stimuli (Strange and Dolan, 2004; van Stegeren et al., 2005, 2006, 2007). Furthermore, administration of either the adrenergic drug yohimbine or hydrocortisone enhanced amygdala and hippocampus activation as well as memory as tested 1 week later (van Stegeren et al., 2010).

The findings of several studies suggest that intense or excessive activation of this noradrenergic system may contribute to the development of posttraumatic stress disorder (PTSD) (Pitman, 2006). Propranolol administered to traumatized patients within several hours after a traumatic experience expressed fewer physiological signs of PTSD when tested 1 month later (Pitman et al., 2002; Vaiva et al., 2003). Additionally, a study of the incidence of PTSD in wounded military personnel reported that patients given morphine within hours after the injury expressed fewer signs of PTSD when examined months after the experience (Holbrook et al., 2010). Because opiates inhibit the release of norepinephrine (McGaugh et al., 1988), a morphine-induced reduction in noradrenergic activation shortly after the trauma may have attenuated the development of PTSD.

EXCEPTIONAL HUMAN MEMORY

The findings summarized above provide the beginnings of understanding why, as William James wondered, some memories endure. Moreover, he suggested that the fact that many, perhaps most, memories are fleeting is adaptive. There is usually no need for memory of every detail of our daily experiences. As James (1890, p. 680) commented, “[s]election is the very keel on which our mental ship is built. If we remembered everything, we should, on most occasions be as ill off as if we remembered nothing.” The fictional character in Borges’ (1944) short story, “Funes the Memorious,” illustrated James’ observation. After he was thrown from a horse, Funes expressed an extraordinary ability to learn and remember. He “remembered not only every leaf of every tree of every wood, but also every one of the times that he had perceived . . . it” (Borges, 1944). Also, he claimed to have "more memories than all mankind has had" (Borges, 1944). However, he also admitted, as James had anticipated, that his memory was like a garbage heap. Borges thus agreed with William James in stressing the importance of forgetting.

Luria (1968) subsequently documented the now well-known case of a subject referred to as S, who had an extraordinarily strong memory ability resembling the ability of Funes. Luria concluded that S's memory capacity and durability were unlimited. Also, he asked, "[h]ow had he come by this capacity for indelible memory traces?" (Luria, 1968, p. 61). Although another individual was subsequently determined to have comparable memory ability (Hunt and Love, 1972), Luria's question remains unanswered. It should also be noted that S's phenomenal memory seemed to be of little help to him in his daily personal life.

A small percentage of autistic individuals are capable of highly exceptional but restricted memory abilities. Calendar calculation is one of the most commonly reported abilities. Some autistic individuals can readily state the day of the week for any specified date over a range of centuries, despite an inability to remember how to do simple addition and subtraction (Hurst and Mulhall, 1988; Heavey et al., 1999). Such complex memory-based ability, like the ability of subject S, remains unexplained.

Recent research has identified a few human subjects who have a remarkable memory ability referred to as highly superior autobiographical memory (HSAM) (Parker et al., 2006; LePort et al., 2012). The first subject identified to have this kind of memory (originally referred to as AJ and now known as Jill Price) wrote: "I am thirty-four years old and . . . have had this unbelievable ability to recall my past. . . . I can take a date, between 1974 and today, and tell you what day it falls on, what I was doing that day and if anything of great importance occurred on that day I can describe that to you as well" (Parker et al., 2006). Extensive testing confirmed her claims. She was remarkably accurate in recalling the experiences of most of the days of her life beginning at about the age of 11 years. Her extensive diary entries confirmed her memories of events that occurred on specific days. Her memory of significant public events is equally superior. Also, importantly, she does not do calendar calculation: unlike autistic savants, she cannot readily provide the day for dates when she was very young or future dates. After the publication of the paper by Parker et al. (2006), testing of many dozens of subjects who claimed to have strong autobiographical memory yielded several dozen subjects who surpassed age- and sex-matched controls in remembering the days and dates of personal and public events as well as details for each event (LePort et al., 2012). All responses were verified by checking available personal and public records. In contrast and perhaps surprisingly, HSAM subjects did not generally excel in learning and remembering information as assessed by laboratory tests (e.g., learning pairs of words and series of digits). Their exceptional memory ability seems to be restricted to experiences of daily life as reflected in episodic remembering. Their memory is not like the memories of Borges' character Funes the Memorious, Luria's subject S, or autistic savants. They are also not like the memory experts, who have learned specific mnemonic tricks enabling the learning of specific kinds of information (Wilding and Valentine, 1997).

MRI scans revealed that several brain regions of HSAM subjects differed from those regions of controls. Several brain regions differed in size and shape (e.g., putamen and caudate) as well as coherence of fiber tracts (e.g., uncinate faciculus) as assessed by diffusion tensor imaging. These results are, of course, only correlational and do not provide critical evidence that these anatomical differences are the bases of or contribute in some way to HSAM. However, it is worth noting that several of the brain regions found to be structurally different in HSAM and control subjects have been implicated in previous studies of autobiographical memory (Kapur et al., 1992; Levine et al., 1998; Steinvorth et al., 2006).

UNUSUAL MEMORY: FLEETING AND LASTING

Studies of unusual memory have significantly influenced memory research as well as our understanding of the neural systems underlying memory. The clinical findings of Ribot (1882) that brain damage impairs most recent memories, sparing older ones, were the first to reveal that lasting memories are consolidated slowly over time. The findings of seminal studies of the patient HM (Scoville and Milner, 1957; Milner, 1972) forced the novel conclusion that different forms of memory are enabled by different brain systems (Mishkin et al., 1984; Packard and McGaugh, 1996; White and McDonald, 2002), and thus they significantly altered research investigating brain systems and memory. The novel finding that some human subjects create highly lasting memories of episodes of their daily experiences as well as memories of significant public events may, ultimately, lead to findings that provide new understanding of how our brains retain and retrieve memories.

Studies have not, as yet, investigated whether the strong memory of HSAM subjects involves experience-induced activation of stress hormones and activation of the amygdala. It may be that the modulatory systems of HSAM subjects are more highly activated by experiences or more sensitive to modestly arousing experiences.

However, HSAM subjects do not remember in precise detail all of their experiences. Like the rest of us, they remember best the more significant events of daily life. Their memories are not like the memories of Funes the Memorious. However, HSAM subjects differ from the rest of us in that they can retain their episodic memories for decades. If lasting memory is important for survival, why is it that so few individuals have this kind of long-lasting memory? It might be that these subjects' memory systems are genetically programmed to retain acquired information. Although the evidence, to date, indicates that none of the HSAM subjects have relatives who have strong memory, additional research is needed to determine whether this ability may have a genetic basis.

We might also wonder whether this ability might have been more common and more commonly used in centuries past. After all, the inventions of the printing press, computers, and cell phones in recent centuries have made it less necessary for us to create lasting records of our experiences. It is said that, before writing was available to keep records of important events, such as a wedding or granting of land, a child was selected to observe an event and then thrown into a river so that the child would subsequently have a lifelong memory of the event. As noted above, for most of us, "[o]ur brains, remarkable as they are, [can]not begin to contain and give equal weight to our every moment of life" (Glore, 1987). Selectively remembering our more important experiences seems to be the best strategy. It is what we generally do, thanks to the modulating influences of emotional arousal on lasting memory.

ACKNOWLEDGMENTS

Research was supported by National Institute of Mental Health Public Health Service Grant MH12526 and the Gerard Family Trust.

10

Concepts and Implications of Altruism Bias and Pathological Altruism

BARBARA A. OAKLEY

The profound benefits of altruism in modern society are self-evident. However, the potential hurtful aspects of altruism have gone largely unrecognized in scientific inquiry. This is despite the fact that virtually all forms of altruism are associated with tradeoffs—some of enormous importance and sensitivity—and notwithstanding that examples of pathologies of altruism abound. Presented here are the mechanistic bases and potential ramifications of pathological altruism, that is, altruism in which attempts to promote the welfare of others instead result in unanticipated harm. A basic conceptual approach toward the quantification of altruism bias is presented. Guardian systems and their overarching importance in the evolution of cooperation are also discussed. Concepts of pathological altruism, altruism bias, and guardian systems may help open many new, potentially useful lines of inquiry and provide a framework to begin moving toward a more mature, scientifically informed understanding of altruism and cooperative behavior.

> Reality must take precedence over public relations, for nature cannot be fooled.
>
> —Richard Feynman

Department of Industrial and Systems Engineering, Oakland University, Rochester, MI 48309. E-mail: oakley@oakland.edu.

Our eyes can be powerless against visual illusions, with our underlying neural machinery leading us to predictably erroneous conclusions about the size or shape of an object (Shepard, 1990). In a similar fashion, our empathic feelings for others, coupled with a desire to be liked, parochial feelings for our in-group, emotional contagion, motivated reasoning, selective exposure, confirmation bias, discounting, allegiance bias, the *Einstellung* ("set") effect, and even an egocentric belief that we know what is best for others, can lead us into powerful and often irrational illusions of helping (Oakley et al., 2012a). In other words, people's own good intentions, coupled with a variety of cognitive biases, can sometimes blind them to the deleterious consequences of their actions. This dynamic of pathological altruism involves subjectively prosocial acts that are objectively antisocial. (Naturally, there are many objective perspectives. One seemingly objective observer's verdict of antisocial terrorism can be another's verdict of prosocial altruism, with the words "objective," "antisocial," "prosocial," "terrorism," and even "altruism" itself varying in meaning depending on the perspective of the putatively objective observer.)

At the core of pathological altruism are actions or reactions based on incomplete access to, or inability to process, the wide range of information necessary to make prudent decisions that align with cultural values associated with altruistic behavior. Various psychological, religious, philosophical, biological, or ideological biases could lead a person or group to misinterpret, selectively discount, or overly emphasize certain aspects of relevant information. Thus, pathologically altruistic behavior can emerge from a mix of accidental, subconscious, or deliberate causes. ["Altruism," in the context of this chapter, is used to signify well-meaning behavior intended to promote the welfare of another; thus altruistic behavior may be motivated by concern for the other, egoistic concerns for the self, or both (e.g., "it makes me feel good to help them") (Batson, 2012). "Pathological" is used in the sense of being excessive or abnormal, without implying any clinical diagnosis.]

Pathological altruism can be conceived as behavior in which attempts to promote the welfare of another, or others, results instead in harm that an external observer would conclude was reasonably foreseeable. More precisely, this chapter defines pathological altruism as an observable behavior or personal tendency in which the explicit or implicit subjective motivation is intentionally to promote the welfare of another, but instead of overall beneficial outcomes, the altruism instead has unreasonable (from the relative perspective of an outside observer) negative consequences to the other or even to the self. This definition does not suggest that there are absolutes but instead suggests that, within a particular context, pathological altruism is the situation in which intended outcomes and actual outcomes (within the framework of how the relative values of "negative" and "positive" are conceptualized), do not mesh.

A working definition of a pathological altruist then might be a person who sincerely engages in what he or she intends to be altruistic acts but who (in a fashion that can be reasonably anticipated) harms the very person or group he or she is trying to help; or a person who, in the course of helping one person or group, inflicts reasonably foreseeable harm to others beyond the person or group being helped; or a person who in reasonably anticipatory way becomes a victim of his or her own altruistic actions (Oakley et al., 2012a). The attempted altruism, in other words, results in objectively foreseeable and unreasonable harm to the self, to the target of the altruism, or to others beyond the target. Examples at an interpersonal level include the codependent wife murdered by the husband she has refused to leave, or the overly attentive "helicopter" father who threatens to sue instructors that give well-deserved bad grades, or the mother who attempts to protect her son by refusing to vaccinate him and who consequently fuels a loss of herd immunity underpinning a local whooping cough epidemic in which an infant dies. Very different personalities can become entangled in pathologies of altruism, ranging from the sensitive hyperempath, to the normal person, to the utterly self-absorbed narcissist. These differing personalities share genuinely good intentions that play out in detrimental ways.

Sometimes there is a blurry line as to whether a problematic outcome for an altruistic action is reasonably foreseeable. This ambiguity can make it difficult to distinguish between altruism and pathological altruism. For example, let's say that, while altruistically helping a friend move to another apartment, you accidentally dropped and broke an expensive statue. Were your actions pathologically altruistic? In the conceptions of pathological altruism outlined here, no. Your altruism would not have been pathologically altruistic, because the bad outcome—the dropped statue—arose as a very unlikely and difficult-to-predict outcome of your good intentions. In a different scenario, however, let's say your brother becomes addicted to painkillers. When he goes through withdrawal, you get more painkillers to help him feel better, and you cover for him when his work supervisor calls. You genuinely want to help your brother, but the reality is that you are enabling his addiction. In this case, your well-meaning altruism is pathological.

These examples help clarify the concept of pathological altruism, but similar situations could be more ambiguous. What if you had dropped your friend's expensive statue after you had consumed a bottle of wine? Or what if your painkiller-addicted brother was waiting to be enrolled in a treatment program? We yearn for the definitive in conceptual definitions, but the reality is that there always will be a residual uncertainty.

Motives are also important. Well-meaning intentions can lead either to altruism or to pathological altruism. Self-servingly malevolent intentions, on the other hand, often have little or nothing to do with altruism, even though such malevolence can easily be cloaked with pretensions of altruism. A con artist soliciting for a "charity" that he uses to personally enrich himself would not be a pathological altruist.

Both altruism and empathy have rightly received an extraordinary amount of research attention. This focus has permitted better characterization of these qualities and how they might have evolved. However, it has also served to reify their value without realistic consideration about when those qualities contain the potential for significant harm.

Part of the reason that pathologies of altruism have not been studied extensively or integrated into the public discourse appears to be fear that such knowledge might be used to discount the importance of altruism. Indeed, there has been a long history in science of avoiding paradigm-shifting approaches, such as Darwinian evolution and acknowledgment of the influence of biological factors on personality, arising in part from fears that such knowledge somehow would diminish human altruistic motivations. Such fears always have proven unfounded. However, these doubts have minimized scientists' ability to see the widespread, vitally important nature of pathologies of altruism. As psychologist Jonathan Haidt (2012) notes, "Morality binds and blinds."

Relevant here are the remarks of historian of science Thomas Kuhn (1970), who observed that when a paradigm shift occurs, scientists see data for the first time. Such is the case with pathologies of altruism, which are not the commonly supposed rare aberrations, "but rather a behavior that overwhelmingly occurs in human social intercourse" (Ayala, 2012). It therefore is realistic to encourage exploration of a new, scientifically based paradigm acknowledging that, even given differing semantic parsings, subjectively altruistic feelings sometimes can be objectively problematic and even ultimately antisocial.

The bottom line is that the heartfelt, emotional basis of our good intentions can mislead us about what is truly helpful for others. Altruistic intentions must be run through the sieve of rational analysis; all too often, the best long-term action to help others, at both personal and public scales, is not immediately or intuitively obvious, not what temporarily makes us feel good, and not what is being promoted by other individuals, with their own potentially self-serving interests. Indeed, truly altruistic actions may sometimes appear cruel or harmful, the equivalent of saying "no" to the student who demands a higher grade or to the addict who needs another hit. However, the social consequences of appearing cruel in a culture that places high value on kindness, empathy, and altruism can lead us to misplaced "helpful" behavior and result in self-deception regarding the consequences of our actions (Fine, 2006; Tavris and Aronson, 2007).

Pathological altruism can operate not only at the individual level but in many different aspects and levels of society, and between societies. Recognizing that feelings of altruism do not necessarily constitute objective altruism provides a new way of framing and understanding altruism. This previously unrecognized perspective in turn may open many new, potentially useful lines of inquiry and provide a framework to begin moving toward a more mature, scientifically informed understanding of altruism and cooperative behavior. The thesis of pathological altruism emphasizes the value of true altruism, self-sacrifice, and other forms of prosociality in human life. At the same time, it acknowledges the potential harm from cognitive blindness that arises whenever groups treat a concept as sacred (Haidt, 2012).

The public as a whole would benefit from knowledge that what might feel subjectively altruistic may have negative unintended consequences that both worsen the situation that was meant to be improved and impact other areas negatively. Even the government can work more efficiently when voters and legislators realize that attempts to help others come with very real costs and can have tradeoffs that worsen the very concerns that were meant to be alleviated.

Along these lines, then, this chapter suggests that pathologies of altruism and of empathic caring should receive concentrated research focus. Specific recommendations are outlined as well. As an underlying motivation, we should remember that in the nineteenth and twentieth centuries, there was an unparalleled improvement in public health as the entire discipline of medicine came under scientific scrutiny. Medical therapies that at one time were thought to be “obviously” beneficial, such as bloodletting and blistering, were finally subjected to review that found them wanting. In a similar vein, if we are truly to help others, this new century at last forms the time for scientists to subject altruistic modern social engineering and activism efforts, as well as academic disciplines that hinge on “helping,” and finally, altruism itself, to far more disciplined scientific scrutiny. It is time for dispassionate exploration of how altruism and empathy themselves can inadvertently bias our efforts to create truly cooperative modern, complex societies.

EVOLUTIONARY CONSIDERATIONS

In one sense, pathological altruism can be thought of as a pattern of nurturing or beneficial behavior with evolutionarily unsuccessful consequences. Evidence for antecedents of such behavior can be seen in the animal world; examples include the unwitting hosts of brood parasitism, as with the wood thrush who devotes substantial resources to raising the offspring of cowbirds. Such antecedent behavior is manifest at even a genetic and molecular level. For example, beneficial replication processes within a cell can be co-opted by viruses (Szathmáry and Maynard Smith, 1997). Consequent cell lysis or exocytosis allows the new viral bodies to spread the contagion.

Molecular perspectives, in fact, can inform how we perceive altruism and cooperative behavior. A stable molecular bond has the property that the bound state is a lower-energy configuration than the unbound state. A physical system tends toward the configuration that minimizes potential energy. Such "cooperative" behavior often needs an initial activation energy—that is, it comes at cost—but the resulting state resides more naturally and easily at the lower energy level for the newly formed single, integrated, cooperating entity. (This entity may or may not have replicative abilities.)

In these situations, pathological altruism or its antecedents might be thought of as arising in two ways. First, it can arise when other entities—systems that are not, or are no longer, integrated into the first cooperating entity—are able to tap into the lowered energy states and possible replicative abilities produced by the first cooperating entity. Tapping into those lowered energy states may weaken or destroy the first entity. (Initially, such secondary entities may be part of the first entity even as they begin their dissociation, as with precancerous cells. It also is worth noting that cooperative "entities" may be composed of different species, as with wrasses that swim with impunity into the mouths of groupers to feed off parasites, or with human intestinal flora.)

Second, pathological altruism or its antecedents can arise when the lowered energy state of the first system allows the system to grow to such a size that it increases the potential for disintegration or destruction from noncooperative mechanisms affiliated with the entity. An example can be found in nuclear fission, where longer-range electrostatic repulsion between protons overcomes the attractive, albeit short-range, nuclear force between nucleons. In more complex cellular processes, the surface area-to-volume ratio limits the cell size. Doubling the size of the cell, for example, requires eight times more nutrients and would have eight times more waste, even though the surface area increased only by a factor of four.

We see these same cooperative versus noncooperative balances playing out on a larger, social scale. For example, the Amazonian Yąnomamö villagers preferred to live in small villages of around 40 people, which seemed to provide an optimal reduction in energy costs affiliated with daily needs for food and safety versus internal strife. However, villages of larger size provided more safety against other, potentially hostile villages. In other words, larger villages could, in some environments, be better at minimizing overall energy costs. Thus, some villages grew to more than 100 inhabitants in size. However, internal repulsive forces increased in the form of disputes that arose as the number of inhabitants in a village increased. Larger villages eventually fissioned, thus beginning the process anew (Chagnon, 2013). At a much higher level of social complexity, there was an initial economic boom as the European Union was first established. This boom has become tempered as internal nominally altruistic and cooperative efforts—the type of efforts that work fairly effectively in less complex social systems—are ultimately proving disputatious and disruptive.

As entities move to higher levels of complexity, the yin and yang of lowered energy states resulting from cooperation, versus noncooperative internal and external forces and effects, can cause boom-and-bust behavior on evolutionary timescales. How entities resolve these issues of cooperation versus noncooperation is a factor in determining whether entities self-destruct, proceed through cycles of growth versus decline, or are able to move successfully to still higher levels of complexity. Whenever higher levels of complexity are achieved, new issues of cooperation versus noncooperation develop, and the cycle begins anew.

One issue is clear. As entities become more complex, they generally develop evolving "guardian" type feedback mechanisms that allow not only the detection and mitigation of the effects of noncooperative mechanisms ("defectors") but also adaptation to changes in those noncooperative mechanisms. Without such flexible guardian systems, entities fall prey to other entities or to their own inherent noncooperative features. On a cellular level, we see that guardian immune systems have evolved from the rudimentary enzyme systems of unicellular organisms, which protect against bacteriophage infections, to the extraordinarily sophisticated immunological defense mechanisms seen in vertebrates.

Similarly, social systems of cooperative behavior must devise effective immunological guardian functions against efforts to siphon away the energetic advantages of cooperative behavior. Such immune guardian functions also must serve to mitigate disruptive internal forces and effects. (Of course, on a biological level, we see from the many varieties of autoimmune disease that immune-type guardian systems, even when designed with care, can create their own host of difficulties and can be hijacked by noncooperative elements, as with leishmaniasis or AIDS. Similar issues would appear to hold true for complex social systems.)

Thus, to the five mechanisms that have been posited for the evolution of cooperation—kin selection, direct reciprocity, indirect reciprocity, network reciprocity, and group selection (Nowak, 2006b)—must be added a sixth, guardian function. For cooperative behavior to continue in complex biological or sociological entities, that is, for entities not to fall prey to ever-present, ever-evolving defectors, some form of evolving active guardian function must be present that detects when debilitating or destructive advantage is being taken of cooperative or altruistic behavior. The guardian system must not only detect but also disable such noncooperative behavior or render the entity immune to the pernicious effects. Without such detection and mitigation mechanisms, we see modeled evolutionary entities that are wiped out by defectors (Nowak, 2006a).

Virtually all the mechanisms for the evolution of cooperation have some degree of overlap. Direct reciprocity, for example, perforce plays a role in indirect reciprocity. In a similar fashion, guardian functions overlap with the other five evolutionary cooperative mechanisms. Reciprocal strategies, such as tit-for-tat, for example, inherently contain what might be thought of as rudimentary and passive guardian functions: If you defect, I will defect. Differences in guardian function between groups could reinforce group selection mechanisms. Guardian functions also could relate to the reputational effects of indirect reciprocity in enhancing cooperation: I may report anyone who does not support the leader, because my family can suffer if I don't. By separating out guardian functions, which address the potential for support or damage to cooperative processes, vitally important mechanisms can be understood and more carefully modeled. Moreover, counterintuitive findings in complex cooperative social systems, such as the importance of selfish behavior and the tradeoffs of religious and ideological mechanisms in inducing and enforcing cooperation, can be clarified (Wilson, 2003; Eldakar and Wilson, 2008). For example, poorly designed guardian functions that do not adequately account for Machiavellian leadership and behavior might play an important role in the failure of social structures. In another example, strong guardian functions that might protect against some internal threats could simultaneously create stifling rigidity that renders the society less able to cope with other challenges. Over previous decades, medical science has come to appreciate the overarching importance of immune systems (themselves examples of guardian systems) in biology. Similarly, awareness of pathological altruism allows those analyzing the evolution of cooperation to appreciate the importance of the full panoply of guardian systems at the many different levels of complexity.

IMPLICATIONS

Let us step back briefly to explore how pathologies of altruism arise at an individual level. Naturally, the small percentage of toddlers and young children who show little concern for others seem predisposed for antisocial behavior as they mature (Rhee et al., 2013). On the other hand, children who manifest altruistic behavior are generally well adjusted.

However, there is a small group of pathologically altruistic children who rate high on altruistic behavior but low on self-actualizing behavior such as showing pleasure at success or doing something on their own. For such children, a psychological cost can arise even at an early age, as shown by high scores in emotional symptoms, including unhappiness, worries, fear, nervousness, and somatization (Oakley et al., 2012b).

As neuroscience and genetics are beginning to elucidate the biological as well as cultural basis of altruistic and empathic behavior, it has become clear that individuals vary in their innate underpinnings involving empathy and altruism (Churchland, 2011). Therefore an educational, religious, and societal "one size fits all" approach to enculturation that uniformly affirms the importance of altruistic caring, without a tempered acknowledgment of the tradeoffs, may inadvertently be harmful for some children in the long run. (In other words, social attempts to blindly encourage altruism become themselves a perfect example of pathological altruism.) Without insight into the undesirable effects arising from empathy and altruistic intentions, children and adults with an existing hypersensitivity toward others find it more difficult to detect and react appropriately to manipulation or to situations in which natural feelings of empathy could lead to undesirable outcomes.

Indeed, it seems that caring for others, helpful as it sometimes may be to those receiving or demanding that care, can have pernicious long-term consequences for the caregiver, including guilt, burnout, depression, and stress disorders (Eisenberg and Eggum, 2009; Najjar et al., 2009). Stress resulting from empathic caring has been shown to produce errors in medical treatment (West et al., 2006). Feelings of empathic caring also appear to lie at the core of dependent personality disorder, codependent behavior, and even anorexia (Oakley et al., 2012a). Caring, empathic, helicopter parents can, with the best of intentions, inflict lasting damage on their children (Locke et al., 2012).

Empathy is not a uniformly positive attribute. It is associated with emotional contagion; hindsight bias; motivated reasoning; caring only for those we like or who compose our in-group (parochial altruism); jumping to conclusions; and inappropriate feelings of guilt in noncooperators who refuse to follow orders to hurt others (Chang, 1998; Frantz and Janoff-Bulman, 2000; Shiller, 2007; Spitzer et al., 2007; Brosnan M et al., 2011; Cikara and Fiske, 2011; Breithaupt, 2012; Gutsell and Inzlicht, 2012). Oxytocin, the "goody-goody hormone" that underlies maternal bonding and many aspects of empathy, also increases both envy and gloating (Shamay-Tsoory et al., 2009). Empathy also can be used by the self-serving, including psychopaths, to deduce how to further their own ends (Dutton, 2012). Being emotionally close to someone who is selfish or dishonest has been found to lead people to becoming more selfish and dishonest themselves (Gino and Galinsky, 2012). Allegiance bias causes forensic scientists to call their findings for the team they believe has hired them (Murrie et al., 2013). [Indeed, the reliability of all types of forensic science evidence, including ostensibly objective techniques such as DNA typing and fingerprint analysis, has been called to question (National Research Council, 2009).] Judges, almost all of whom are lawyers, favor the legal system in their decisions; this bias has far-reaching and deleterious effects on American law (Barton, 2010).

Quietly going along with the flow—refusing to blow the whistle on objectively criminal behavior, for example—also sometimes may be a form of pathological altruism that grows from our feelings of empathy. In other words, the altruism and empathy we feel often isn't really about the person or group ostensibly being helped but instead often are about us. Sometimes they relate to the pain we might feel at being ostracized or shunned for thinking or acting differently. Or they relate to building our reputation—we wish to be publicly perceived as being altruistic, whether or not our efforts are truly altruistic, so that we can receive the reputational benefits of indirect reciprocity. (Juries are notoriously magnanimous with other peoples' money.) Some would say that, once egoism is involved, the result is no longer altruism, so there is no such thing as pathological altruism. However, such an interpretation would also mean there is no altruism, because egoistic reward circuitry appears to be an important determinant of altruistic behavior.

As the work of Nobel laureate Daniel Kahneman, Jonathan Haidt, and others has shown, humans possess both intuitive fast and rational slow cognitive processes (Cushman et al., 2010; Kahneman, 2011; Haidt, 2012). Intuitions come first; reasoning follows to support that intuition (Zajonc, 1980; Haidt, 2001). Empathy is driven by fast processes. We often make snap judgments as a result of empathy and superficial notions of altruism [related to the "moral heuristics" described by Sunstein (2005)]. Then, as both Kahneman and Haidt have explored in depth, we are experts at justifying emotionally based decisions with backfilled rationality. *Einstellung*, the inability to see another solution once an initial solution is prefixed in mind (Bilalić et al., 2008), means that a superficially helpful approach can become reified, further reinforced by motivated reasoning, selective exposure, belief perseverance, and growing overconfidence (Mercier and Sperber, 2011), along with moral heuristics such as those involving omission bias and outrage (Sunstein, 2005).

However, surprisingly, an individual can be oblivious to the consequences of these interwoven effects as a consequence of "bias blind spot" (Pronin and Kugler, 2007). In this fashion, an initial snap, commonsense judgment about what seems right in helping others can gel quickly into formidable certitude without consideration of important relevant facts. As noted by Mercier and Sperber (2011), "there is considerable evidence that when reasoning is applied to the conclusions of intuitive inference, it tends to rationalize them rather than to correct them . . . reasoning pushes people not towards the best decisions but towards decisions that are easier to justify." Intelligence is no safeguard regarding these confirmation bias-related issues. Highly intelligent people, for example, do not reason more even-handedly and thoroughly; they simply are able to present more arguments supporting their own beliefs (Perkins et al., 1991). As Columbia's Mark Lilla (2003) has pointed out "Distinguished professors, gifted poets, and influential journalists summoned their talents to convince all who would listen that modern tyrants were liberators and that their unconscionable crimes were noble, when seen in the proper perspective. Whoever takes it upon himself to write an honest intellectual history of twentieth-century Europe will need a strong stomach." In fact, combating extreme confirmation bias has been called one of psychology's most pressing research priorities (Lilienfeld et al., 2009).

Sometimes it is appropriate to turn off or distance oneself from feelings of empathy, and it appears such emotional distancing can be learned (Chiesa and Serretti, 2009; Decety et al., 2010). In fact, it is clear that turning off empathy—becoming dispassionate—is normal in certain conditions, such as a surgeon performing surgery. Indeed, many hospitals have policies forbidding surgeons from operating on family members, a circumstance in which it would be more difficult to maintain a dispassionate stance.

In psychology, lack of awareness of limitations and tradeoffs regarding empathy has spilled over into the therapeutic process itself. Older therapists remember sayings such as "empathy defeats therapy" (Friedman, 2008), but such attitudes have fallen away as psychologists increasingly have placed a premium on empathic care during the therapeutic process. In a related vein, within the field of nursing, the importance of empathy and compassion for patients is emphasized so unrelentingly that it would be reasonable to explore the possibility of a causal relationship between the unilateral focus on caring and the severe issue of burnout among nurses (Kowalski et al., 2010). Health care workers are not taught about the potential hazards of excessive or misplaced empathy; consequently, a gradual dehumanization process unfolds (Haque and Waytz, 2012). An unconditional support of empathy and altruism makes matters so difficult for some members of general society that a counterculture of popular literature and support groups involving codependency has arisen. However, such approaches suffer from a lack of scientific merit or rigor (McGrath and Oakley, 2012).

It is clear that, without the support of science, it is impossible to steer societal mores toward a more nuanced understanding of altruism and empathy that ultimately can benefit everyone.

EXTENDED IMPLICATIONS

There are broader implications related to these issues, particularly regarding the policy aspects of the scientific enterprise. Good government is a foundation of large-scale societies; government programs are designed to minimize a variety of social problems. Although virtually every program has its critics, well-designed programs can be effective in bettering people's lives with few negative tradeoffs. From a scientifically based perspective, however, some programs are deeply problematic, often as a result of superficial notions on the part of program designers or implementers about what is genuinely beneficial for others, coupled with a lack of accountability for ensuing programmatic failures (Sowell, 2012). In these pathologically altruistic enterprises, confirmation bias, discounting, motivated reasoning, and egocentric certitude that our approach is the best—in short, the usual biases that underlie pathologies of altruism—appear to play important roles.

For example, teen pregnancy has received substantive focus in recent years. Teenagers in the United States become pregnant, contract sexually transmitted diseases, and have abortions at much higher rates than teenagers in most other industrialized countries. However, the most effective, scientifically proven approaches to reducing teen pregnancy are often ignored. As psychologist Timothy Wilson (2011) noted in summarizing the many problematic efforts in this area: "The fact that policy makers learned so little from past research—at huge human and financial cost—is made even more mind-boggling by being such a familiar story. Too often, policy makers follow common sense instead of scientific data when deciding how to solve social and behavioral problems." Policy makers and policy supporters, in other words, are shaped by cohesive cognitive biases regarding their intentions to help others.

In yet another area, ostensibly well-meaning governmental policy promoted home ownership, a beneficial goal that stabilizes families and communities. The government-sponsored enterprises Freddie Mac and Fannie Mae allowed less-than-qualified individuals to receive housing loans and encouraged more-qualified borrowers to overextend themselves. Typical risk–reward considerations were marginalized because of implicit government support (Acharya et al., 2011). The government used these agencies to promote social goals without acknowledging the risk or cost. When economic conditions faltered, many lost their homes or found themselves with properties worth far less than they originally had paid. Government policy then shifted to the cost of this "altruism" to the public, to pay off the too-big-to-fail banks then holding securitized subprime loans. For those who care about helping the needy in this country, or those who object to corporate bailouts, these trillion-dollar costs bring into high relief the immediate need for scientifically informed planning and evidence-based reevaluation. What is of primary concern here is that altruistic intentions played a critical role in the development and unfolding of the housing bubble in the United States, which in turn had enormous impact on the U.S. economy. This recent history emphasizes the importance of studying not only altruism but also its biases and the consequences of those biases.

In foreign aid, $2 trillion dollars have been provided to Africa over the past 50 years. As chronicled by economist and former World Bank consultant Dambisa Moyo, a native of Zambia, such aid has resulted in measurably worsened outcomes in a broad variety of areas, supporting despotism and increasing corruption and a sense of dependency in Africans (Moyo, 2009). In some cases, the money has been directly responsible for extraordinary damage (Easterly, 2006; Polman, 2010). Experienced foreign aid worker Ernesto Sirolli echoes many when he notes that much Western aid arises from narcissistic paternalism and patronization (Sirolli, 1999). We see here yet another situation where preconceived altruistic notions render it more difficult to focus on and react to indications supplied by data.

Viewing altruistic behavior as a source of both potentially positive and potentially negative influences may provide a framework for understanding better a variety of complex challenges. For example, one of the most important national issues of our time, as outlined in the National Academy Press publication *Choosing the Nation's Fiscal Future,* is the looming federal deficit (National Research Council and National Academy of Public Administration, 2010). Ralph Cicerone, President of the National Academy of Sciences, and Jennifer Dorn, President and Chief Executive Officer of the National Academy of Public Administration, jointly wrote: "Much is at stake. If we as a nation do not grapple promptly and wisely with the changes needed to put the federal budget on a sustainable course, all of us will find that the public goals we most value are at risk."

How can such budgetary policies arise and continue? Arguably, their establishment and growth are cultivated by broadly Judeo-Christian cultural values and educational processes related to empathy and altruism. [Cultures can conceptualize empathy, altruism, and associated values in different ways (Haidt, 2012; Traphagan, 2012).] In this cultural perspective, empathy and altruistic intentions often are viewed as monolithically positive, nearly sacred qualities with negligible tradeoffs, whether or not the empathy is genuinely beneficial or the outcome of the altruistic intentions is truly altruistic. "It's the thought that counts," as the saying goes when discounting negative consequences of altruism.

A supportive bias for claimed altruistic efforts appears to have contributed not only to a plethora of economic woes but also to a continuing record of difficulties in the social sciences, where programs, theories, and therapies with altruistic intent—particularly those that coincide with preconceived "obviously beneficial" notions of helping—do not appear to receive the same careful scientific scrutiny as less obviously well-intentioned programs (Cole, 2001; Wright and Cummings, 2005; Wilson, 2011). This lack of critical appraisal has been seen in vitally important areas such as the mitigation of posttraumatic stress disorder, the reduction of family violence, the elimination of racial prejudice, the reduction of sex differences in mathematics, and the lessening of adolescent behavior problems and drug use (Petrosino et al., 2000, 2003; Kalev et al., 2006; Lilienfeld, 2007; Mills, 2008; Eidelson and Soldz, 2012; Sander and Taylor, 2012; Stoet and Geary, 2012). In one example, a therapy called "critical incident stress debriefing" was broadly implemented throughout the United States to reduce posttraumatic stress disorder, even though this costly program simply did not work and, in fact, sometimes worsened the very stress it was meant to resolve (Lilienfeld, 2007).

Well-meaning but unscientific approaches toward altruistic helping can have the unwitting effect of ensuring that the benefits of science and the scientific method are kept away from those most in need of help. In the final analysis, it is clear that when altruistic efforts in science are presented as being beyond reproach, it becomes all too easy to silence rational criticism (Sommers, 1995, 2001; Satel, 2000; Wright and Cummings, 2005; Mills, 2008; Straus, 2007, 2008, 2009; Sunstein, 2009). Few wish to run the gauntlet of criticizing poorly conducted, highly subjective "science" that is purported to help, or indeed, of daring to question the basis of problematic scientific paradigms that arise in part from good intentions. Edward O. Wilson ran into just such a well-meaning buzzsaw with the publication of his *Sociobiology,* as did Judith Rich Harris with *The Nurture Assumption* and Napoleon Chagnon with his studies of rates of violence among the Amazonian Yąnomamö (Pinker, 2002; Dreger, 2011; Chagnon, 2013).

To object to a scientific theory is one thing, but to object to a scientific theory that connects however tenuously to feelings of morality is quite another. Once morality plays a role, even at the most subliminal level, the formidable cognitive biases of altruism and its pathologies can swing into play. Perhaps for that reason different academic disciplines and specific topics within those disciplines show differing requirements for rigor. In disciplines related to helping people (which can encompass a surprisingly broad swathe of even hard-science topics), scientists' differing treatment of research findings that elicit altruism bias can skew the findings of seemingly objective science (Margolis, 1993). As Robert Trivers (2011) has noted: "It seems manifest that the greater the social content of a discipline, especially human, the greater will be the biases due to self-deception and the greater the retardation of the field compared with less social disciplines."

One of the most valuable characteristics of science is that, despite the obvious imperfection of biases in ostensibly objective scientists, it provides a potential mechanism for overcoming those biases. At the same time, altruism bias may be one of the most pernicious, hard-to-eradicate biases in science, because it involves even-handed examination of what groups of seemingly objective rational scientists subliminally have come to regard as sacred. [Biases and belief systems can have a sense of the sacred even when not formalized as religions (Haidt, 2012).]

As noted previously, many government programs are indeed beneficial, and some are invaluable in allowing the population as a whole to live meaningful lives supported by a safety net for life's inevitable difficulties. However, the publication *Choosing the Nation's Fiscal Future* (National Research Council and National Academy of Public Administration, 2010) documents that the federal deficit is clearly heading for a crisis. In other words, as a result of manifold individual decisions, many of which were based on very real intentions to help others, everyone is at risk for serious harm. Such crises may arise, not as a tragedy of the commons, but rather, as a tragedy of altruism.

In the small social groups, which characterized most of human history, altruism bias and pathologies of altruism would have had few means for extending broad influence. In modern times, with the mass outreach potential of a few well-intentioned individuals or influential groups, who often have little or no ultimate accountability for programmatic failures or other detrimental effects, pathologies of altruism can assume enormous importance. It is reasonable to help shift the scientific and cultural paradigm and set the stage so that it becomes culturally acceptable, even expected, that one should attempt to quantify objectively purported claims of altruism. This paradigm shift is particularly important with regard to the budgetary tradeoffs and planning that form important aspects of effective government that promotes cooperative behavior. The reality is, as made clear in the joint statement by the presidents of the National Academy of Sciences and the National Academy of Public Administration (20100, that unless these types of considerations are made expeditiously, extraordinary cuts must be made in even the most genuinely beneficial programs. A voting public encouraged to follow a short-term, superficial, "feel good," emotionally based heuristic for helping others is a voting public that much more easily can make poor long-term decisions.

TOWARD A CONCEPTUAL FRAMEWORK

As scientists and engineers know well, "all models are wrong, but some are useful" (Box and Draper, 1987). Embedded in any model is perspective, that is, the framework perceived by the developer. In the past, altruism (or cooperation) generally has been conceived and modeled as lying on a continuum between nonexistent and existent, much like the concept of eusociality (in which the opposite of eusociality is asociality, that is, no tendencies for grouping or socializing at all (Trivers, 1971; Darlington, 1978; Sober and Wilson, 1998; Fehr and Fischbacher, 2003). ("Asocial" may also be considered, in some conceptions, to be "selfish" or "egoistic.") More recently, altruism has been conceived on a positive-to-negative continuum where negative altruism involves malevolent intentions, Machiavellianism, and psychopathy (Baron-Cohen, 2012).

However, altruism can be framed in a third way, as a positive-to-negative continuum where negative altruism is altruism with antithetical consequences, that is, pathological altruism. Viewing altruism in this way provides insights that relate to both individual personality traits and to large-scale modeling. There are tradeoffs to virtually all forms of altruism, and considering altruism as possessing both positive and negative aspects allows one to take more careful consideration of who is helped (the beneficiary) and who is harmed (the victim). Sometimes the same individual or group may be both helped and harmed. Parochial altruism—the combination of in-group altruism and out-group hostility—is positive altruism within one group but negative altruism for another. High taxes, for example, may be considered as positive altruism for one group and as negative altruism for another.

It should be noted that these conceptions formulate the problem primarily in terms of the altruism provider and stress the liability arising from, among other things, empathy and identification. It also is possible to formulate altruism as a dynamic process controlled in part by the altruism seeker (Halabi and Nadler, 2009). Moreover, the entitlements pressed for by the altruism seeker may be either objectively helpful (e.g., a scholarship sought by a hardworking student) or harmful (e.g., alcohol sought by an alcoholic). In other cases, the altruism seeker may desire seemingly infinitesimal acts of altruism that ultimately play a role in widespread long-term negative outcomes, as seen with grade inflation and social promotion. Jean Twenge and her research group have pointed toward substantive increases in narcissism in the population over the past decades, "Trends in positive self-views are correlated with grade inflation . . . but are not explained by changes in objective performance" (Twenge et al., 2008, 2012). It also may be that the actual help needed by those seeking or expecting help, as with Munchausen by Internet (in which Internet users feign a variety of ills to draw attention), involves something entirely different from what is sought.

Studies suggest that those involved in altruistic transactions benefit differentially from them, and egoism can play surprising roles. For example, sensitive children may have better personal outcomes if they behave egoistically in some instances. However, as shown with Twenge's work, other children appear to have unrealistic expectations when egoistic considerations are encouraged. The question thus arises: When and for whom is egoistic behavior beneficial or harmful? What is the relationship of egoism to altruism and—most importantly for our purposes—to pathologies of altruism? Further, how can we study these issues scientifically without our own judgments and moral righteousness intruding, guiding answers toward what we are certain will be helpful for others to hear rather than toward what the data actually reveal?

We can find clues as to how to proceed by examining prospect theory, where outcomes are assigned differing values depending on whether there are gains or losses. Losses hurt more than "feel good" gains. With altruism bias, it appears that people assign varying values to outcomes based on their underlying moral assessment. An example of such altruism bias was seen in subjects who were given a posthypnotic suggestion to feel a flash of disgust (an intimate part of moral judgment) when hearing a particular arbitrary word. Moral judgment—that sense of whether something is or is not helpful for others—could be made more severe by the presence of the arbitrary word (Wheatley and Haidt, 2005). Researchers were surprised to find that even in a control situation where there was no apparent moral issue, the arbitrary words caused some subjects to make more negative moral judgments; later, the subjects confabulated stories to explain their behavior. Many factors have been shown to influence moral judgment at a subconscious level (Haidt, 2012).

It appears that when a person attempts rationally (using the "slow" system) to calculate the utility of something that he or she already has judged through "fast" cognitive processes to be morally beneficial, skewed judgments are made, inflating the good outcomes and deflating the bad. Analogously, one can imagine that if malevolence was the goal, as with ill intentions by a parochial in-group toward an out-group, benefits would be deflated and harms inflated.

A PATH FORWARD

Personal-Scale Studies

Pathologies arising from altruism can be studied on an individual level. For example, many of the errors of judgment cited in the extensive listing in Krueger and Funder (2004) could result in altruism bias, or altruism bias could underlie and help lead to those judgment errors. In this regard, does the brain use a simple underlying "thumbs up" moral heuristic that leads "rational" thought processes to a foregone conclusion, as with the allegiance effect? Can such a heuristic be seen as a characteristic signature in medical imaging? Do individuals vary in their ability to influence their underlying moral heuristics? Are some individuals addicts of their feelings of self-righteousness? What varying effect does culture have on different individual's moral heuristics? On a side note, it appears that altruism bias, like many such biases, is a Jamesian fringe phenomenon of consciousness, much like the feeling of familiarity. It seems to grow from or relate to that little studied sense of rightness, of certitude—a tip-of-the-tongue feeling built on a web of biases, influences, and perceptions that one thing is beneficial, whereas another is not (Mangan, 2001; Brin, 2012; Burton, 2012). Self-righteousness and pathologies of certitude have received almost no research emphasis (Brin, 2012; Burton, 2012).

Narcissism, one of the most strongly heritable of all personality traits (Torgersen et al., 2000), has been similarly neglected. Narcissism is comorbid with many of the most troublesome personality disorders and dysfunctions, including psychopathy, borderline personality disorder, and bipolar disorder. So it comes as a surprise to learn that there are almost no hard-science imaging studies focusing on narcissism, although many other syndromes, as well as the positive aspects of empathy, have received keen research focus (Garrity et al., 2007; Allen et al., 2011; Zaki and Ochsner, 2012). Narcissism, in other words, deserves priority in imaging research.

Similarly, the vital topic of codependency has received almost no hard-science research focus, leaving "research" to those with limited or no scientific research qualifications (McGrath and Oakley, 2012). An indication of the popular need for and interest in this area is that a single book, *Codependent No More,* has sold more than five million copies over several decades. It is reasonable to wonder if the lack of scientific research involving codependency may relate to the fact that there is a strong academic bias against studying possible negative outcomes of empathy. Codependency, like narcissism, would thus be an important area of research in the elucidation of pathologies of altruism.

Broad-Scale Studies

At a larger scale, almost any data-driven model or projection in any discipline or government enterprise that even indirectly impacts an area of fairness or morality, or which contains significant potential for disciplinary bias, can be examined to see how well it actually has performed in the context of unfolding real-world data. Unexpected performance of the model or projection could be an indicator of altruism bias, and the bias could be quantified as to when, where, why, how, and to what extent it occurred. For example, a better understanding of altruism bias in data analysis and program development and implementation may provide insights regarding a great variety of phenomena, including the artificially inflated values of economic bubbles or various inadequate statistical measures (e.g., those involving unemployment and economic growth) that can falsely boost the effects of well-meaning efforts. Concepts of pathological altruism thus can serve a normative purpose, helping us create better policies. Knowledge of how altruism bias distorts objective scientific inquiry can and should be considered a confounding factor when developing formal models.

It should be noted, however, that those possessing altruism bias would be most strongly biased to object to the very concept of altruism bias (Pronin et al., 2002). Research has shown the near impossibility of reaching biased individuals using rational approaches, no matter their level of education or intelligence; such attempts can be likened to squaring the circle (Perkins et al., 1991; Lilienfeld et al., 2009).

In another vein, researchers from outside a given discipline, and who are thus less vested in the theories of that domain themselves, could initiate studies to determine whether insufficient statistics, exaggerated claims, drawing the wrong conclusions from other papers, or using data selectively to confirm hypotheses might differ among studies that relate to disciplinary biases or moral issues (many hard-science topics ultimately impact issues of deep moral concern) versus those that do not. Within scientific disciplines, the appearance of group-norm–enforcing signed petitions could be used as indicators of the potential for pathologies of altruism; such petitions might communicate important, albeit unintended, information about the health of a discipline. Are entire disciplines shaped by papers that are not submitted because of legitimate fears of rejection? As Santiago Ramón y Cajal (1937), the father of modern neuroscience, perceptively wrote: "the good will of scientists is usually so paradoxical that they are more pleased by the defence of an obvious error which has become wide-spread than by the establishment of a new fact." These thoughts were echoed recently in a predictably controversial paper by John Ioannidis pointing toward the shockingly high publication rate of false research findings. Ioannidis (2005) noted: "for many current scientific fields, claimed research findings may often be simply accurate measures of the prevailing bias." Can disciplinary biases be quantified, perhaps in studies put forth by interdisciplinary groups (including non-academics) from largely outside the discipline in question? Group-think within disciplines, particularly in regard to differing editorial standards of proof required for studies that do not hold to a discipline's underlying moral paradigm, would be a particularly rich, important, and provocative area of study.

Lilienfeld (2007) points toward psychological treatments that "may produce harm in relatives or friends of clients in addition to, or instead of, clients themselves. For example, some treatments that are otherwise innocuous or even effective with clients could produce a heightened risk of false abuse allegations against family members." Is it possible that some social advocacy and social justice efforts result in the same types of pernicious effects on a societal scale so that efforts to build cooperation instead inhibit it? We often do not know, because well-meaning advocates have made raising those questions a taboo. Framing issues in the form of pathologies of altruism and altruism bias forms a mechanism for breaking through the taboo and making dispassionate studies of when helping is truly helping and when it is contributing inadvertent harm.

Forensic studies of allegiance bias (Murrie et al., 2013) could profitably inform academic disciplines as to how to examine the effects of altruism bias both within and outside academia, and indeed, in regard to greater academia itself. In the later regard, it seems academia is reaching multiple crises, often arising from well-meaning efforts; such crises include administrative bloat, college tuitions that have vastly outpaced inflation, and students who are left academically adrift (Arum and Roksa, 2010).

Potential Steps to Address Altruism Bias in Academic Disciplines and the Scientific Enterprise

There are active steps that could be taken to prevent the potential for altruism bias within the scientific enterprise. In all-important journal review processes, for example, mixed panels of reviewers (e.g., cognitive psychologists and neuroscientists reviewing social psychological papers) could become standard practice (Stoet and Geary, 2013). Doctoral programs can place heavier emphasis on the scientific method and careful use of statistics so that graduate students, who are themselves future journal reviewers, can learn to spot problematic submissions more easily and perhaps be less likely to conduct problematic research themselves. The many aspects of altruism bias and the problems as well as benefits of empathy can be much more broadly discussed and emphasized in textbooks, beginning even in high school and the early years of college. Disciplines heavily involved in social advocacy, whose primary goal involves truly benefiting others, should be among the first to take interest in incorporating these concepts and approaches into research and training programs, editorial efforts, and textbooks.

CONCLUSIONS

Science has put extraordinary emphasis on studying the helpful aspects of altruism, and this emphasis has helped reify altruism's benefits among the general population. However, if science is truly to serve as an ultimately altruistic enterprise, then science must examine not only the good but also the harm that can arise from our feelings of altruism and empathetic caring for others. In support of this idea, it is important to note that during the twentieth century, tens of millions of individuals were killed under despotic regimes that rose to power through appeals to altruism (Waite, 1977; Li, 1994; Montefiore, 2004; Short, 2004; Chang and Halliday, 2005). The study of pathological altruism, in other words, is not a minor, inconsequential offshoot of the study of altruism but instead is a topic of overwhelming scientific and public importance.

ACKNOWLEDGMENTS

The author thanks Philip Oakley and Joseph Carroll for extended discussions and Amy Alkon, Gary Barber, Augustine Brannigan, Bernard Berofsky, Kenny Felder, David C. Geary, Joachim Krueger, Hugo Mercier, Karol Pessin, Sally Satel, John Traphagan, and Carolyn Zahn-Waxler for cogent critical suggestions. The suggestions of the anonymous editor and reviewers also were very beneficial.

11

Justice- and Fairness-Related Behaviors in Nonhuman Primates

SARAH F. BROSNAN

A distinctive feature across human societies is our interest in justice and fairness. People will sometimes invest in extremely costly behavior to achieve fair outcomes for themselves and others. Why do people care so much about justice? One way to address this is comparatively, exploring behaviors related to justice and fairness in other species. In this chapter, I review work exploring responses to inequity, prosocial behavior, and other relevant behaviors in nonhuman primates in an effort to understand both the potential evolutionary function of these behaviors and the social and ecological reasons for the individual differences in behavior. I also consider how these behaviors relate to human behavior, particularly in the case of experimental studies using games derived from experimental economics to compare nonhuman primates' responses to those of humans in similar experimental conditions. These results emphasize the importance of a comparative approach to better understand the function and diversity of human behavior.

A feature of humans that apparently sets us apart as a species is our focus on others' well-being, as well as our own (Eisenberg and Mussen, 1989; Henrich et al., 2004). We will, sometimes at

---

Georgia State University, Departments of Psychology and Philosophy, Neuroscience Institute, Atlanta, GA 30302. E-mail: sbrosnan@gsu.edu.

great personal cost, protest outcomes that we consider unfair, whether they personally affect us or have no direct impact on our lives. What is it that causes people to behave in this way? One possibility is that it is attributable to culture. In fact, only English has a word for the concept of "fairness"; other languages have adopted the English word, indicating a culturally broad interest in the concept but potentially implying that the concept is not ubiquitous (Wilson, 2012). Another possibility is that we have evolved to be interested in the well-being of others. Although there are clear fitness benefits to considering one's own well-being, there are also (more delayed) benefits to considering others' well-being. There may be costs to helping others in the short term, but if there are long-term benefits, either because of continued interactions based on reciprocity or, more indirectly, because of gaining a reputation as a "fair" person, then the behavior could be selected (Frank, 1988). If this behavior has evolved, we may find similar behaviors, or precursor behaviors, in other species. Other species will not show these behaviors in the same way that humans do. Among other reasons for this, many behaviors related to fairness and justice, such as the ability to share information about a third party's previous behavior, require language. Nonetheless, an important question is the degree to which fairness and justice have evolved from similar or related behaviors in other species. This evolutionary approach provides insight into understanding our own behavior.

In humans, the concept of fairness is closely related to that of justice. Distinguishing the two, fairness involves voluntary interactions with other individuals, whereas justice is meted out by an impartial third party (Wilson, 2012). Based on these definitions, most of the experimental work discussed below relates to fairness, rather than justice, because the subjects being studied are involved in the interactions and outcomes in question. Outside of the experimental context, observations suggest impartial interventions in others' interactions, indicating that these species may also be sensitive to justice concerns. There are many different aspects of justice and fairness, including distributive, procedural, retributive, restorative, etc. Most experimental studies involving nonhuman species measure subjects' responses to different distributions of food rewards and, hence, concern distributive justice or fairness. In humans, two common distribution mechanisms are egalitarianism, in which all individuals get the same outcome (e.g., equality) and equity, in which individuals' benefits are proportional to their inputs. Both of these are amenable to study in other species and are the feature most commonly manipulated in the aforementioned experimental studies (e.g., by altering subjects' payoffs compared with their partner's). Outside of the experimental realm, observational studies indicate that nonhuman primates are also sensitive to nondistributional aspects of justice and fairness, such as judging the appropriateness of another's behavior, providing a broader context in which to consider justice or fairness in these species.

Studying other species' behaviors in these situations allows us to elucidate the evolutionary function of justice and fairness by exploring behaviors that are related, either because the behavior itself is a component of justice or fairness or because it represents a precursor to human behavior. This comparative approach is informative in two complementary ways, through homology and convergence. Homologies occur when a behavior exists in multiple species because the behavior existed in a shared common ancestor. This pinpoints when in the taxon's phylogenetic history the trait evolved. Convergences occur when a behavior evolved in multiple species because of common selective pressures but without shared descent from a common ancestor. Convergences may be particularly informative when studying the function of a behavior because, through comparison across species, they may indicate which traits co-occur and the social or ecological pressures that may have selected for the behavior.

My goal in this review is to bring together data regarding behaviors related to justice and fairness in nonhuman primate species (hereafter, primates). Observations have highlighted situations in which primates act as if their behavior is guided by an interest in the outcomes of others (de Waal, 1991). A decade ago, the first experimental studies emerged, focusing on one aspect of justice and fairness: how individuals responded to getting less than a partner (Brosnan and de Waal, 2003; Brosnan et al., 2005). These studies used methods derived from game theory and showed that, in experimental settings in which inequity between two individuals was introduced, subjects responded negatively to inequity not in their favor. Since that time, this task has been extended to 14 species, including 10 primate species, allowing for a broad phylogenetic view that provides insight into the evolutionary function of inequity (Brosnan, 2011). Additionally, responses to inequity have been explored in more species-specific contexts and situations (de Waal and Berger, 2000; Brosnan et al., 2006). These results highlight the correlation between inequity and cooperation, as well as emphasizing the socioecological factors that influenced the emergence of justice- and fairness-related behavior. This comparative analysis is beginning to shed light on the factors that may have led to the evolution of justice- and fairness-related behaviors in humans and other primates.

JUSTICE- AND FAIRNESS-RELATED BEHAVIOR IN OTHER SPECIES

One hypothesis for the evolution of fairness is that recognizing inequities helped individuals ascertain the value of their partners in cooperative interactions (Fehr and Schmidt, 1999; Brosnan, 2011). Individuals should not continue to work with others if they do not, on average, benefit from the relationship. Whether outcomes are equitable may be used as a proxy; if one's outcomes are routinely wanting compared with one's partner's, then it is likely that an interaction with another partner, even one chosen at random, will lead to a more beneficial outcome. This leads to a partner choice mechanism in which individuals sample other partners when they are experiencing high levels of inequity with the current partner or partners (Brosnan, 2006). Note that individuals thus recognize and respond to inequity without any understanding of why they are doing so. Additionally, this provides a benefit even if the individual's outcomes in the less advantageous interaction are net positive, because the currency of natural selection is relative, rather than absolute, gains.

Although this hypothesis linking inequity and cooperation emerged in the context of humans, other species also cooperate with one another, so behaviors related to inequity may occur in other cooperative species as well. Comparative research presents challenges. First, the manifestations of justice and fairness may be different in different species, making it difficult for human experimenters to recognize relevant behaviors. Second, nonhuman species are nonverbal, with the dual implications that we cannot ask them about their motivations for their behavior, nor can we ask them about outcomes that did not result in an overt change in their behavior. Thus, we will miss any response that does not have a behavioral manifestation. As a result, experiments focus on whether other species act in a certain way, not whether they mean to act in that way. This is different from the measure used in many human studies, and ideally results should only be compared if the variable of interest is subjects' behavioral reactions, not subjects' reported motivations or reactions. Finally, the limitation to measuring behavioral changes means that the methods used in humans typically differ substantially from those used in other primates, which can complicate comparative analyses.

There have been two approaches to comparative work on justice and fairness. The first is to adapt game theory methods to explore decision making in other species. Game theory is a powerful approach that allows complex decision making to be modeled experimentally as a series of carefully controlled choices, which can be experimentally manipulated to rigorously explore the behavior of interest (Smith, 1987). The advantage of game theory for comparative research is the focus on very simple choices to uncover complex behavior, making these techniques amenable to use in a wide variety of other species. Procedures can be designed that require no verbal instruction whatsoever and that can be used in the same form in humans and other species, allowing for direct comparisons and subsequent explorations of shared outcomes or cognitive mechanisms

(Brosnan et al., 2013). Although we cannot assume that different species (or different individuals within the same species) interpret even identical procedures in the same way, if procedures differ between species, then we are never able to disentangle whether any resulting differences in behavior are attributable to species differences or differences in the procedure. One procedural challenge to such experimental approaches is that humans interact with an experimenter of the same species, whereas other species interact with an experimenter of a different species (a human). Although this is a practical necessity, other species did not evolve to interact with humans, and so careful controls are needed to determine that the nonhuman subjects were evaluating their outcomes relative to their conspecific partner, not the experimenter or another aspect of the environment. Additionally, experimental approaches are artificial, and so we may miss situations in which justice-related behavior occurs. Despite these drawbacks, game theoretic approaches have the advantage of being comparable to the human literature and so are indispensable for comparative research.

A second approach is to explore behaviors that may be related to justice and fairness in species-specific contexts. This includes observational studies, in which behavior is observed during unconstrained interactions. This approach has the advantage of being the more natural, which leads to likely candidate behaviors and a better understanding of how justice or fairness manifest in the species' typical interactions. Moreover, because these studies are not reliant on manipulating outcomes and measuring subjects' subsequent behavior, there is greater opportunity to study justice outside of the context of food distributions. The disadvantages are that these results are less comparable across species, particularly if methods or the contexts in which individuals are attentive to inequity differ, and the underlying motivations for subjects' behavior are not known. The ideal is to combine insights from both approaches.

USING GAME THEORY TO EXPLORE JUSTICE-RELATED BEHAVIOR

The Ultimatum Game

In 1982, Werner Guth presented the Ultimatum Game (UG), designed to explore fairness in bargaining behavior in humans (Guth et al., 1982) (Fig. 11.1). In this game, one individual, a proposer, is given a set sum and told to allocate it between himself or herself and a partner. If the partner, called the responder, accepts the allocation, both parties receive the money as allocated, but if the responder rejects it, neither party receives anything. Hundreds of experiments across the last three decades have shown that modern Western humans typically allocate about 40 percent of the sum

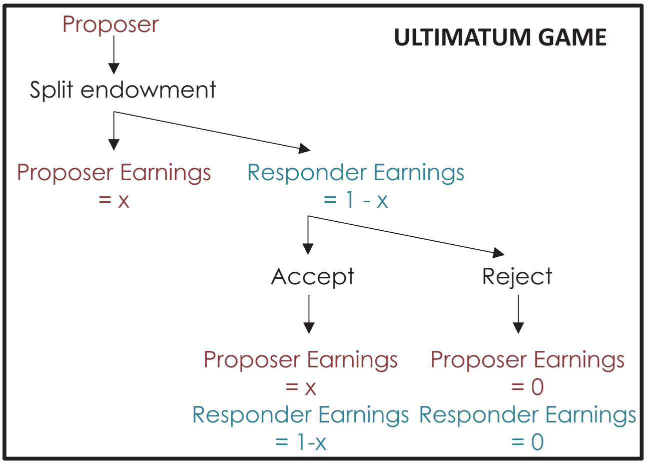


FIGURE 11.1 Schematic diagram of the UG.

to the responder, and responders typically reject any offer under about 20 percent of the allocation (Camerer, 2003). Allocations are higher than those seen in a related game, the Dictator Game (DG), in which the responder has no recourse to the proposer's allocation, indicating that the proposer alters his or her allocations dependent upon whether the responder can influence the outcome.

The UG is often considered to measure fairness preferences; thus, it is particularly relevant to considerations of fairness and justice in other species. There have been two studies in chimpanzees, both relying on a limited-form version of the game in which proposers make a choice from between two preset distributions. In neither case did chimpanzee responders refuse allocations; however, proposers' behavior differed between the studies. In the first, proposers chose between the two trays, each of which contained foods for them and their partner (neither chimpanzee could reach their partner's food). After the proposer chose one option, by pulling the corresponding tray within reach of the responder, the responder could choose whether or not to accept the offer by pulling the tray in such a way that both the proposer and the responder could access their rewards. In this study, proposers consistently chose the larger outcome for themselves and responders accepted virtually any offer (Jensen et al., 2007). However, responders accepted more than half of zero offers (i.e., they received nothing themselves), indicating that they may not have understood the task. A subsequent study showed that human responders rarely refused in a similar situation, possibly because of the difficulty of inhibitory responses

(Smith and Silberberg, 2010), indicating that the deviation from behavior typically seen in the UG could have been attributable to the experimental design rather than a species difference.

In a more recent study (Proctor et al., 2013), subjects were trained that one token represented an equal 3/3 split of six food items, whereas the other represented a 5/1 split of the foods in favor of the proposer. Proposers could choose a token and pass it to the responder, who could then trade it out to the experimenter (accepting the proposal) or not (refusing it). Proposers' choices in the UG were compared with those in a DG-like condition in which the responder was present but had no recourse (proposers passed the chosen token directly back to the experimenter). The procedure was repeated using children paired with another familiar individual from their daycare class to ensure that humans would respond similarly to chimpanzees in this procedure.

Despite responders never refusing offers, all chimpanzee proposers' choices shifted from preferring the more beneficial 5/1 token in the DG-like condition to preferring the equal 3/3 split in the UG condition. Validating the procedure, children responded in the same way. These results differ from typical UG results because neither the children nor the chimpanzees ever refused the low offer. However, in typical human UGs, responders are interacting with anonymous partners in a one-shot situation, and their only recourse is to refuse the offer. In this study, responders were interacting with individuals from their social group and had options besides refusal, such as punishment or the threat of punishment, which are less costly means of protest than refusing a positive, if relatively smaller, outcome (Milinski, 2013). Similarly, in typical UGs, proposers' refusals decrease when they are given other options, even in one-shot games [e.g., the responder can write a note to the proposer (Xiao and Houser, 2005)]. These results do not necessarily mean that the chimpanzees showed a sense of fairness, because if this were the case, they should have preferred the equal token in both the DG and the UG conditions. This also does not mean that proposers had prosocial motivations, because they may have changed their preference to avoid refusals by the responder. Nonetheless, both humans and chimpanzees were apparently sensitive to how their choices influenced their partner's decisions and changed their behavior accordingly.

The Impunity Game

Closely related to the UG is the Impunity Game (IG) (Fig. 11.2). The IG is similar to the UG, but if the responder refuses the proposer's offer, the responder gets nothing, whereas the proposer receives their portion of the allocation as indicated by the proposer (Bolton et al., 1998). This game

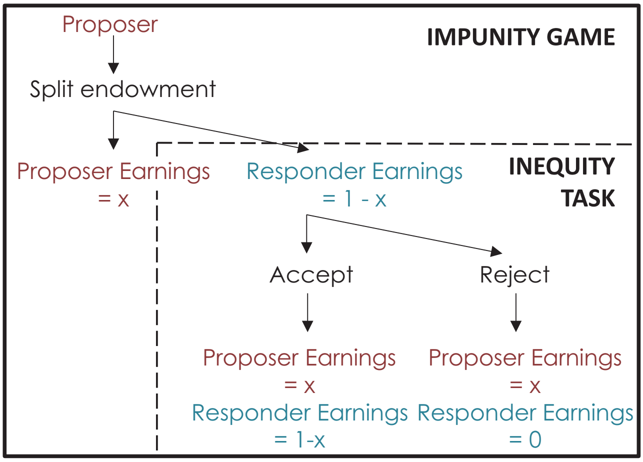


FIGURE 11.2 Schematic of the IG. The full IG has not yet been explored with other species; however, a typical inequity procedure is reminiscent of the responder's choice in the IG (indicated by the dashed line).

has received very little attention in the human literature. In part, this is due to the assumption that no rational responder would ever refuse an offer, because this action leaves them with both absolutely and relatively less than the proposer (in the UG, a refusal leaves the responder with absolutely less but relatively the same as the proposer). Nonetheless, in a study that used the same procedure for both games, human subjects refused in the IG about half as often as in the UG for a given distribution (Yamagishi et al., 2009).

Much as in the UG, the challenge of the IG with primates is assuring that the responders understand that their choice was constrained by the actions of the proposer. Most studies of primates to date have explored only responses to unequal distributions, to learn how individuals respond to inequity when they cannot alter their partner's outcomes [reviewed in Price and Brosnan (2012)]. In a typical experiment, paired subjects alternate completing a task (such as exchanging a token) with a human experimenter. The experimenter rewards subjects with the same rewards (Equity condition) or gives one a more preferred reward (Inequity condition). To rule out the possibility of contrast effects (Reynolds, 1961; Roma et al., 2006), in which subjects compare their outcomes to those present in the environment without attending to the social component, pairs are given a Contrast condition, in which both partners are shown the preferred reward but, after completing the task, receive the less-preferred one (Brosnan et al., 2010b; Talbot et al., 2011). These responses are referred to as Inequity and Equity rather than Inequality and Equality because, despite the fact that the outcomes are identical (or not), we cannot know whether they are perceived identically by subjects because of differences in rank, hunger level, etc.

Initial studies confirmed that both capuchin monkeys (Brosnan and de Waal, 2003; van Wolkenten et al., 2007; Fletcher, 2008) and chimpanzees (Brosnan et al., 2005, 2010b) were more likely to refuse to complete the interaction (e.g., return the token or accept the subsequent food reward) in the Inequity condition compared with either the Equity condition or the Contrast condition, although there was variation within and between studies [discussed below in more detail (Brosnan et al., 2005; Bräuer et al., 2009; Silberberg et al., 2009)]. Because humans refuse more frequently in situations in which they do not like the outcome (e.g., in the UG game), this similar behavior in other species has been interpreted as responding negatively to inequitable outcomes. The response is also sensitive to context, with refusals occurring only after subjects have completed a task but not when rewards are simply handed out for "free" (Bräuer et al., 2006; Roma et al., 2006; Dindo and de Waal, 2007; Neiworth et al., 2009; Silberberg et al., 2009). Despite this, subjects do not change their rate of refusal when they have to work harder than a partner to achieve their reward [Fontenot et al. (2007), but see Takimoto and Fujita (2011) for a response to effort using a different paradigm]. This indicates that although subjects are sensitive to inequity in the context of joint action, it is the difference in outcome rather than effort that is important for their decision making. This may indicate that subjects are more sensitive to distributional inequities than procedural ones.

Demographic variables also influence individuals' responses, but not always in consistent ways. For instance, not all studies find a dominance effect, although for those that do, dominant individuals always respond more strongly than do subordinates, presumably because they are more accustomed to receiving higher-valued rewards (Bräuer et al., 2009; Brosnan et al., 2010b). There are also no consistent sex differences (Brosnan et al., 2005, 2010b), possibly because of relatively small sample sizes (although several dozen chimpanzees have been tested across three facilities, a large sample for captive primate studies, this is a very small sample size for untangling individual variation). The degree to which individual differences influence behavior—both in nonhuman and human primates—is a topic that requires additional exploration.

Finally, not all primate species refuse in conditions of inequity. The same procedure to elicit inequity has now been used to test seven primate species, and similar procedures have been used with several others (Table 11.1). Comparing these different species' responses allows us to consider which social or environmental factors may have played a role in shap-

TABLE 11.1 Summary of Inequity Studies by Species, Including Whether Inequity Aversion Has Been Found with Different Methods and the Influence of Effort and Social Context

		Task Used/Results			Effects of . . .	
Species	Respond to Inequity?	Exchange	Other Task	No Task	Effort?	Social Context?
Chimpanzee	Yes	Yes (Brosnan et al., 2005, 2010b; Bräuer et al., 2009)	—	No (Bräuer et al., 2006)	No (Brosnan et al., 2010b)	Social closeness (Brosnan et al., 2005) Sex (Brosnan et al., 2010b) Rank (Bräuer et al., 2006; Brosnan SF et al., 2010b)
Bonobo	Possibly	Trend toward yes (Bräuer et al., 2009)	—	No (Bräuer et al., 2006)	—	—
Gorilla	Yes	—	—	No (Bräuer et al., 2006)	—	Social play (van Leeuwen et al., 2011)
Orangutan	No	No (Bräuer et al., 2009; Brosnan et al., 2011)	—	No (Bräuer et al., 2006)	—	—

Macaque	Yes	Yes (Hopper et al., 2013)	Yes (Massen et al., 2012)	—	Yes (Massen et al., 2012)	Rank (Massen et al., 2012) Social relationship (Massen et al., 2012) Ontogeny (Hopper et al., 2013)
Capuchin	Yes	Yes (Brosnan and de Waal, 2003; van Wolkenten et al., 2007)	Yes (Fletcher, 2008; Brosnan et al., 2010a; Takimoto et al., 2010)	No (Roma et al., 2006; Dindo and de Waal, 2007)	Yes (Takimoto and Fujita, 2011)	Rank (Takimoto et al., 2010)
		No (Fontenot et al., 2007; Silberberg et al., 2009)			No (Fontenot et al., 2007; van Wolkenten et al., 2007)	
Squirrel monkey	No	No (Talbot et al., 2011)	—	—	—	—
Tamarin	No	No (Neiworth et al., 2009)	—	—	—	—
Marmoset	No	No (Freeman et al., 2013)	—	—	—	—
Owl monkey	No	No (Freeman et al., 2013)	—	—	—	—

NOTE: Dashes indicate that no study has yet been done on the topic.

SOURCE: Adapted from Price and Brosnan (2012) with permission from Springer Science+Business Media B.V.

ing the evolution of the response. Although more species will need to be tested to verify these conclusions, patterns are emerging. For instance, responding negatively to inequity is not a homology within the primates. Among the great apes, bonobos may respond similarly to chimpanzees and humans, indicating that the last common ancestor of *Pan* and *Homo* shared this behavior. Only five bonobos have been tested, making statistical analyses difficult; however, their refusal rates doubled from 10 to 20 percent in the Inequity compared with the Equity condition (Bräuer et al., 2009). On the other hand, orangutans showed no response to inequity (Bräuer et al., 2009; Brosnan SF et al., 2011), eliminating the possibility of a homology within the great apes. Additionally, the behavior is not a homology within the New World monkeys, because of the five New World monkeys tested, only capuchins responded differently to the Inequity condition. The orangutan's behavior also rules out the possibility that this is related to increased brain size or advanced cognitive capabilities, because orangutans have a brain-to-body ratio and cognitive skills similar to the other great apes.

Thus far, negative response to inequity correlates positively with whether a species cooperates routinely with nonkin [reviewed in Brosnan (2011)] (Fig. 11.3). Chimpanzees, bonobos, and capuchin monkeys cooperate with nonkin, for instance in coalitions and alliances, and all three species responded to inequity in these experiments. Macaques, too, both responded negatively to inequity (Massen et al., 2012; Hopper et al., 2013) and showed cooperation in the form of coalitions and alliances (Maestripieri, 2007). However, in squirrel monkeys, a species confamilial (and sympatric) with capuchins but lacking extensive social cooperation, males responded more strongly to the Contrast condition than either the Inequity or Equity conditions, indicating that their reactions were more strongly influenced by their previous offers than by rewards received by another monkey (Talbot et al., 2011). Again considering orangutans, one way in which they differ from chimpanzees and bonobos is their relative lack of social cooperation. A potential challeng to this hypothesis arises with the species that show biparental care. These species cooperate extensively, working together to raise offspring, but thus far there is no indication that such species respond negatively to inequity in this experimental paradigm (Neiworth et al., 2009; Freeman et al., 2013). However, the proposed function of responding to inequity is to judge the value of cooperative partners to determine whether to search for a new partner. It is very costly to find a new pair mate, so it is possible that even if individuals in biparental care species do notice inequities, they have evolved to respond only to very costly inequities, which do not include receiving a less-preferred reward than their mated partner.

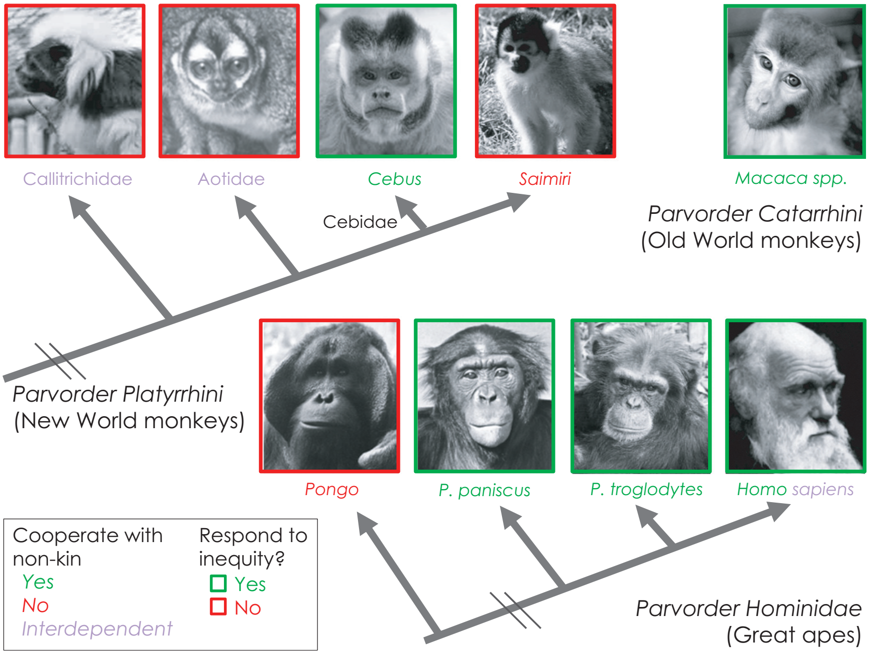


FIGURE 11.3 Schematic diagram indicating the responses to inequity of species that have been tested using the typical inequity procedure in which subjects exchange tokens for rewards while sitting next to a partner. The photos representing species that show a negative response to inequity in this task are outlined in green, and those that do not are outlined in red. The names of species that show extensive social cooperation, such as coalitions and alliances, are in green, those that do not are in red, and interdependent species (e.g., those that show biparental care) are in violet. Humans show both extensive social cooperation and biparental care. Note that this diagram excludes gorillas, for whom too little information is known. The photographs of the macaque and bonobo are by F. B. M. de Waal. The photograph of the orangutan is by C. Talbot. The photograph of Darwin is from the public domain. All other photographs are by the author. [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

Related to this, subjects should be more sensitive to inequity when forming a relationship, which is a time when the costs of finding a new partner are less, than after the relationship is established and there is joint investment in offspring (Brosnan, 2011). One drawback to our understanding of human behavior is that most studies to date have involved unrelated individuals, mostly strangers, virtually always in conditions of anonymity, and often without repeated interactions, which removes the possibility of reputations forming. Although these conditions are informative for exploring the degree to which humans will cooperate without either a relationship or social knowledge, this is not as informative for telling us about typical human cooperative behaviors, which primarily take place within established relationships with known partners. Additional experiments that explore differences in behavior in the context of different social relationships and with different degrees of anonymity will be essential to understand how inequity functions in the context of the relationship.

Prosocial Games

Despite children's calls of "that's not fair" when they receive a less-preferred outcome than another child, responding negatively to receiving less than one's partner is only one part of a sense of fairness. A sense of fairness or justice requires responding not only to inequities that affect oneself but also to those that affect others (Hatfield et al., 1978; Fehr and Schmidt, 1999). In other species, this has most commonly been experimentally explored using procedures reminiscent of the Dictator Game. In the typical experimental game with primates, the subject has the option to provide rewards, or not, to a social partner. Importantly, the subject's behavior when the subject is with a social partner is compared with their behavior when alone, ruling out the possibility that they are choosing the prosocial option because there are a greater number of rewards visible than in the nonprosocial option. The critical difference between these games and the DG is that choosing to reward the partner does not reduce the subject's own payoffs in these prosocial games; thus, there are no disincentives for prosocial behavior.

Although reward structures have varied across experiments, making direct comparisons difficult, a sufficient number of these studies exist that patterns are emerging. Chimpanzees choose to provide rewards to their partners in some experiments (Horner et al., 2011) but not others (Silk et al., 2005; Jensen et al., 2006), and it is not yet clear which features lead to prosocial behavior in this ape. It is also not clear that these results are reflective of chimpanzees' prosocial tendencies. Results in the inequity studies described above imply that chimpanzees may recognize when they receive a better outcome than a partner even when they chose not to act to change the situation. In one study, subjects sometimes refused preferred rewards when their partners got less-preferred ones and did so at greater rates than when both received preferred rewards (Brosnan et al., 2010b). This does not mean that the subject's motivations were prosocial, because the subject may have feared the partner's reaction to receiving a less-preferred reward than the subject, but these results verify that chimpanzees recognized when they received better outcomes than a partner.

Among the monkeys, capuchin monkeys preferentially chose the prosocial option (de Waal et al., 2008; Lakshminarayanan and Santos, 2008) and were more likely to reward kin than either nonkin group mates or nongroup mates (de Waal et al., 2008). Callithrichids, one of the taxa that show biparental care, also chose the prosocial option that rewarded a group mate (Burkart et al., 2007; Cronin et al., 2010), although like the chimpanzees, they did not do so in all experiments (Cronin et al., 2009). Finally, long-tailed macaques also showed prosocial behavior, but in this study, dominants chose the prosocial option, whereas subordinates did not (Massen et al., 2010). Again, these studies measured behavior, not motivations, so they cannot shed light on why the monkeys behaved prosocially (i.e., they cannot disentangle whether subjects were prosocially motivated to help their partners or were selfishly motivated to avoid repercussions for not helping their partners). Nonetheless, although there is still debate about the contexts under which each of these species shows prosocial behavior and the selective pressures underpinning it, in some circumstances, all of the primates tested thus far actively chose an outcome that benefited a partner as well as themselves.

Species-Specific Approaches to Justice and Fairness Inequity in the Context of Cooperation

If responding to inequity is a mechanism for identifying good cooperative partners, then inequity should influence behavior when cooperation is required. This can be experimentally explored by introducing inequity into an experimental cooperation paradigm. Capuchin monkeys have been studied extensively in the realm of cooperation, and there is evidence that they understand the contingencies of cooperative tasks and are sensitive to their partner's behavior [reviewed in Brosnan (2010)]. In the first study to explore cooperation in a situation of inequity, capuchin monkeys could work together to pull in a heavy tray to obtain food, but only one monkey got the food. Monkeys worked together, but only if the individual who received the food shared with the individual who did not. Perhaps anticipating this, the monkey who got the food was more likely to share in this condition than in a control condition in which they could acquire the food without their partner's help. This indicates a sensitivity to their partner's reaction and an anticipation of their need for their partner's help (de Waal and Berger, 2000).

In a study more explicitly exploring inequity and cooperation, monkeys were tested in a similar paradigm in which both monkeys always received food, but these foods differed in the degree to which the monkeys preferred them. Thus, sometimes both monkeys received the (same) preferred food, sometimes they received the (same) less-preferred food, and sometimes one received the preferred food, whereas the other received the less-preferred food. The monkeys were not separated nor were their roles predetermined by the experimenter, so in all cases, the monkeys had to negotiate between themselves who would pull from which location, which also determined who got which food item. The pair's pulling success was not dependent upon the value of the rewards; pairs pulled in the tray just as often for two identical rewards as for two different ones. Instead, the monkeys were sensitive to their partner's behavior. In some partnerships, individuals shared access to the more preferred reward when the rewards differed, each receiving it approximately half of the time. In these partnerships, cooperative pulling success was high (~70 percent) in all three conditions. On the other hand, for partnerships in which one member dominated the preferred reward in the different-reward condition, they succeeded in pulling in the tray only about 30 percent of the time across all three conditions (Brosnan et al., 2006).

These results show two important things. First, subjects in the inequitable partnerships apparently reacted against their partner, not the reward distribution. That is, when one member dominated the preferred reward in the different-reward condition, pulling rates dropped across all conditions, even the two conditions in which both monkeys got the same reward. This supports the hypothesis that recognizing inequity helps to identify cooperative partnerships, because these subjects refused to work with a specific partner rather than refusing a certain outcome. Second, in the partnerships in which neither individual dominated the preferred rewards, subjects were, by definition, receiving the less-preferred reward on half of all different-reward trials, and yet cooperation was maintained. The reality of cooperation is that it is unlikely that every individual will receive the same reward on every trial, and these results indicate that capuchins are somehow able to extrapolate across multiple trials and therefore reap the gains of cooperation despite variation in outcome.

Inequity in Interactions with the Experimenter

Although the above data relate to primates' rewards in comparison with each other, how do primates react toward the experimenter who caused the inequity? A recent study explored which of two novel experimenters the monkeys preferred to interact with in a task in which the monkey returned a token to an experimenter to get a food reward. Subjects first gained experience with both experimenters, one of whom consistently provided the offered rewards and one of whom failed to provide the offered reward (or any reward) on up to 50 percent of trials.

When the monkeys then had free choice as to which experimenter they would return the token to, subjects were equally likely to interact with both experimenters (Brosnan and de Waal, 2009). Although it may be that capuchin monkeys do not form preferences for experimenters based on reliability [they do show preferences between experimenters in other situations (Paukner et al., 2009)], it is also possible that the relationship between humans and captive nonhuman primates influenced the results. Despite the fact that subjects in Brosnan and de Waal (2009) had never interacted with the experimenters who participated in the study (novel experimenters were used for each condition), they did have extensive experience with experimenters in general, as well as with trials in which rewards were not given (e.g., because of incorrect responses). Thus, they may have responded to this situation by trying to "correct" their response, rather than recognizing the experimenter′s unreliability. Pet dogs, who may have a different relationship with humans, do discriminate between human experimenters in a similar task (Horowitz, 2012).

Inequity in Social Interactions

Some of the best evidence in favor of a sense of justice or a sense of fairness comes from observational studies of nonhuman primates' interactions during their natural behavior. These interactions also offer the opportunity to look beyond distributional equity. Unfortunately, in many cases, these events are extremely rare, making it difficult to make strong statements about these behaviors. Moreover, observational work yields correlations, which cannot tell us causation without controlled studies that alter one variable at a time. Nonetheless, these situations may be the best window we have into primates' sense of fairness and justice because they are natural interactions, unconstrained by interactions with humans or experimental contingencies.

Chimpanzees display a sense of "social regularity" that has been linked to the human sense of justice (de Waal, 1991). Chimpanzees appear to have expectations about others' behavior and are known to express frustration, sometimes aggressively, when these expectations are violated. Moreover, such responses are not limited to the apes. Apes and monkeys both engage in policing behavior in which individuals, typically the highest-ranking males, intervene in fights to maintain group stability. Some of the best evidence for the utility of policing behavior comes from studies done with macaques. In these studies, the group's behavior was compared on typical days and those in which the highest ranking males were removed. Results demonstrated the males' necessity in stabilizing the group's interactions (Flack et al., 2005, 2006). Similarly, both macaque and chimpanzee males, once they have established high status, will intervene in fights on the side of the loser (de Waal, 1978; Watanabe, 2001). Although there are many potential reasons for such behavior, it again indicates that these males recognized social inequalities in others' interactions and were willing to act against their own short-term self-interest to rectify them. Of course, in the longer term, maintaining group stability always benefits a high-ranking male, and a physical intervention may additionally emphasize his power to others in his group. Nonetheless, there are short-term costs to entering into any fight, particularly in favor of an individual who is losing.

Recently, inequity has also been linked with play fighting in gorillas. Gorillas who gained the upper hand during a bout of play fighting worked to maintain it, possibly indicating that they were aware of the social dynamics and strove to maintain their competitive advantage (van Leeuwen et al., 2011). The authors emphasized the benefit of studying inequity in a natural social context and considered how responses to inequities may vary depending on whether the individual in question has the social advantage. Again, for practical experimental reasons, much work focuses on inequity of food rewards, but attention to inequity may have evolved in the social realm and only more recently adapted to physical outcomes, such as food. Future work will help to determine how responses to inequity vary depending upon the commodity in question.

INEQUITY AND RELATED BEHAVIORS

Inequity likely interacts with other behaviors, although, thus far, there have been few studies to explore these interactions.

Punishment

Recognizing inequity is only one of several behaviors that likely underpin cooperation. Punishment may also support cooperation. Cleaner fish, which cooperate with nonkin during the cleaning interaction, do not respond to inequity of rewards compared with a social partner (Raihani et al., 2012). However, the fish do punish one another for acting against the pair's interests (Raihani et al., 2010). Thus, it may be that in species or situations in which finding a new partner would be difficult or costly, punishment to change the current partner's behavior is used in lieu of finding a new partner (Raihani and McAuliffe, 2012).

Inequity and Contrast Effects

It seems likely that responses to inequity share cognitive mechanisms with behaviors such as loss aversion and contrast effects, both of which involve reactions to unexpectedly lesser outcomes. These are rather difficult to untangle experimentally, given that inequity is essentially a contrast effect with another's outcome as the referent (similarly, inequity is a loss with another's outcome as the referent). However, we can compare the relative strengths of these motivations using well-designed experiments. For instance, whereas some species (e.g., chimpanzees and capuchin monkeys) were more sensitive to inequity with one's partner than to contrast with previously offered outcomes, others (e.g., squirrel monkeys) showed the reverse. Mapping such preferences may help to determine the underlying influences on the expression of these behaviors, providing insight into the relative strength of social and nonsocial environmental stimuli on a species' decision making.

FUTURE DIRECTIONS AND CONCLUSIONS

Although in the previous decade we have learned much about nonhuman primates' responses to inequity, there remains much to learn. First and foremost, humans are primates, which makes nonhuman primates a natural group for comparison, yet other species also respond to inequity (Range et al., 2009; Horowitz, 2012; Raihani et al., 2012; Wascher and Bugnyar, 2013). More work is needed to identify which species respond to inequity, whether these responses are similar across species, and the nature of individual differences in response in these species. This will also provide a stronger test of the hypothesis that inequity responses correlate with cooperation.

Another important area of inquiry is distinguishing situations in which nonhuman species notice versus respond to inequity. All of the studies described above focus on behavioral responses to differing outcomes, but subjects may notice an inequitable situation that they do not respond to, for instance, because they are unable to inhibit their desire for the reward, because of social pressure, or for other reasons not yet known. One way to address this question is to explore changes in individuals' affect across different conditions to identify responses that occur in the absence of an overt behavioral change. This approach has been successful in identifying recognition of inequity in young children (LoBue et al., 2009).

Inequity also occurs in a variety of contexts that are not yet reflected in the nonhuman literature because of the focus on distributional concerns in experimental tests. One major focus of human research that has received little attention in the nonhuman literature is procedural inequity (Skitka, 2012). Although preliminary investigations reveal no change in subjects' behavior based on procedural variations (Brosnan et al., 2010b), nonhuman primates have expectations about others' behaviors and it is reasonable to assume that they are sensitive to procedural differences in some contexts.

All of the experimental work to date has involved an egocentric approach to fairness and justice, yet observational studies of natural behavior indicate that primates will intervene in the interactions of others, in some cases impartially. Although challenging, it is possible to study fairness in the laboratory removed from egocentric reactions. Experimental studies on reputation in chimpanzees indicates that these apes are able to form opinions about human experimenters from watching these experimenters interact with other chimpanzees (Subiaul et al., 2008). A fruitful line of inquiry would be to explore nonhuman primates' judgments of the equity of others' interactions. Such third-party assessments of others' distributions would be the first research to experimentally examine justice in other species.

Finally, studies of justice and fairness will advance significantly when work from the laboratory is combined with what we know about animals' natural behaviors in the wild (Janson and Brosna, 2013). In this way, we will better understand the social and ecological conditions under which these preferences manifest, which lends additional insight into their function. Additionally, combining these behavioral studies with what we know about cognition may yield insights into these behaviors, such as the overlap between inequity and delay of gratification (Price and Brosnan, 2012).

Humans are not alone in responding negatively to differential treatment as compared with a partner. This response is shared with other species and appears to be instrumental in successful cooperation. Understanding the evolution of this response provides insight into our own behavior. Although nonhuman primates do not show a sense of justice or fairness in the same way as humans do, gaining knowledge about the evolution of justice and fairness from comparative studies will improve our understanding of these judgments in humans as well as in other animals.

ACKNOWLEDGMENTS

I thank L. Salwiczek for helpful comments on an earlier draft of this manuscript. Funding was provided by National Science Foundation (NSF) Faculty Early Career Development Award SES 0847351 and NSF Grant SES 1123897.

12

Powering Up with Indirect Reciprocity in a Large-Scale Field Experiment

EREZ YOELI,[*] MOSHE HOFFMAN,[†‡] DAVID G. RAND,[‡§]
AND MARTIN A. NOWAK[‡‖#**]

A defining aspect of human cooperation is the use of sophisticated indirect reciprocity. We observe others, talk about others, and act accordingly. We help those who help others, and we cooperate expecting that others will cooperate in return. Indirect reciprocity is based on reputation, which spreads by communication. A crucial aspect of indirect reciprocity is observability: reputation effects can support cooperation as long as peoples' actions can be observed by others. In evolutionary models of indirect reciprocity, natural selection favors cooperation when observability is sufficiently high. Complementing this theoretical work are experiments where observability promotes cooperation among small groups playing games in the laboratory. Until now, however, there has been little evidence of observability's power to promote large-scale cooperation in real-world settings. Here we provide such evidence using a field study involving 2,413 subjects. We collaborated with a utility company to study participation in a program designed to prevent blackouts. We show that observability triples participation in this public goods game. The effect is nearly seven times larger than offering a $25 monetary incentive, the com-

---

[*] Federal Trade Commission, Washington, DC 20580; [†] Department of Computer Science and Engineering, University of California at San Diego, La Jolla, CA 92093; [‡] Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138; [§] Department of Psychology, Yale University, New Haven, CT 06520; and Departments of [‖] Mathematics and [#] Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138. [**] To whom correspondence should be addressed. E-mail: martin_nowak@harvard.edu.

pany's previous policy. Furthermore, as predicted by indirect reciprocity, we provide evidence that reputational concerns are driving our observability effect. In sum, we show how indirect reciprocity can be harnessed to increase cooperation in a relevant, real-world public goods game.

Cooperation occurs when we take on costs to benefit the greater good. By this definition, everyone is better off when everyone cooperates, but self-interest undermines cooperation and leads to free-riding. Promoting cooperation is a central challenge for human societies, both today and over our evolutionary history (Hardin, 1968; Axelrod, 1984; Ostrom, 1990; Levin, 2006; Helbing and Yu, 2009; Walker et al., 2009; Sigmund, 2010; Nowak and Highfield, 2011; Oakley et al., 2011; Churchland, 2012). There are five mechanisms for the evolution of cooperation (Nowak, 2006b): direct and indirect reciprocity, spatial selection, group selection, and kin selection. Each of these mechanisms is an interaction structure that can lead cooperators to outperform noncooperators, and therefore be favored by selection.

Direct and indirect reciprocity involve repeated interactions, creating future consequences for one's actions: it can pay to cooperate today to receive cooperation from others tomorrow. Spatial selection occurs when players' interactions are structured rather than occurring at random. As a result, cooperators may be more likely to interact with other cooperators and thus preferentially receive the benefits of cooperation. Spatial selection operates when cooperaters cluster in physical space, on social networks, in sets, or in phenotype space (Nowak et al., 2010). Group selection (or multilevel selection) occurs when competition and reproduction happen at multiple levels: not only do players compete with others in their group, but groups compete with each other. If cooperative groups outcompete noncooperative groups, then group-level selection can favor the evolution of cooperation. Finally, kin selection may be defined as preferring to cooperate with those who are closely related. Kin recognition can allow players to cooperate with close genetic relatives and defect otherwise.

Most of the literature on the evolution of cooperation uses the Prisoner's Dilemma and related frameworks: players can pay a cost to give a greater benefit to one or more others. Thus, within the context of these games, cooperation is good for everyone. However, cooperation need not be good for everyone more generally (Oakley et al., 2011; Dasgupta, 2012). There are situations in which cooperating may give a benefit to some, but impose costs on others. For example, in intergroup conflict and war, people cooperate with members of their own group in an attempt to harm members of other groups (Choi and Bowles, 2007).

Or in the context of markets, companies may collude to keep prices high, benefiting each other but harming consumers (Carlton and Perloff, 1994). The five mechanisms for the evolution of cooperation may promote both total welfare-enhancing cooperation, as well as these more pernicious forms of cooperation.

All of these mechanisms are relevant for the evolution of human cooperation, but direct reciprocity and indirect reciprocity occupy a central place: most of our key interactions are repeated and reputation is usually at stake. Direct reciprocity is based on repeated encounters between the same two individuals: my behavior toward you depends on what you have done to me. Indirect reciprocity is based on repeated encounters in a group of individuals: my behavior toward you also depends on what you have done to others (Fig. 12.1). We take a keen interest in who does what to whom and why, which requires sophisticated social intelligence. We talk to each other about others. As David Haig said: "For direct reciprocity you need a face, for indirect reciprocity you need a name" (Nowak and Highfield, 2011). The evolution of indirect reciprocity is linked to the evolution of human language. Supported by human language, reputation systems allow us to track the good and bad behavior of others and to use this information to incentivize cooperation. Whatever is specifically human about our mental machinery is derivative of human language, social intelligence, and thus indirect reciprocity (Cela-Conde and Ayala, 2007; Nowak and Highfield, 2011).

The evolution of cooperation via indirect reciprocity has been a topic of great interest in recent years. Mathematical models and computer simulations have demonstrated the power of indirect reciprocity for promoting cooperative behavior (Kandori, 1992; Nowak and Sigmund, 1998a,b, 2005; Nowak, 2000; Leimar and Hammerstein, 2001; Panchanathan and Boyd, 2003, 2004; Ohtsuki and Iwasa, 2004, 2006, 2007; Brandt and Sigmund, 2006; Pacheco et al., 2006; Masuda and Ohtsuki, 2007; Suzuki and Akiyama, 2007a,b; Fu et al., 2008; Ohtsuki et al., 2009; Uchida and Sigmund, 2010; Berger, 2011; Nakamura and Masuda, 2011; Manapat and Rand, 2012; Manapat et al., 2013; Mani et al., 2013). In these models, players typically engage in a series of one-shot interactions with others selected at random from the population. In some of those interactions, players' previous decisions are observable by their partners. Observability allows players to use conditional strategies that base their actions on the partner's behavior in the past. When past actions are sufficiently observable, natural selection can favor strategies that cooperate as long as the partner has behaved well in the past. What constitutes "good" behavior worthy of receiving cooperation depends on the social norm. A simple social norm is called "image scoring" and prescribes cooperating with those who have cooperated in sufficiently many previous interactions (Nowak and Sigmund,

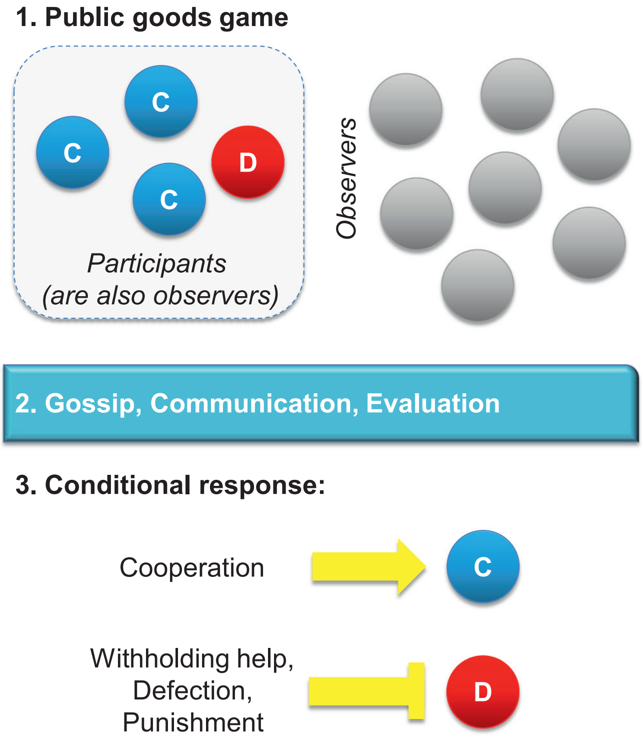


FIGURE 12.1 Indirect reciprocity can support contributions to public goods, as depicted here. In indirect reciprocity, my behavior toward you depends on how you have behaved toward both me and others. This process occurs in three stages. First, people engage in a public goods game (C = cooperators and D = defectors). Peoples' behavior is observed, both by other players and third parties. Second, information about this behavior can spread from person to person. Based on the information received, peoples' opinions about the players are updated. Third, as a result, public goods cooperators will receive cooperation in future interactions whereas defectors will be denied cooperation, defected upon, or punished. Thus, indirect reciprocity creates an incentive to contribute to public goods and can promote the evolution of cooperation.

1998a). More complicated norms also take into account the behavior of the partner's previous partners. For example, under the "standing" norm, players can maintain their good reputation by defecting against those with bad reputation (Ohtsuki and Iwasa, 2006). The many models of indirect reciprocity differ in their details, yet across a wide range of assumptions, making previous decisions observable allows cooperators to selectively target their cooperation at other cooperators and withhold cooperation from defectors. Thus, free-riders are at a disadvantage, and cooperation can spread.

This body of theoretical work is supported by behavioral experiments where subjects play economic games in the laboratory. People are substantially more cooperative when their decisions are observable and when others can respond accordingly (Wedekind and Milinski, 2000; Milinski et al., 2001, 2002a,b; Wedekind and Braithwaite, 2002; Andreoni and Petrie, 2004; List et al., 2004; Rege and Telle, 2004; Bolton et al., 2005; Semmann et al., 2005; Rockenbach and Milinski, 2006; Seinen and Schram, 2006; Tadelis, 2007; Linardi and McConnell 2008; Andreoni and Bernheim, 2009; Rand et al., 2009; Ule et al., 2009; Jacquet et al., 2011; Pfeiffer et al., 2012; Choi and Ahn, 2013). Subjects understand that having a good reputation is valuable in these settings (Pfeiffer et al., 2012) and so are willing to pay the cost of cooperation. Observability particularly increases cooperation when the prosocial nature of the cooperative choice is made salient (Rege and Telle, 2004; Kossmeier et al., 2009). Moreover, experimental evidence indicates that indirect reciprocity is deeply entrenched in human psychology: subtle cues of observability have large effects on cooperation levels (Haley and Fessler, 2005; Burnham and Hare, 2007; Ernest-Jones et al., 2011; Powell et al., 2012), and our initial impulse to cooperate in one-shot anonymous settings (Cornelissen et al., 2011; Rand et al., 2012, 2013; Schulz et al., in press) is likely the result of adaptation in a world dominated by reputational concerns (Rand et al., 2012, 2013).

These laboratory experiments are extremely valuable. They generate powerful insights into human psychology and provide clear evidence for the importance of indirect reciprocity. To do so, however, they typically use abstract economic games and involve the interaction of only a handful of subjects. Thus, the question of whether observability affects large-scale cooperation in real-world settings outside of the laboratory remains largely unexplored [exceptions include Lacetera and Macis (2010), Ashraf et al. (2012), and Karlan and McConnell (2012)]. The extent to which findings from theory and the laboratory generalize to natural field settings is of great importance, both for scientific understanding and for public policy (Levitt and List, 2007).

Here, we address this question by running a large-scale field experiment on the effect of observability in a public goods game (PGG). We collaborated with a major electric utility company to enroll consumers in a “demand response” program. This program is designed to help prevent blackouts by reducing excessive use of air conditioning during periods of high electricity demand. The cost of electricity production can spike hundredsfold during demand peaks. However, the price consumers pay is typically constant across time. Thus, during peak periods, there is a dramatic mismatch between price and actual cost, leading to excessive energy use. This mismatch reduces grid reliability, drives up energy costs, increases the risk of blackouts, and harms the environment. In recent years, reducing excessive peak energy use has become a target of regulatory efforts to increase efficiency in the electricity industry.

Encouraging participation in demand response programs such as the one used in this study is the primary policy tool available for reducing peak energy use (U.S. Committee on Technology, 2011). Demand response programs are voluntary programs in which people allow their utility to remotely restrict their energy consumption during peak hours. To do so, the utility usually installs a remote switch in-line with the circuitry of an appliance such as a hot water heater or air conditioner. Estimates suggest that these voluntary programs could reduce the need to invest in additional generation capacity by at least 38 percent over the next two decades, generating cost savings of at least $129 billion (Chupka et al., 2008). Voluntary energy efficiency and demand response programs have been widely available for years, but participation is frustratingly low (Federal Energy Regulatory Commission, 2011). Demand response programs exemplify the public goods dilemma: participation helps reduce on-peak demand, benefiting all energy grid users, but energy consumers find participating inconvenient. Participation is socially optimal because the inconvenience is minimal for most individuals relative to the societal costs of a blackout.

To explore the effect of observability on this real-world public goods problem, we solicited residents of 15 homeowners associations (HOAs) to participate in a demand response program. Residents who volunteered for this program allowed the utility to install a device that remotely curbs their central air conditioners when necessary: on days with unusually high demand or in the case of an unexpected plant or transmission failure. Residents who volunteered therefore contributed to a public good by improving the stability of the electrical grid in all of California, at the cost of some personal inconvenience. We solicited volunteers by delivering mailers to residents and asking them to participate. Sign-up sheets were posted in a communal area near their home, usually by a shared mailbox kiosk. In our primary manipulation, we varied whether residents' neighbors could tell who had signed up for the program. We did so by varying whether the publicly posted sheets required residents to print their name and unit number (observable treatment) or only a code that does not reveal their identity (anonymous treatment).

RESULTS

We found that residents in the observable treatment are nearly three times as likely to participate in the demand response program as residents in the anonymous treatment (fraction of residents participating:

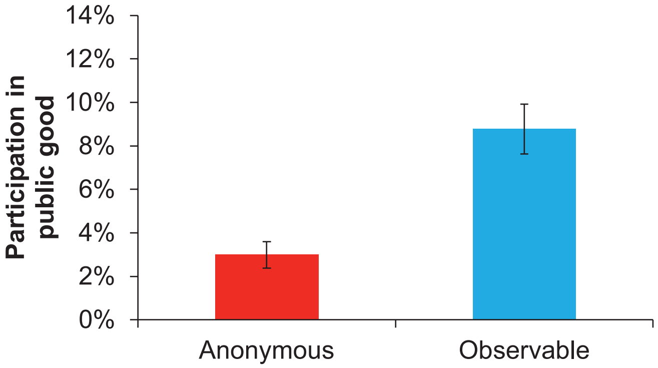


FIGURE 12.2 We solicited 1,408 customers of a major electric utility for participation in a program designed to prevent blackouts. Residents signed up for the program on sheets posted in a communal area near their home, usually by a shared mailbox kiosk. We varied whether residents' neighbors could tell who signed up for the program: publicly posted sheets required residents to print their name and unit number (observable treatment) or only a code that does not reveal their identity (anonymous treatment). Observability tripled participation in the program.

anonymous = 0.030, observable = 0.088, $P < 0.01$, $n = 1{,}408$; Fig. 12.2). All statistics presented are from probit regressions including various controls, with SEs clustered at the HOA level

The effect of the observable treatment was nearly seven times that of offering a $25 incentive (the estimated effect of the incentive is 0.009; a Wald test rejects that the coefficients on observability and the $25 incentive are identical, $P = 0.024$). This incentive was what the utility had used before the experiment, and they had previously argued the incentive would be far more effective than observability. In fact, this incentive appears to have been too small to be effective, and such small financial incentives are known to sometimes backfire (Gneezy and Rustichini, 2000). For the sake of comparison, we followed convention and estimated how large the financial incentive would have to be to achieve the same results if its effect is linear (Bertrand et al., 2010). We found that the utility would have had to offer an incentive of $174 to increase participation as much as our observable treatment.

We now explore the mechanism through which observability functions to increase participation. Indirect reciprocity theory is based on reputational concerns: when groups of people interact repeatedly and actions are observable, it becomes advantageous to be seen contributing to public goods. Based on this account, we predict that observability will have a greater effect among populations where ongoing relationships and reputations are expected to play a larger role. We evaluate this prediction in two ways.

First, we tested whether the effect of the observable treatment was greater in apartment buildings compared with row houses and individual homes. In apartment buildings, residents are more likely to interact with their neighbors in public spaces, and signup sheets were typically posted in especially conspicuous locations. Thus, indirect reciprocity theory predicts that observability will have a larger effect in apartment buildings. As shown in Fig. 12.3*A*, the results confirm this prediction: observability increased participation among those living in apartment buildings (fraction of residents participating: anonymous = 0.048, observable = 0.114, $P < 0.01$, $n = 582$), whereas it had little effect on the inhabitants of row houses or individual homes (fraction of residents participating: anonymous = 0.024, observable = 0.038, not significant, $n = 826$; yielding an estimated interaction of 0.052, $P = 0.04$).

Second, we tested whether observability had a larger effect among those who own their homes/apartments relative to those who rent. Renters are more transient and therefore likely to be less invested in relationships with their neighbors. Thus, indirect reciprocity theory predicts that observability will have a larger effect among owners. As shown in Fig. 12.3*B*, the results were again consistent with this prediction: observability dramatically increased participation among owners (fraction of residents participating: anonymous = 0.024, observable = 0.099, $P < 0.01$, $n = 1{,}015$) but had little effect on renters (fraction of residents participating: anonymous = 0.045, observable = 0.059, not significant, $n = 393$; yielding an estimated interaction of 0.046, $P < 0.01$).

Residents of apartment buildings and individual homes differ on any number of dimensions, as do those who own versus rent their homes. Thus, although the results are consistent with the predictions of the indirect reciprocity framework, alternative explanations of these results are possible. To partially address this issue, we ran the same analysis with additional controls such as Spanish language preference, ethnicity, missed payments, rebate use, and historical electrical use, and found even stronger results. Therefore, differences on these dimensions do not account for the differential effects of observability seen in Figs. 12.2 and 12.3.

Finally, we provide evidence that the effect of observability is unique to public goods. Not participating in the program should carry the threat of social sanctions only if participation is considered to be a public good. Therefore, indirect reciprocity theory predicts that observability should not increase participation among subjects who do not think of participa-

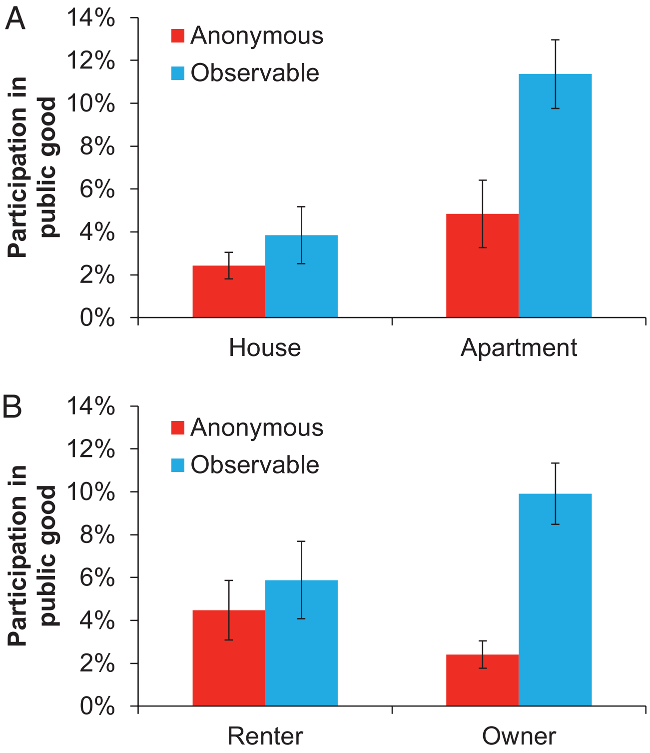


FIGURE 12.3 Observability increased participation more in settings where reputational concerns matter more. (*A*) Observability increased participation more in apartment buildings where residents are more likely to interact with their neighbors in public spaces and sign-up sheets were typically posted in especially conspicuous locations, compared with row houses or individual homes, where neighbors are less likely to interact and sign-up sheets were less easily visible by others. (*B*) Similarly, observability increased participation more among those who own their homes/apartments relative to those who rent because renters are more transient and therefore likely to be less invested in long-term relationships with their neighbors.

tion as a public good. To test this prediction, an additional 1,005 subjects received exactly the same treatment as described above, except that the mailers they received were stripped of any language that framed the demand response program as a public good. Consistent with our hypothesis, Fig. 12.4 shows that the effect of observability was reduced in this cohort (fraction of residents participating: anonymous = 0.061, observable = 0.086, not significant, n = 1,005; estimated interaction

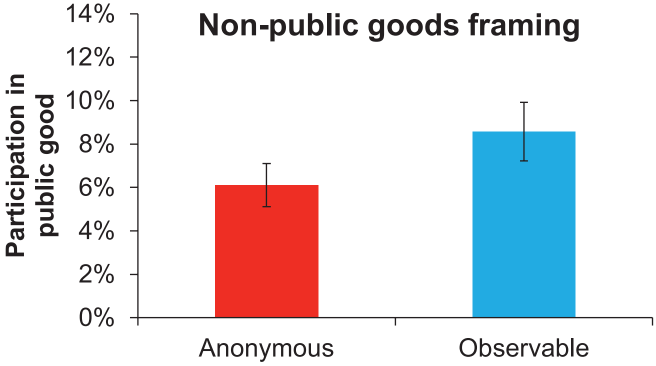


FIGURE 12.4 We solicited an additional 1,005 customers with exactly the same treatment as described earlier, except that the informational materials they received were stripped of any language that framed the blackout prevention program as a public good. The effect of observability was dramatically reduced among subjects who did not receive the public good framing.

between observability and the public good message in a pooled regression is 0.035, $P = 0.098$).

DISCUSSION

We have shown that indirect reciprocity promotes cooperation in a real-world public goods game affecting thousands of people. Making participation in the public good observable substantially increased sign-ups and did so significantly more than offering a cash incentive. Moreover, the effect of observability was larger in settings where individuals were more likely to have future interactions with those who observed them, and when participation was framed as a public good. These results provide evidence that reputational concerns were the driving force behind the effect of observability in our study.

Our study is part of a nascent literature exploring reputation and prosociality using field experiments. Consistent with our findings in the domain of energy efficiency, there is evidence that publicizing the names of donors increases the frequency of blood donation (Lacetera and Macis, 2010) as well as the level of giving to a college charity (Karlan and McConnell, 2012). Nonfinancial incentives involving reputation have also been shown to outperform monetary incentives in motivating the sale of condoms on behalf of a health organization in Namibia (Ashraf et al., 2012). Our work adds to these studies by directly manipulating observability, allowing a comparison with monetary incentives while avoiding other potential confounds present in previous experiments. We also test specific hypotheses generated by indirect reciprocity theory regarding when observability will and will not increase cooperation. Taken together, this body of work provides clear evidence that reputational incentives can be a powerful force for increasing cooperation in the field. Our paper in particular adds to efforts aimed at promoting energy conservation via nonfinancial incentives, such as providing people information about their own energy use and how it compares with the energy use of their neighbors (Minosi et al., 2003; Thompson, 2007; Ayres et al., 2009; Costa and Kahn, 2010).

A question arising from our study is the extent to which our subjects were conscious of their indirect reciprocity motives. One possibility is that they explicitly considered the reputational costs of not participating in the observable public goods treatment. Alternatively, they may have learned or evolved sensitivity to subtle cues that subconsciously increased their desire to participate when their decisions were observable, as has been shown in other settings (Haley and Fessler, 2005; Bateson et al., 2006; Burnham and Hare, 2007; Ernest-Jones et al., 2011). Perhaps the degree of "warm glow" they feel is sensitive to the degree of observability in their environment and the likelihood of interacting with observers in the future. Subsequent studies should further investigate this issue.

A related issue is the universality of reputation concerns. Observability can promote cooperation, but only in populations where the proper social norms are in place. For example, in a laboratory experiment in the United States, making public goods contributions observable by linking the PGG to a set of pairwise Prisoner's Dilemma games led to high contributions (Rand et al., 2009). However, when the same experiment was run using students in Romania, no such positive effects were observed because the Romanians did not sanction bad behavior in the PGG (Ellingsen et al., 2012). Similarly, providing feedback on how one's energy use compares with one's neighbors had reduced consumption among American liberals but may have had the opposite effect among conservatives (Costa and Kahn, 2010). Studying the interaction between norms and institutional policies is an important direction for future research.

In our experiment, the observability mechanism was designed so that participation was automatically displayed to all: because sign-up sheets were posted in public areas, no special effort was required by individuals to spread reputational information. Most indirect reciprocity models, however, rely on individuals communicating information about the observed actions of others (Nowak and Sigmund, 2005). Fortunately, we are more than happy to talk about how others have behaved: gossip is a central element of human communication (Dunbar et al., 1997;

Sommerfeld et al., 2007). However, why did we come to have this predilection for gossiping about the previous behavior of others? Why spend time and effort on evaluating others, and why give honest evaluations of competitors? Indirect reciprocity itself offers a potential answer: providing honest information or not is another game of cooperation and defection, which is also linked to reputation. Your reputation can be damaged not just by defection in the primary public goods game, but also by the distribution of incomplete or false information. Another important question involves large-scale reputation systems such as those used by the online market eBay (Resnick et al., 2006) or the business rating website Yelp (Luca, 2011): to what extent does our intrinsic desire to gossip extend to these more distributed settings? Why do people bother to leave evaluations, and how can secondary reputation systems be designed to encourage honest feedback? Exploring these issues is an important direction for further study.

Indirect reciprocity offers a powerful tool for promoting cooperation in contexts of great societal importance. Here, we offer quantitative evidence for one example: curbing electricity use during periods of high demand. However, this is just one of many such opportunities (Rand and Nowak, 2009; Lacetera and Macis, 2010; Ashraf et al., 2012; Karlan and McConnell, 2012). For example, people might be induced to drive more efficient cars if all vehicles bore a visible indication of fuel efficiency, perhaps via mandated color coding of license plates for the most efficient and most wasteful vehicles. Or home energy use might be reduced if utility companies made individuals' power use statistics publicly available. One might even apply this logic to scientific discovery: a measure of "scientific carbon efficiency" could be calculated by dividing an author's number of citations (or h-index) by the number of miles flown to attend conferences. Of course, privacy is an important issue that must be balanced against the benefits of reputational pressure. However, there are also indirect reciprocity applications that do not infringe on the privacy rights of individuals. For example, businesses might reduce their environmental impact if they were required to disclose the overall carbon footprint of their operations. Reputational concerns might discourage financial institutions from taking excessive risk because of changes in the price at which they have to borrow. Or government agencies might reduce waste if the relevant statistics were readily accessible to the public. Developing interventions that harness indirect reciprocity is a promising direction for future public policy initiatives.

METHODS

We administered the field experiment with the collaboration of the Pacific Gas and Electric Company (PG&E), a regulated utility that operates the majority of Northern California's retail residential electricity market. The experiment was incorporated into a routine marketing effort for a demand response program called SmartAC, which is designed to help prevent or shorten power interruptions by curbing demand from central air conditioners on days with unusually high demand, or in the case of an unexpected plant or transmission failure. The program is voluntary; subjects who participate contribute to a public good by contributing to the stability of the electrical grid in all of California, at the cost of some personal inconvenience and possibly some discomfort. The SmartAC switch is installed free-of-charge. At the time of the program, participants received a $25 check for signing up. The SmartAC program is a typical demand-side management, direct load control, or load shedding program.

Subjects in the field experiment were residential customers living in homeowners associations (HOAs) and one rental complex in Santa Clara County. We focused on tenants of HOAs because it was necessary to choose residences with public spaces where sign-up sheets could be posted. We focused on Santa Clara County because PG&E had not marketed in this area before the field experiment. Furthermore, Santa Clara County is hot enough that customers there were likely to have air conditioners, and dense enough to have a sufficient number of HOAs. Finally, we restricted the analysis to HOAs where all residents were known to have central air conditioning because central air conditioning was required to participate in the SmartAC program.

We invited subjects to participate in the program by sliding marketing materials under subjects' doors, placing them on their doorstep, or mailing materials to subjects. The materials included an informational letter describing the program and an instruction card that directed subjects to sign up for the program on sign-up sheets posted next to their mailboxes or in another central location. We left the sign-up sheets up for 3 to 10 days, depending on managers' preferences, the weather, and other conditions. After distributing the marketing materials, we removed the sign-up sheets, noted subjects' participation decisions, and provided the list of participants to PG&E's contractor for processing and installation. Note that subjects were not aware that they were participating in an experiment. This study is therefore classified as a natural field experiment (Harrison and List, 2004).

In the experiment's main treatment, we varied observability by varying the design of the sign-up sheets on which subjects register for the program: some sheets were designed so that subjects' identities were easily revealed to others who observed the sign-up sheet whereas others were designed to conceal subjects' identities. In the latter "anonymous'" design, the fields for subjects' names and apartment numbers were omitted from the sign-up sheet. Instead, subjects were identified only by their randomly generated personal code.

Simultaneously, we varied the design of the marketing materials along two dimensions. First, we varied whether the materials framed the decision to sign up as a contribution to a public good that would benefit others, or just as a new feature being offered by PG&E. Second, we varied whether subjects were offered a $25 incentive for signing up for the program.

ACKNOWLEDGMENTS

This research was partially funded by National Science Foundation Proposal 0752818, Russell Sage Foundation Award 980803, the Stigler Center for the Study of the Economy and the State's Energy Initiative, the University of Chicago Graduate School of Business, and the John Templeton Foundation. Any opinions expressed in this article are those of the authors and not of the Federal Trade Commission or any individual Commissioner.

13

From Perception to Pleasure: Music and Its Neural Substrates

ROBERT J. ZATORRE*‡ AND VALORIE N. SALIMPOOR*†

Music has existed in human societies since prehistory, perhaps because it allows expression and regulation of emotion and evokes pleasure. In this review, we present findings from cognitive neuroscience that bear on the question of how we get from perception of sound patterns to pleasurable responses. First, we identify some of the auditory cortical circuits that are responsible for encoding and storing tonal patterns and discuss evidence that cortical loops between auditory and frontal cortices are important for maintaining musical information in working memory and for the recognition of structural regularities in musical patterns, which then lead to expectancies. Second, we review evidence concerning the mesolimbic striatal system and its involvement in reward, motivation, and pleasure in other domains. Recent data indicate that this dopaminergic system mediates pleasure associated with music; specifically, reward value for music can be coded by activity levels in the nucleus accumbens, whose functional connectivity with auditory and frontal areas increases as a function of increasing musical reward. We propose that pleasure in music arises from interactions between cortical loops that enable predictions and expectancies to emerge from sound patterns and subcortical systems responsible for reward and valuation.

---

*Montreal Neurological Institute, McGill University, Montreal, QC, Canada H3A 2B4; and †Rotman Research Institute, Baycrest Centre, University of Toronto, Toronto, ON, Canada M6A 2E1. ‡To whom correspondence should be addressed. E-mail: robert.zatorre@mcgill.ca.

Some 40,000 years ago, a person—a musician—picked up a vulture bone that had delicately and precisely incised holes along its length and blew upon it to play a tune. We know this thanks to recent remarkable archeological finds (Fig. 13.1) near the Danube, where several such flutes were uncovered (Conard et al., 2009). What bears reflection here is that, for an instrument to exist in the upper Paleolithic, music must have already existed in an advanced form for many thousands of years already; else it would have been impossible to construct something as technologically advanced as a flute that plays a particular scale. We may safely infer therefore that music is among the most ancient of human cognitive traits.

MUSICAL ORIGINS

Knowing that music has ancient origins is important in establishing it as part of our original "human mental machinery," but it does not tell us why it may have developed. The answer to this question may always remain unknown, but for insight we may turn to Darwin. One of his most well-known comments about music, from *The Descent of Man,* is this one: "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least direct use to man in reference to his ordinary habits of life, they must be ranked among the most mysterious with which he is endowed" (Darwin, 1871). Ten years later, in his autobiography, he reflected on and lamented his own musical anhedonia with these words: "if I had to live my life again, I would have made a rule to read some poetry and listen to some music at least once every week; for perhaps the parts of my brain now atrophied would thus have been kept active through use. The loss of these tastes is a loss of happiness, and may pos-

FIGURE 13.1 Ancient bone flute. The flute, made from the radius bone of a vulture, has five finger holes and a notch at the end where it was to be blown; fine lines are precisely incised near the finger holes, probably reflecting measurements used to indicate where the finger holes were to be carved. Radiocarbon dating indicates it comes from the Upper Paleolithic period, more than 35,000 years ago. Adapted from Conard et al. (2009) with permission from Macmillan Publishers, copyright 2009.

sibly be injurious to the intellect, and more probably to the moral character, by enfeebling the emotional part of our nature" (Darwin, 1887). This insightful remark contains a possible answer to the mystery alluded to in the earlier quote, for here Darwin articulates a thought that most people would intuitively agree with: that music can generate and enhance emotions, and that its loss results in reduced happiness. He even goes so far as to suggest that music might serve to prevent atrophy of neural circuits associated with emotion, an intriguing concept.

Enhancement, communication, and regulation of emotion no doubt constitute powerful reasons for the existence, and possibly for the evolution, of music, a topic that others have addressed more specifically than we will here (Wallin et al., 2000; Hauser and McDermott, 2003; Mithen, 2005). Such lines of inquiry will not tell us why music might have such properties, however. Music is the most abstract of arts: its aesthetic appeal has little to do with relating events or depicting people, places, or things, which are the province of the verbal and visual arts. A sequence of pitches—such as might have been produced by an ancient flute—concatenated in a certain way, cannot specifically denote anything, but can certainly result in emotions. Psychological models suggest a number of distinct mechanisms associated with the many different emotional responses that music can elicit (Juslin and Sloboda, 2001). However, in the present contribution, we focus specifically on a particular aspect of musically elicited affective response: pleasure. Because pleasure and reward are linked, and there is a vast literature concerning the neural basis for reward, studying musical pleasure gives us a set of hypotheses that serve as a framework for studying what might otherwise appear as an intractable question. To understand how we get from perception to pleasure, we therefore start with an overview of the perceptual analysis of musical sounds, and then move to the neurobiology of reward, before attempting a synthesis of the two.

NEUROBIOLOGY OF MUSICAL COGNITION

In thinking of how evolution may have specifically shaped the human auditory system, we should consider what is most characteristic of the way we use sound. One obvious feature that stands out is that humans use sound to communicate cognitive representations and internal states, including emotion. Both speech and music can be thought of in this way (Patel, 2008), and one could go so far as to say they constitute species-specific signals. However, unlike the call systems of other species, ours is generative and highly recursive; that is, complex structures are created out of a limited set of primitives in a combinatorial manner by the application of syntactic rules. An important property of both speech and music that is relevant to their innate nature is that they appear in the vast majority of members of the species fairly early in development, following a relatively fixed sequence, and taking as their input sounds from the immediate environment. A neural architecture must therefore exist such that it allows for these capacities to emerge.

Such neural organization necessarily had to emerge from precursors, and it is therefore useful to consider some of the features of nonhuman primate auditory cortex to identify both homologies and unique properties (Rauschecker and Scott, 2009; Zatorre and Schönwiesner, 2011). Primate auditory cortex, like visual and somatosensory systems, can be thought of as organized in a hierarchical manner, such that core areas are surrounded by belt and parabelt regions within the superior portion of the temporal lobe, with corresponding patterns of feedforward and feedback projections (Rauschecker and Scott, 2009) (Fig. 13.2); both the cytoarchitecture and connectivity of the different subfields support this organization (Kaas et al., 1999). Another organizational feature

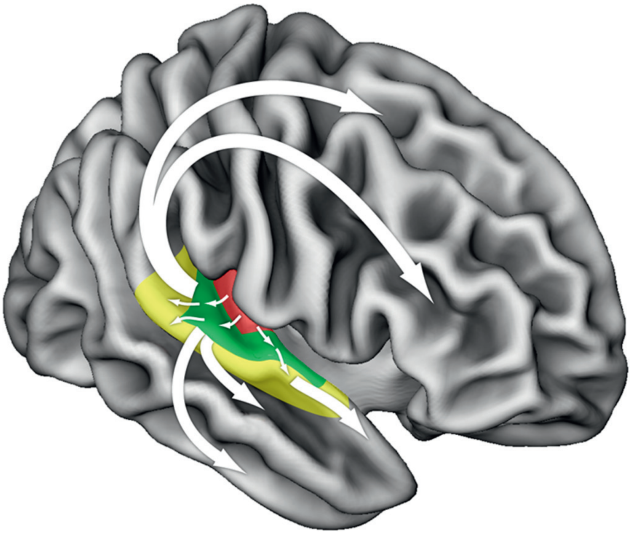


FIGURE 13.2 Schematic of putative functional pathways for auditory information processing in the human brain. Pathways originating in core auditory areas project outward in a parallel but hierarchical fashion toward belt and parabelt cortices (colored areas). Subsequently, several distinct bidirectional functional streams may be identified: Ventrally, processing streams progress toward targets in superior and inferior temporal sulcus and gyrus, eventually terminating in the inferior frontal cortex. Dorsally, projections lead toward distinct targets in parietal, premotor, and dorsolateral frontal cortices. Adapted from Zatorre and Schönwiesner (2011). [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

present across species is the distinct pathways starting in the core areas and proceeding in two directions: one dorsally and posteriorly toward parietal areas, the other ventrally and anteriorly within the temporal lobe (Rauschecker and Scott, 2009); both pathways have eventual targets in separate areas of the frontal cortices and are best thought of as bidirectional. This architecture creates a series of functional loops that allow for integration of auditory information with other modalities; they also permit interactions between auditory and motor systems related to action, and to planning or organization of action, and to memory systems. These interactions with planning and memory functions result in the ability to make predictions based on past events, a topic we shall return to below.

Functional loops between frontal and temporal cortices also play a particularly important part in working memory. Unlike visual events, which can often be static (a scene, an object), auditory events are by their very nature evanescent, leaving no traces other than those that the nervous system can create. To be able to concatenate discrete auditory events such that meaning can be encoded or decoded thus requires a working memory system that can maintain information dynamically for further processing. Here may lie one important species difference: monkeys seem to have a very limited capacity to retain auditory events in working memory (Fritz et al., 2005; Scott et al., 2012) compared with their excellent visual working memory; this limitation may help explain their relative paucity of complex, combinatorial auditory communication ability. In contrast, humans have excellent ability to maintain auditory information as it comes in, which accounts for our ability to relate one sound to another that came many seconds or minutes earlier (consider a long spoken sentence whose meaning is not clear until the last word; or a long melody that only comes to a resolution at the end). Several neuroimaging studies have pointed to interactions between auditory cortices and inferior frontal regions, especially in the right hemisphere, in the processing of tonal information, in part due to working memory requirements for tonal tasks (Zatorre et al., 1994; Gaab et al., 2003). Indeed, congenital amusia, or tone deafness (Ayotte et al., 2002), may be caused by a disruption of this system (Hyde et al., 2007; Loui et al., 2009a).

The organization of frequency maps, which are similarly topographic across both monkeys (Kaas and Hackett, 2000; Petkov et al., 2006) and humans (Schönwiesner et al., 2002; Formisano et al., 2003), presents another relevant homology. However, a more relevant feature for our discussion is sensitivity to the perceptual quality of pitch. Pitch results from periodicity; such sounds have biological significance because in nature they are almost exclusively produced by vocal tracts of other animals, compared with aperiodic natural sounds (wind, water). The ability to track pitch would thus be a useful trait for an organism to develop in navigating an acoustic environment. Neurophysiological studies have identified pitch-sensitive neurons in marmosets that respond in an invariant manner to sounds that have the same pitch but vary in their harmonic composition (Bendor and Wang, 2005), thus allowing for pitch information to be processed despite irrelevant acoustical variation. Several lines of evidence converge to suggest that a similar neural specialization for pitch may exist in the human auditory cortex, in one or more regions located lateral to core areas (Zatorre, 1988; Patterson et al., 2002; Penagos et al., 2004).

However, in humans, pitch also serves an important information-bearing function because it serves as a medium for encoding and transmitting information. Both speech and music make use of pitch variation; but its use in music seems to have some particular properties that distinguish it from its use in speech (Zatorre and Baum, 2012). Notably, pitch as used in music across many cultures tends to be organized as discrete elements, or scales (as opposed to in speech where pitch changes tend to be continuous), and these elements generally have fixed, specific frequency ratios associated with them. These properties are precisely what would be produced by an instrument such as our ancient flute, with its fixed finger holes producing discrete tones at specific pitches. Thus, music requires a nervous system able to encode and produce pitch variation with a great degree of accuracy. Substantial evidence implicates mechanisms in the right cerebral hemisphere, including pitch-specialized cortical areas, in this fine-grained, accurate pitch mechanism both in perception (Zatorre et al., 2002; Hyde et al., 2008; Zatorre and Gandour, 2008) and production (Ozdemir et al., 2006), as contrasted with the left auditory cortical system, which instead seems to be specialized for speech sounds that do not require as great accuracy in pitch tracking.

Melodies consist of combinations of individual pitches; so once separate tones are encoded by this early cortical system, combinations of pitches need to be processed. Tonal melodies can be structured in terms of the scales that they are constructed from, and the pitch contours. Both lesion (Zatorre, 1985; Stewart et al., 2006) and neuroimaging studies (Griffiths et al., 1998; Patterson et al., 2002) demonstrate that cortical areas beyond the pitch-related regions come into play as one goes from single sounds to patterns, and that these involve both the anteroventral and posterodorsal pathways, following a hierarchical organization. The global picture that emerges is that areas more distal from core and belt regions are likely involved in performing computations beyond pitch extraction, involving combinations of tonal elements, for example, related to analysis of musical interval size (Klein and Zatorre, 2011) and/or melodic contour (Lee Y-S et al., 2011). However, perhaps because of the feedback connectivity from distal regions back to core and belt areas, there is also evidence that auditory category information may sometimes be encoded in a more distributed fashion (Ley et al., 2012).

The perceptual processing steps just described only allude to the mechanisms involved in passively listening to a sequence of sounds. However, perception of something like a melody does not proceed in a simple sequential manner. It also involves an active component, such that expectancies are generated based upon a listener's implicit knowledge about musical rules that have been acquired by previous exposure to music of that culture. Thus, hearing a particular set of tones leads one to expect certain specific continuations with greater probability than others (Krumhansl, 1990; Huron, 2006). This phenomenon is significant because it points to our highly adaptive ability to predict future events based on past regularities. There is good evidence that the relevant sequential contingencies are encoded based on a process of statistical learning (Schön and François, 2011), which emerges early in life for both speech and music (Saffran, 2003) and is also operative in adulthood (Loui et al., 2009b). This dependency on environmental exposure also means that different individuals will have different sets of perceptual templates to the extent that they have been exposed to different musical systems or cultures, a point we return to below.

The neural substrates associated with musical expectancies and their violation have been measured using electrophysiological markers. These studies show that there is sensitivity to predictions based on a variety of features including contour (Tervaniemi et al., 2001) and interval size (Trainor et al., 2002), as well as harmonies (Koelsch et al., 2000; Leino et al., 2007). The localization of these processes is complex and not fully deciphered, but most likely involves interactions between belt/parabelt auditory cortices and inferior frontal cortices, using the anteroventral pathway described above (Opitz et al., 2002; Schönwiesner et al., 2007). In keeping with the concept of hierarchical organization, violations of more abstract features are associated with changes coming from frontal areas: for example, if a chord is introduced that is itself consonant but is unexpected in terms of the harmonic relationships established by earlier chords, there will be a response in the inferior frontal cortex, typically stronger on the right side (Maess et al., 2001; Tillmann et al., 2006).

Melodies of course contain temporal patterns as well as pitch patterns. Cognitive science has identified some relevant hierarchical organization in the way rhythms are processed (Large and Palmer, 2002; Patel, 2008) such that there are more local and more global levels. Meter, defined as repeating accents that structure temporal events, would be a key level of global organization; it gains importance in our context because it can be thought of as providing a temporal framework for expected events. That is, in metrically organized music, a listener develops predictions about when to expect sounds to occur (a parallel to how tonality provides the listener with a structure to make predictions about what pitches to expect). Neuroimaging studies have suggested that this metrical mechanism may depend on interactions between auditory cortices and the more dorsal pathways of the system, particularly with the premotor cortex and dorsolateral frontal regions [for a review, see Zatorre et al. (2007)], although subcortical basal ganglia structures also play an important role (Grahn and Rowe, 2009; Kung et al., 2013). The interaction with motor-related areas provides a possible explanation for the close link between temporal structure in music and movement. It is not far-fetched to suppose that the people listening to that ancient flute were also dancing.

The findings of these various lines of research point toward the conclusion that interactions between auditory and frontal cortices along both the ventral and dorsal streams generate representations of structural regularities of music, which are essential for creating expectancies of events as they unfold in time. This system no doubt plays a critical role in many aspects of perception. In fact, similar phenomena have been described for linguistic expectancies (Friederici et al., 2003; Patel, 2003). However, as we shall see below, these same systems may also hold part of the key to understanding why music can induce pleasure.

A final important phenomenon in considering the role of auditory cortex in complex perceptual processes is that it is also involved in imagery, that is, the phenomenological experience of perception in the absence of a stimulus. Musical imagery is a particularly salient form of this experience, as almost anyone can imagine a musical piece "in the mind's ear." Cognitive psychology has shown that imaginal experiences are psychologically real insofar as they can be quantified, and because they share features of real perception, including temporal accuracy and pitch acuity (Halpern, 1988; Janata, 2012). Several neuroimaging studies have shown the neural reality of this phenomenon because, even in the absence of sound, portions of belt or parabelt auditory cortex are consistently recruited when people perform specific imagery tasks (Zatorre and Halpern, 2005; Herholz et al., 2008). This imagery ability is relevant here because it shows that the auditory cortex must contain memory traces of past perceptual events, and that these traces are not merely semantic in nature, but rather reflect perceptual attributes of the originally experienced sound. In the case of music, we may say that these traces, accumulated over time, can also be thought of as templates, containing information about sound patterns that recur in musical structures. One might also ask how this information, if it is stored in these cortical areas, is accessed or retrieved. Although the mechanism is far from being understood, it appears that the frontotemporal loops mentioned above are also relevant for retrieval; this conclusion is supported by evidence that functional interactions between temporal and frontal cortices are enhanced during musical imagery (Herholz et al., 2012). Moreover, the degree of activity in this network is predictive of individual differences in subjective vividness of imagery, supporting a direct link between engagement of this frontotemporal system and ability to imagine music. This network, as we shall see, may also play an important role in musically mediated pleasure, and recruitment of the reward network, the topic to which we now turn.

NEUROBIOLOGY OF REWARD

A reward can be thought of as something that produces a hedonic sense of pleasure. Because this is a positive state, we tend to be reinforced to repeat the behavior that leads to this desirable outcome (Thorndike, 1911). A biological substrate for reinforcement was discovered in Montreal over half a century ago, when Olds and Milner (1954) reported that electrical stimulation of a specific part of a rat's brain caused the animal to continuously return to the location where this stimulation had occurred. Subsequent studies demonstrated that, if rats are given a chance to stimulate these areas, they would forgo all other routine behaviors, such as grooming, eating, and sleeping (Routtenberg and Lindy, 1965; Wise, 1978). The electrical stimulation was targeting pathways leading to the mesolimbic striatum, and it has now been widely demonstrated that dopamine release in these regions can lead to reinforcement of behaviors (Schultz, 2007; Leyton, 2010; Glimcher, 2011).

In the animal kingdom, the phylogenetically ancient mesolimbic reward system serves to reinforce biologically significant behaviors, such as eating (Hernandez and Hoebel, 1988), sex (Pfaus et al., 1995), or caring for offspring (Hansen et al., 1993). In humans, dopamine release and hemodynamic activity in the mesolimbic areas has also been demonstrated to reinforce biologically adaptive behaviors, such as eating (Small et al., 2003) and behaviors related to love and sex (Aron et al., 2005; Komisaruk and Whipple, 2005). However, as animals become more complex, additional factors become important for successful survival. For example, among human societies, having a certain amount of money can predict successful survival. Not surprisingly, obtaining money is highly reinforcing, and has also been demonstrated to involve the mesolimbic striatal areas (Knutson et al., 2001). The reinforcing qualities of such secondary rewards suggest that humans are able to understand the conceptual value of an abstract item that does not contain inherent reward value. In line with this, many people obtain pleasure from other stimuli that are conceptually meaningful, with little direct relevance for survival, and listening to music is one example. As Darwin observed, music has no readily apparent functional consequence and no clear-cut adaptive function (Hauser and McDermott, 2003). However, listening to music is ubiquitous throughout human societies since at least Paleolithic times. How does a seemingly abstract sequence of sounds produce such potent and reinforcing effects?

HOW DOES MUSIC CAUSE PLEASURE?

It is widely believed that the pleasure people experience in music is related to emotions induced by the music, as individuals often report that they listen to music to change or enhance their emotions (Juslin and Sloboda, 2001). To examine this link, we performed an experiment in which we asked listeners to select highly pleasurable music and, while listening to it, rate their experience of pleasure continuously as we assessed any changes in emotional arousal (Salimpoor et al., 2009). Increased sympathetic nervous system activity is implicated in "fight or flight" responses (Cacioppo et al., 2007) and thought to be automated; therefore it serves as a reliable measure of emotional arousal. We measured heart rate, respiration rate, skin conductance, body temperature, and blood volume pulse amplitude to track changes that correspond to increasing levels of self-reported pleasure. The results revealed a robust positive correlation between online ratings of pleasure and simultaneously measured increases in sympathetic nervous system activity, thus showing a link between objective indices of arousal and subjective feelings of pleasure.

Next we turn to the mechanisms through which emotional arousal can become rewarding. If emotional responses to music target dopaminergic activity in the reinforcement circuits of the brain, there should be a mechanism through which these responses could be considered rewarding. To examine this question, our laboratory has performed two studies in which participants selected music that they find highly emotional and pleasurable (Blood and Zatorre, 2001; Salimpoor et al., 2011). To have an objective measure of peak emotional arousal, people brought in music that gives them "chills," which are believed to be physical manifestations of peak emotional responses (Panksepp, 1995; Blood and Zatorre, 2001; Rickard, 2004), and related to increased sympathetic nervous system arousal (Salimpoor et al., 2009). In the first study, we demonstrated that the ventral striatum and other brain regions associated with emotion were recruited as a function of increasing intensity of the chills response (Blood and Zatorre, 2001). This finding thus importantly identified that the mesolimbic reward system could be recruited by an abstract aesthetic stimulus. Several other studies have shown consistent findings (Koelsch et al., 2006; Menon and Levitin, 2005); however, because all these studies measured hemodynamic responses, they did not address whether the dopaminergic system was involved. Therefore, we performed another study (Fig. 13.3*A*) with ligand-based positron emission tomography (PET) (Salimpoor et al., 2011), using raclopride, a radioligand that binds competitively with dopamine receptors. We compared dopamine release in response to pleasurable vs. neutral music and confirmed that strong emotional responses to music lead to dopamine

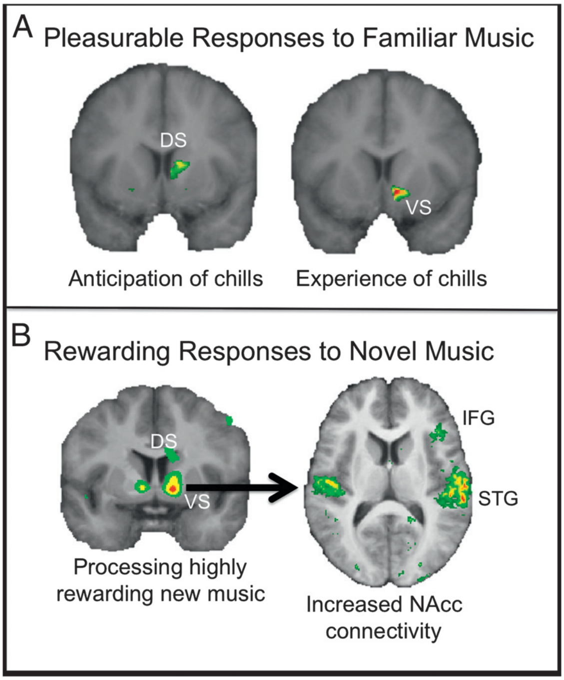


FIGURE 13.3 Neural correlates of processing highly rewarding music. (*A*) Spatial conjunction analysis between [^{11}C]raclopride positron emission tomography and fMRI while listeners heard their selected pleasurable music revealed increased hemodynamic activity in the ventral striatum (VS) during peak emotional moments (marked by "chills"), and the dorsal striatum (DS) preceding chills, in the same regions that showed dopamine release. Adapted from Salimpoor et al. (2011). (*B*) fMRI scanning showing that the best predictor of reward value of new music (as marked by monetary bids in an auction paradigm) was activity in the striatum, particularly the NAcc; the NAcc also showed increased functional connectivity with the superior temporal gyri (STG) and the right inferior frontal gyrus (IFG) as musical stimuli gained reward value. Adapted from Salimpoor et al. (2013). [NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

release in the mesolimbic striatum, which can help explain why music is considered rewarding, and links music directly to the other, biologically rewarding stimuli outlined above.

If the pleasures associated with music are at least in part related to the dopaminergic systems that we share with numerous other vertebrates, why do they seem to be uniquely a part of human behavior? Can animals tell the difference between ancient flutes, Mahler, and Britney

Spears? And if so, do they care? The closest phenomena to music in the animal kingdom are biologically significant vocalizations. However, these musical sounds are thought to be limited to an adaptive role toward territory defense and mate attraction, rather than for abstract enjoyment (Catchpole and Slater, 1995; Marler, 1999). When given a choice between listening to music versus silence, our close evolutionary relatives (tamarins and marmosets) generally prefer silence (McDermott and Hauser, 2007). Some animals may be capable of processing basic aspects of sound with relevance for music. For example, rhesus monkeys do demonstrate an ability to judge that two melodies are the same when they are transposed by one or two octaves (Wright et al., 2000). However, this ability is limited: the monkeys failed to perform this task if melodies were transposed by 0.5 or 1.5 octaves. There is also some evidence (Izumi, 2000; Fishman et al., 2001) that monkeys can distinguish between consonance and dissonance. However, they do not seem to consider consonant sounds more pleasurable, based on the finding (McDermott and Hauser, 2004) that cotton-top tamarins showed a clear preference for species-specific feeding chirps over distress calls, but no preference for consonant versus dissonant intervals. Although certain individuals of some species do demonstrate motor entrainment to externally generated rhythmic stimuli (Patel et al., 2009; Schachner et al., 2009), there is no evidence that primates do so; moreover, such behaviors have been observed in interactions with humans, and not in natural settings. Thus, overall, there is scant evidence that other species possess the mental machinery to decode music in the way humans do, or to derive enjoyment from it.

Why do certain combinations of sounds seem aesthetically pleasant to humans, but not to other animals, even primates? To better understand how we can obtain pleasure from musical sounds, it is important to realize that the mesolimbic systems do not work in isolation, and their influence will be largely dependent on their interaction with other regions of the brain. Mesolimbic striatal regions are found in many organisms, including early vertebrates (O'Connell and Hofmann, 2011); however, the anatomical connectivity of these regions with the rest of the brain varies across species depending on the complexity of the brain (Northcutt and Kaas, 1995). For example, the mesolimbic reward system becomes highly interconnected with the prefrontal cortices in mammals (Cardinal et al., 2002). Furthermore, as animals become more complex, the concept of reward can take on different forms. For example, we humans enjoy activities as diverse as attending concerts, reading fiction, visiting museums, or taking photographs, as well as less "high-brow" but still aesthetic pursuits such as decorating our vehicles, matching our wardrobes, or planting flowers. Aesthetic rewards are often highly abstract in nature and generally involve important cognitive components. In particular, they are highly culture dependent and therefore imply a critical role for learning and social influences. These features suggest that they may involve the "higher-order" and more complex regions of the brain that are more evolved in humans. Brain imaging studies of aesthetic reward processing lend support to this idea by demonstrating activity in the cerebral cortex, particularly the prefrontal cortex (Cela-Conde et al., 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004), which is most evolved in humans (Haber and Knutson, 2010). The cerebral cortex contains stores of information accumulated throughout an organism's existence. As such, cortical contributions to aesthetic stimulus processing are consistent with the idea that previous experiences may play a critical role the way an individual may experience certain sounds as pleasurable or rewarding. Although evidence exists for some basic similarities in how people across cultures respond to certain cues (Fritz et al., 2009), the rewarding nature of aesthetic stimuli is not entirely universal, differing significantly across cultures, and between individuals within cultures. These responses are related to subjective interpretation of the stimulus, which is likely to be related to previous experiences with a particular stimulus or other similar stimuli. It has been proposed that all individuals have a "musical lexicon" (Peretz and Coltheart, 2003), which represents a storage system for musical information that they have been exposed to throughout their lives, including information about the relationships between sounds and syntactic rules of music structure specific to their prior experiences. This storage system may contain templates that can be applied to incoming sound information to help the individual better categorize and understand what he or she is hearing. As such, each time a sequence of sounds is heard, several templates may be activated to fit the incoming auditory information. This process will inevitably lead to a series of predictions that may be confirmed or violated, and ultimately determine its reward value to the individual.

To examine the neural substrates of predictions and reward associated with music, and how these may contribute to pleasurable responses, in a new study, we scanned people with functional MRI (fMRI) as they listened to music that they had not heard before and examined the neural activity associated with the reward value of music (Salimpoor et al., 2013). We assessed the reward value of each piece of music by giving individuals a chance to purchase it in an auction paradigm (Becker et al., 1964), such that higher monetary bids served as indicators of higher reward value. We were interested in examining the neural activity associated with hearing musical sequences for the first time, and examining the neural activity that can distinguish between musical sequences that become "rewarding" to an individual compared with those that they do not care to hear again. The results (Fig. 13.3*B*) revealed that activity in the mesolimbic striatal areas, especially the nucleus accumbens (NAcc), was most associated with reward value of musical stimuli, as measured by the amount bid. The NAcc has been implicated in making predictions, anticipating, and reward prediction errors—that is, the calculated difference between what was expected and the actual outcome (McClure et al., 2003; O'Doherty, 2004; Pessiglione et al., 2006). A prediction may result in a positive, zero, or negative prediction error, depending on the organism's expectations and the outcome (Montague et al., 1996; Schultz, 1998; Sutton and Barto, 1998), and a number of studies have demonstrated that prediction errors are related to dopamine neurons in the midbrain (Morris et al., 2004; Bayer and Glimcher, 2005) and may be measured in the NAcc (O'Doherty, 2004; Pessiglione et al., 2006). This result therefore provides evidence that temporal predictions play an important role in the way in which individuals obtain pleasure from musical stimuli. A second and perhaps more important finding was that auditory cortices in the superior temporal gyrus (STG), which were highly and equally active during processing of all musical stimuli, showed robustly increased functional interactions with the NAcc during processing of musical sequences with high, compared with low, reward value. As discussed above, auditory cortices are the site of processing not only of incoming auditory information, but also of more abstract computations related to perception, imagery, and temporal prediction. Increased functional connectivity between the NAcc and STG as reward value increases suggests that predictions were linked with information contained in the STG, which we think is related to templates of sound information gathered through an individual's prior experiences with musical sounds (likely based in part on implicit knowledge, such as might arise via statistical learning). This functional interaction between subcortical reward circuits involved in prediction and highly individualized regions of the cerebral cortex can explain why different people like different music, and how this may be a function of their previous experiences with musical sounds. Moreover, consistent with the studies reviewed above linking the STG with the inferior frontal cortex and implicating this region with hierarchical expectations during music processing, we found increased connectivity also of frontal cortex with the NAcc during highly rewarding music processing. These corticostriatal interactions exemplify the cognitive nature of rewarding responses to music and help to explain why the complexities of the highly evolved human brain allow for the experience of pleasure to an abstract sequence of sound patterns.

In the experiment described, we used new music to rule out veridical expectations (Bharucha, 1994), or explicit expectations of how musical passages may unfold based on familiarity with the musical selections. However, explicit expectations can also lead to activity in the mesolimbic striatal regions. In the earlier study (Salimpoor et al., 2011), we found activity in the dorsal striatum (caudate nucleus) during the period immediately preceding the chills, that is, during a phase of anticipation (Fig. 13.3*A*). Indeed, this dorsal component of the mesolimbic striatum has previously been associated with anticipation (Boileau et al., 2006). The dorsal striatum has intricate anatomical connections with various parts of the prefrontal cortex (Monchi et al., 2006; Postuma and Dagher, 2006). The frontal lobes, particularly the prefrontal cortices, are involved in executive functions, such as temporal maintenance of information in working memory and relating information back to earlier events, temporal sequencing, planning ahead, creating expectations, anticipating outcomes, and planning actions to obtain rewards (Stuss and Knight, 2002; Petrides and Pandya, 2004). These cognitive processes are highly significant during musical processing, and it would be consistent that striatal circuits would provide a mechanism for the temporal nuances that give rise to feelings of anticipation and craving. Therefore, it is likely that the cerebral cortex and striatum work together to make predictions about potentially rewarding future events and assess the outcome of these predictions. Additional support implicating the caudate in anticipation comes from other studies that implicate the dorsal striatum in anticipating desirable stimuli, when the behavior is habitual and expected (Boileau et al., 2006; Belin and Everitt, 2008). In this way, the signals that predict the onset of a desirable event can become reinforcing per se. In the case of music, this prediction may include sound sequences that signal the onset of the highly desirable part of the music. Previously neutral stimuli may thus become conditioned to serve as cues signaling the onset of the rewarding sequence. Frontal cortices (Tillmann et al., 2003; Koelsch et al., 2008), and their interactions with the basal ganglia (Seger et al., 2013), have also been implicated in processing syntactically unexpected events during music, suggesting that they might be involved in keeping track of temporal unfolding of sound patterns and their structural relationships, further supporting the role of striatal connectivity with the most evolved regions of the human brain during music processing. It is important to note that the NAcc has also been demonstrated to play a role in anticipation with other types of stimuli, such as monetary rewards (Knutson and Cooper, 2005). The functional roles of these structures are therefore not simply attributable to any one dimension, but are dynamically altered as a function of a variety of factors, not all of which have yet been identified.

The NAcc played an important role with both familiar and novel music. In the case of familiar music, hemodynamic activity in the NAcc was associated with increasing pleasure, and maximally expressed during the experience of chills, which represent the peak emotional response; these were the same regions that showed dopamine release. The NAcc is tightly connected with subcortical limbic areas of the brain, implicated in processing, detecting, and expressing emotions, including the amygdala and hippocampus. It is also connected to the hypothalamus, insula, and anterior cingulate cortex (Haber and Knutson, 2010), all of which are implicated in controlling the autonomic nervous system, and may be responsible for the psychophysiological phenomena associated with listening to music and emotional arousal. Finally, the NAcc is tightly integrated with cortical areas implicated in "high-level" processing of emotions that integrate information from various sources, including the orbital and ventromedial frontal lobe. These areas are largely implicated in assigning and maintaining reward value to stimuli (O'Doherty, 2004; Chib et al., 2009) and may be critical in evaluating the significance of abstract stimuli that we consider pleasurable.

PUTTING IT ALL TOGETHER

The studies we have reviewed begin to point the way to a neurobiological understanding of how patterns of otherwise meaningless sounds can result in highly rewarding, pleasurable experiences. The key concepts revolve around the idea of temporal expectancies, their associated predictions, and the reward value generated by these predictions. As we have seen, auditory cortical regions contain specializations for analysis and encoding of elementary sound attributes that are found in music, particularly pitch values and durations. These elements are processed in a hierarchical manner within auditory areas to represent patterns of sounds as opposed to individual sounds. The interactions between auditory areas and frontal cortices via the ventral and dorsal routes are critical in allowing working memory to knit together the separate sounds into more abstract representations, and in turn, in generating tonal and temporal expectancies based on structural regularities found in music. These expectancies are rooted in templates derived from an individual's history of listening, which are likely stored in auditory cortices.

The reward system, phylogenetically old, may be most parsimoniously explained as a mechanism to promote certain adaptive behaviors, with dopaminergic circuits playing a critical role in establishing salience and reward value of relevant stimuli and the sensations generated by them. An important part of this system seems to be devoted to reward prediction; as indicated above, fulfillment of prediction leads to dopamine release in the striatum, with a greater response associated with better-than-expected reward. The findings of enhanced functional interactions between the auditory cortices, valuation-related cortices, and the striatum as a function of how much a new piece of music is liked provide a link between these two major lines of research. We suggest that the interactions that we observed represent greater informational cross-talk between the systems responsible for pattern analysis and prediction (cortical) with the systems responsible for assigning reward value itself (subcortical). Thus, the highly evolved cortical system is able to decode tonal or rhythmic relationships, at both local and more global levels of organization, that are found in music, such that it can generate expectations about upcoming events based on past events. However, the emotional arousal associated with these predictions, we think, is generated by the interactions with the striatal dopaminergic system. This framework, and others like it (Kringelbach and Vuust, 2009), could also be thought of more broadly as applicable to other types of aesthetic rewards: for example, some authors have suggested that visual aesthetic experiences may arise from interactions across cortical regions involved in perception and memory (Biederman and Vessel, 2006); also, Cela-Conde et al., Chapter 16, this volume, emphasize synchronization across cortical fields as important for visual aesthetics.

Our ability to enjoy music can perhaps now be seen as a little less mysterious than Darwin thought, when viewed as the outcome of our human mental machinery, both its phylogenetically ancient, survival-oriented circuits and its more recently evolved cortical loops that allow us to represent information, imagine outcomes, make predictions, and act upon our stored knowledge. We have little doubt that the ancient musicians, armed with the same machinery as us, and able to coax patterns of tones from a vulture bone, experienced and communicated pleasure, beauty, and wonder, just as much as we do today.

14

Learning Where to Look for a Hidden Target

LEANNE CHUKOSKIE,* JOSEPH SNIDER,*
MICHAEL C. MOZER,*‡ § RICHARD J. KRAUZLIS, ‖ AND
TERRENCE J. SEJNOWSKI*†#**

Survival depends on successfully foraging for food, for which evolution has selected diverse behaviors in different species. Humans forage not only for food, but also for information. We decide where to look over 170,000 times per day, approximately three times per wakeful second. The frequency of these saccadic eye movements belies the complexity underlying each individual choice. Experience factors into the choice of where to look and can be invoked to rapidly redirect gaze in a context- and task-appropriate manner. However, remarkably little is known about how individuals learn to direct their gaze given the current context and task. We designed a task in which participants search a novel scene for a target whose location was drawn stochastically on each trial from a fixed prior distribution. The target was invisible on a blank screen, and the participants were rewarded when they fixated the hidden target location. In just a few trials, participants rapidly found the hidden targets by looking near previously rewarded locations and avoiding previously unrewarded locations. Learning trajectories were well characterized by a simple reinforcement-learning (RL) model that maintained and continu-

---

*Institute for Neural Computation and †Division of Biological Sciences, University of California at San Diego, La Jolla, CA 92093; ‡Department of Computer Science and §Institute of Cognitive Science, University of Colorado, Boulder, CO 80309; ‖Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD 20892; and #Howard Hughes Medical Institute and Computational Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, CA 92037. **To whom correspondence should be addressed. E-mail: terry@salk.edu.

ally updated a reward map of locations. The RL model made further predictions concerning sensitivity to recent experience that were confirmed by the data. The asymptotic performance of both the participants and the RL model approached optimal performance characterized by an ideal-observer theory. These two complementary levels of explanation show how experience in a novel environment drives visual search in humans and may extend to other forms of search such as animal foraging.

The influence of evolution can be seen in foraging behaviors, which have been studied in behavioral ecology. Economic models of foraging assume that decisions are made to maximize payoff and minimize energy expenditure. For example, a bee setting off in search of flowers that are in bloom may travel kilometers to find food sources. Seeking information about an environment is an important part of foraging. Bees need to identify objects at a distance that are associated with food sources. Humans are also experts at searching for items in the world, and in learning how to find them. This study explores the problem of how humans learn where to look in the context of animal foraging.

Our daily activities depend on successful search strategies for finding objects in our environment. Visual search is ubiquitous in routine tasks: finding one's car in a parking lot, house keys on a cluttered desk, or the button you wish to click on a computer interface. When searching common scene contexts for a target object, individuals rapidly glean information about where targets are typically located (Potter, 1975; Itti and Koch, 2000; Neider and Zelinsky, 2006; Oliva and Torralba, 2006; Torralba et al., 2006; Rayner et al., 2009; Castelhano and Heaven, 2010, 2011; Võ and Henderson, 2010). This ability to use the "gist" of an image (Oliva and Torralba, 2006; Torralba et al., 2006) enables individuals to perform flexibly and efficiently in familiar environments. Add to that the predictable sequence of eye movements that occurs when someone is engaged in a manual task (Hayhoe and Ballard, 2005) and it becomes clear that despite the large body of research on how image salience guides gaze (Itti and Koch, 2000; Parkhurst and Niebur, 2003), learned spatial associations are perhaps just as important for effectively engaging our visual environment (Chun and Jiang, 1998; Hayhoe and Ballard, 2005; Tatler and Vincent, 2009). Surprisingly, however, little research has been directed to how individuals learn to direct gaze in a context- and task-appropriate manner in novel environments.

Research relevant to learning where to look comes from the literature on eye movements, rewards, and their expected value. Like all motor behavior, saccades are influenced by reward, occurring at shorter latency for more valued targets (Milstein and Dorris, 2007). In fact, finding something you seek may be intrinsically rewarding (Xu-Wilson et al., 2009).

Refining the well-known canonical "main sequence" relationship between saccade amplitude and velocity, the value of a saccade target can alter details of the motor plan executed, either speeding or slowing the saccade itself depending upon the value of that target for the subject (Shadmehr, 2010; Shadmehr et al., 2010). This result is especially interesting in light of the research indicating that the low-level stimulus features, which have an expected distribution of attracting fixations (Reinagel and Zador, 1999), are different (Tatler et al., 2006) and perhaps also differently valuable (Açık et al., 2010) depending on their distance from the current fixation location. Taken together these results underscore the complex interplay of external and internal information in guiding eye movement choice.

Two early foundational studies from Buswell (1935) and Yarbus (1967) foreshadowed modern concepts of a priority or salience map by showing that some portions of an image are fixated with greater likelihood than others. Both researchers also provided early evidence that this priority map effectively changes depending on the type of information sought. Yarbus observed that the patterns of gaze that followed different scene-based questions or tasks given to the observer were quite distinct, suggesting that the observer knew where to find information in the scene to answer the question and looked specifically to areas containing that information when it was needed. Henderson and coworkers (Castelhano et al., 2009) have replicated this result for the different tasks of visual search and image memorization. However, Wolfe and coworkers (Greene et al., 2012), using a slightly different question and task paradigm, failed to find evidence that saccade patterns were predictive of specific mental states. Regardless of specific replications of Yarbus's demonstration, it is clear that scene gist—context-specific information about where objects are typically found—emerges very quickly and guides target search of a scene with a known context (Torralba et al., 2006). For example, when shown a street scene, an observer would immediately know where to look for street signs, cars, and pedestrians (Fig. 14.1*A*).

Castelhano and Heaven (2011) have also shown that in addition to scene gist itself, learned spatial associations guide eye movements during search. Subjects use these learned associations as well as other context-based experience, such as stimulus probability, and past rewards and penalties (Geng and Behrmann, 2005; Stritzke and Trommershäuser, 2007; Schütz et al., 2012) to hone the aim of a saccadic eye movement. A recent review and commentary from Wolfe et al. (2011) explores the notion of "semantic" guidance in complex, naturalistic scenes as providing knowledge of the probability of finding a known object in a particular part of a scene. This perspective relates work on scene gist together with more classic visual search tasks, offering a framework for considering how indi-

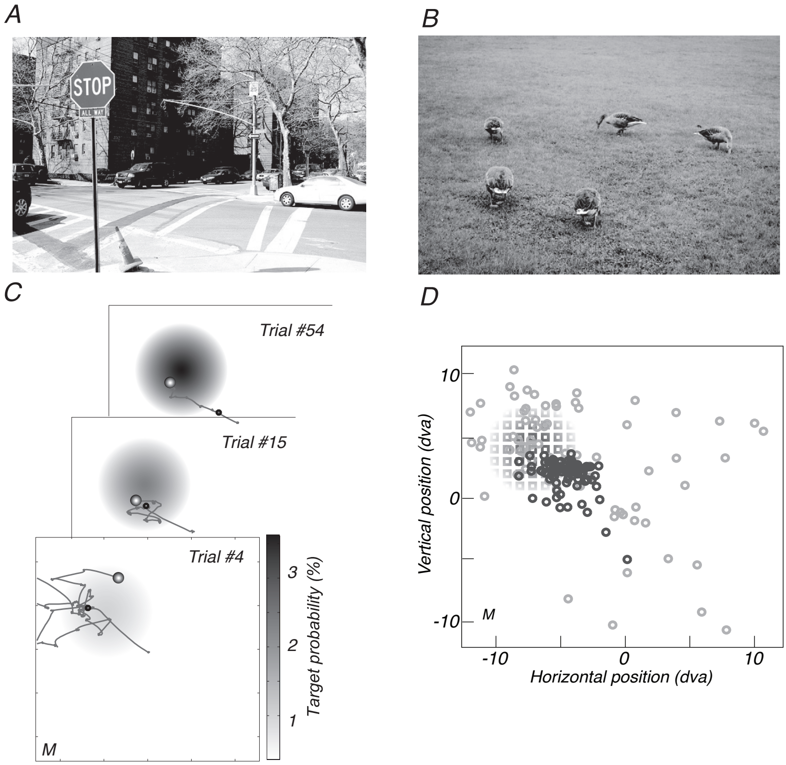


FIGURE 14.1 Visible and hidden search tasks. (*A*) An experienced pedestrian has prior knowledge of where to look for signs, cars, and sidewalks in this street scene. (*B*) Ducks foraging in a large expanse of grass. (*C*) A representation of the screen is superimposed with the hidden target distribution that is learned over the session as well as sample eye traces from three trials for participant M. The first fixation of each trial is marked with a black circle. The final and rewarded fixation is marked by a shaded grayscale circle. (*D*) The region of the screen sampled with fixation shrinks from the entire screen on early trials (light gray circles; 87 fixations over the first five trials) to a region that approximates the size and position of the Gaussian-integer distributed target locations (squares, shading proportional to the probability as given in *A*) on later trials (dark gray circles; 85 fixations from trials 32–39). Fixation position data are from participant M.

viduals might use past experience to direct gaze in both real-world scenes as well as in the contrived scenarios of our laboratories.

Quite distinct from the literature on visual search is the literature on another sort of search that is commonly required of animals and people: foraging. Foraging agents seek food, which is often hidden in the environment in which they search (Fig. 14.1*B*). The search for hidden food rewards changes not only with the position of the reward, but also with the size of the distribution of rewards (Charnov, 1976). Other work has cast foraging behavior in terms of optimal search (Bénichou et al., 2005). What distinguishes foraging from visual search tasks is that visual search tasks have visible cues that drive search, in addition to contextual information that specifies probable target location. To make visual search more like foraging, we can strip the visible cues from visual search. A visual search task devoid of visual cues would allow us to determine whether there are underlying commonalities between these two types of search and whether general principles of search might emerge from such an investigation.

The importance of searching for hidden and even invisible targets is underscored by human participants engaged in large-scale exploration approximating animal foraging (Gilchrist et al., 2001; Smith et al., 2005). In one such paradigm (Smith et al., 2005), children were told to explore a room with a floor composed of box-like floor tiles, one of which contained a reward item. Interestingly, children explored the environment differently when they were instructed to search with their nondominant hand than with their dominant hand. Specifically, more "revisits" were necessary in the nondominant hand condition. This result suggests that learning and motor effort factor into performance on tasks that might seem to be automatic, which suggests methods for modeling foraging-like behavior. The additional motor effort that would be required to reduce metabolically expensive revisits in a foraging scenario seemed to have engaged memory systems to a greater degree than what is typically observed in traditional "visual" search tasks.

The reinforcement-learning (RL) framework has become widely accepted for modeling performance in tasks involving a series of movements leading to reward (Sutton, 1988; Montague and Sejnowski, 1994). In addition, for organisms across many levels of complexity, RL has been shown to be an appropriate framework to consider adaptive behavior in complex and changing environments (Niv et al., 2002; Lee et al., 2012). Here we describe performance in our task in terms of an RL perspective. Participants' learning trajectories were well characterized by a simple RL model that maintained and continually updated a reward map of locations. The RL model made further predictions concerning sensitivity to recent experience that were confirmed by the data. The asymptotic performance of both the participants and the RL model approached optimal performance characterized by an ideal-observer theory assuming perfect knowledge of the static target distribution and independently chosen fixations. These two complementary levels of explanation show how experience in a novel environment drives visual search in humans.

RESULTS

Humans Rapidly Learn to Find Hidden Targets

In visual search, previous experiments failed to isolate completely the visual appearance of a target from the learned location of the reward; in all cases a visual indication of a target, or a memory of a moments-ago visible target (Stritzke and Trommershäuser, 2007) and its surroundings, were available to guide the movement. To understand how participants learn where to look in a novel scene or context where no relationship exists between visual targets and associated rewards or penalties, we designed a search task in which participants were rewarded for finding a hidden target, similar to the scenario encountered by a foraging animal (Fig. 14.1*C*).

Participants repeatedly searched a single unfamiliar scene (context) for a target. However, to study the role of task knowledge in guiding search apart from the visual cues ordinarily used to identify a target, the target was rendered invisible. The participants' task was to explore the screen with their gaze and find a hidden target location that would sound a reward tone when fixated. Unbeknownst to each participant, the hidden target position varied from trial to trial and was drawn from a Gaussian distribution with a centroid and spread (target mean and SD, respectively) that was held constant throughout a session (Fig. 14.1*C*).

At the start of a session, participants had no prior knowledge to inform their search; their initial search was effectively "blind." As the session proceeded participants accumulated information from gaining reward or not at fixation points and improved their success rate by developing an expectation for the distribution of hidden targets and using it to guide future search (Fig. 14.1*D*).

After remarkably few trials, participants gathered enough information about the target distribution to direct gaze efficiently near the actual target distribution, as illustrated by one participant's data in Fig. 14.1*C* and *D*. We observed a similar pattern of learning for all participants: Early fixations were broadly scattered throughout the search screen; after approximately a dozen trials, fixations narrowed to the region with high target probability.

A characterization of this effect for all participants is shown in Fig. 14.2*A*. The average distance from the centroid of the target distribution to individual fixations in a trial drops precipitously over roughly the first dozen trials. Fig. 14.2*A* shows this distance for all participants in the 2° target spread condition. The asymptotic distance from centroid increased monotonically with the target spread (Table 14.1).

A measure of search spread is the SD of the set of fixations in a trial. The search spread was initially broad and narrowed as the session progressed, as shown in Fig. 14.2*B* for all participants in the 2° target-spread condition. The asymptotic search spread monotonically increased with the target-spread condition (Table 14.1). These data suggest that participants estimated the spread of the hidden target distribution and adjusted their search spread accordingly. Also, the median number of fixations that participants made to find the target (on target-found trials) decreased rapidly within a session to reach an asymptote (Fig. 14.2*C*).

Humans Approach Ideal-Observer Performance

We now consider the behavior of participants once performance had stabilized. Taking trials 31–60 to reflect asymptotic behavior, we examined the efficiency of human search in comparison with a theoretical optimum. An ideal observer was derived for the Hidden Target Search Task assuming that fixations are independent of one another and that the target distribution is known, and the expected number of trials is minimized. The dashed lines in Fig. 14.2 mark ideal-observer performance. Ideal search performance requires a distribution of planned fixation "guesses" that is √2 broader than the target distribution itself (Snider, 2011). As seen in Fig. 14.2*B* and *C*, the performance of participants hovered around this ideal search distribution after about a dozen trials.

Subjects showed a ~1° bias toward the center of the screen relative to the target distribution, but the calculation of the ideal behavior assumed subjects searched symmetrically around the center of the target distribution. Although the addition of the bias makes the math untenable analytically, a simulated searcher approximated the expected number of saccades required to find a target with a systematic 1° bias (Fig. 14.3). There was essentially no change in the predicted number of saccades or the search spread (location of the minimum in Fig. 14.3), except for the case of the 0.75° target distribution, where the optimum shifted from a search spread of 0.56° to 0.85°. Intuitively, the effect of bias was small because the bias was less than the 2° target radius. Nonetheless, at a 95 percent confidence level across the three target distributions, the number of steps, search spread, and step size all qualitatively and quantitatively match the predictions assuming the number of saccades was minimized.

Reinforcement-Learning Model Matches Human Learning

In addition to the ideal-observer theory, which characterizes the asymptotic efficiency of human search, we developed a complementary, mechanistic account that captured the learning, individual differences, and dynamics of human behavior. RL theory, motivated by animal learning and behavioral experiments (Yu and Cohen, 2008), suggests a simple and intuitive model that constructs a value function mapping locations in

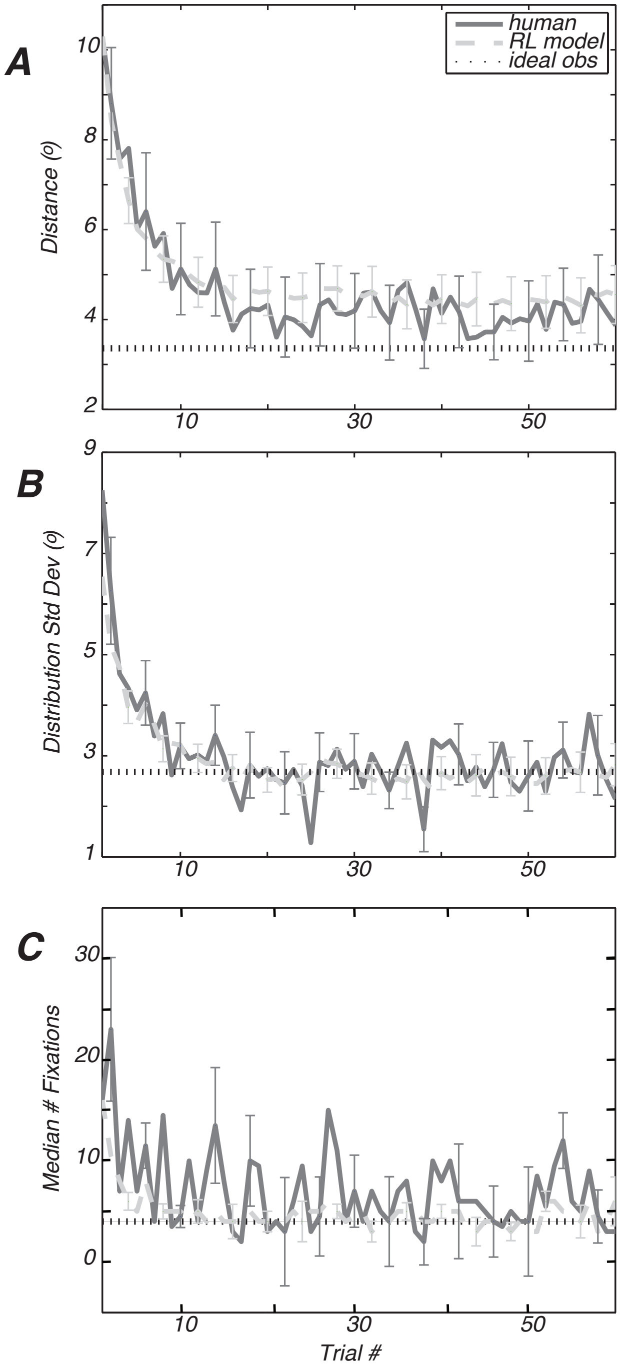

A
B
C
human
RL model
ideal obs
Distance (º)
Distribution Std Dev (º)
Median # Fixations
Trial #
10
8
6
4
2
9
7
5
3
1
30
20
10
0
10
30
50

TABLE 14.1 Performance at Asymptote of Learning for Participants, the Ideal-Observer Theory, and a Reinforcement-Learning Model

Target Spread Condition, deg	Mean Distance from Target Centroid to Fixations on Trials 31–60, deg	Search Spread on Trials 31–60, deg
Participant data		
0.75	1.97	1.14
2.00	4.08	2.80
2.75	4.39	3.70
Ideal-observer theory		
0.75	0.70	0.56
2.00	3.36	2.68
2.75	4.74	3.78
Reinforcement-learning model		
0.75	3.21	1.56
2.00	4.46	2.61
2.75	6.07	4.29

NOTE: Data, theory, and model statistics for the mean fixation distance and search spread for 0.75-, 2.0-, and 2.75-degree target distribution conditions.

FIGURE 14.2 Learning curves for hidden-target search task. (*A*) The distance between the mean of the fixation cluster for each trial to the target centroid, averaged across participants, is shown in dark and light gray and indicates the result of 200 simulations of the reinforcement-learning model for each participant's parameters. The SEM is given for both. The ideal-observer prediction is indicated by the black dotted line. (*B*) The SD of the eye position distributions or "search spread" is shown for the average of all participants (dark gray) and the RL model (light gray) with SEM. The dashed line is the ideal-observer theoretical optimum in each case, assuming perfect knowledge of the target distribution. (*C*) The median number of fixations made to find the target on each trial is shown (dark gray) along with the RL model prediction (light gray) of fixation number. The SEM is shown for both.

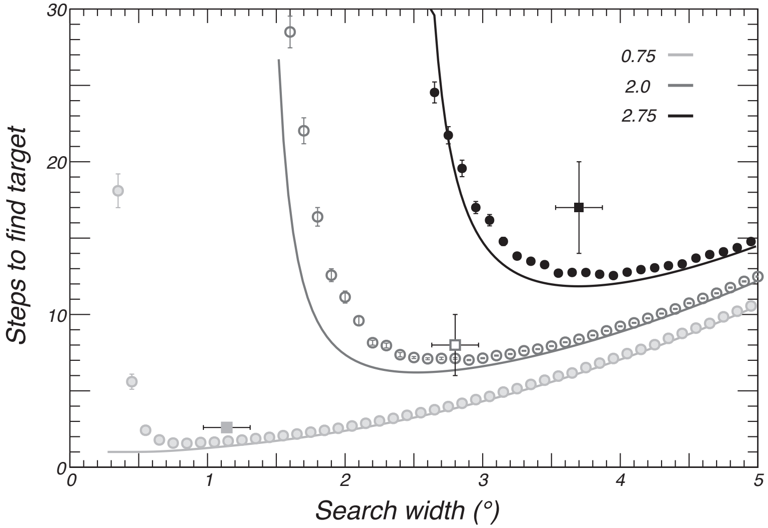


FIGURE 14.3 Optimal search model. Theoretical number of search steps to find the target for target distributions of size 0.75° (light gray, filled), 2° (dark gray, open), and 2.75° (black) was estimated by simulation (circles with mean and SEs from 100,000 trials per point) and from the theoretical calculation (solid lines). The simulation included the observed 1° bias seen in the subjects, but the theory lines did not. Solid boxes indicate the observed values for the subjects (mean and SE). With the added bias, the minimum moved slightly to the right but was only significant for the 0.75° target distribution. The cost in terms of extra saccades for nonoptimal search spreads (away from the minimum) was higher for the larger target distributions, and the comparatively shallow rise for search spreads above optimal meant that if subjects were to err, then they should tend toward larger spreads. Indeed, the tendency for larger spreads was evident as subjects started with large spreads and decreased toward the minimum (Fig. 14.2). The extra steps that subjects took to find the target for the 2.75° distribution (*Upper Right*) was consistent with the tendency toward small saccades even though they were quite close to the correct minimum: The largest saccades may have been broken up into multiple short saccades.

space to expected reward. The value function is updated after each fixation based on whether or not the target is found and is used for selecting saccade destinations that are likely to be rewarded.

We augmented this intuitive model with two additional assumptions: First, each time a saccade is made to a location, the feedback obtained generalized to nearby spatial locations; second, we incorporated a proximity bias that favored shorter saccades. A preference for shorter saccades was present in the data and has been noted by other researchers (Yarbus, 1967; Sutton and Barto, 1998), some of whom have shown that it can override knowledge that participants have about the expected location of a target (Rayner, 1998). Incorporating a proximity bias into the model changed the nature of the task because the choice of the next fixation became dependent on the current fixation. Consequently, participants must plan fixation sequences instead of choosing independent fixations.

We modeled the task using temporal difference methods (Sutton, 1988), which are particularly appropriate for Markovian tasks in which sequences of actions lead to reward (*Reinforcement Learning Model* gives details). The model's free parameters were fitted to each subject's sequence of fixations for each of the first 20 trials. Given these parameters, the model was then run in generative mode from a de novo state to simulate the subject performing the task.

Fig. 14.2 shows the mean performance of the model side by side with the mean human performance. The model also predicted an asymptotic search spread that increased with the target spread (Table 14.1), consistent with the participants' aggregate performance. Similar to the human performance observed in Fig. 14.2*A*, the RL model approaches, but does not reach, the theoretical asymptote. Like the human participants, the RL model is responsive to nonstationarity in the distribution, whereas the ideal-observer theory assumes that the distribution is static. In addition, the model accounted for individual differences (*Reinforcement Learning Model*). There are several reasons why the observed consistency between participants and simulations may be more than an existence proof and could provide insight into the biological mechanisms of learning (Araujo et al., 2001). The RL model itself had emergent dynamics that were reflected in the human behavior (Fig. 14.4 and sequential effects discussed below). Also the criterion used to train the model was the likelihood of a specific fixation sequence. A wide range of statistical measures quite distinct from the training criterion was used to compare human and model performance: mean distance from target centroid, SD of the distribution of eye movements, and the median number of fixations (Fig. 14.2). Finally, only the first 20 trials were used to train the model, but all of the comparisons shown in Table 14.1 were obtained from trials 31–60.

Fig. 14.2 suggests that participants acquire the target distribution in roughly a dozen trials and then their performance is static. However, in the RL model the value function is adjusted after each fixation, unabated over time. A signature of this ongoing adjustment is a sequential dependency across trials—specifically, a dependency between one trial's final fixation and the next trial's initial fixation. Dependencies were indeed observed in the data throughout a session (Fig. 14.4*A*), as predicted by the model (Fig. 14.4*B*) and explained some of the trial-to-trial variability in performance (Fig. 14.2 and *Reinforcement Learning Model*). Participants were biased to start the next trial's search near found target locations from recent trials.

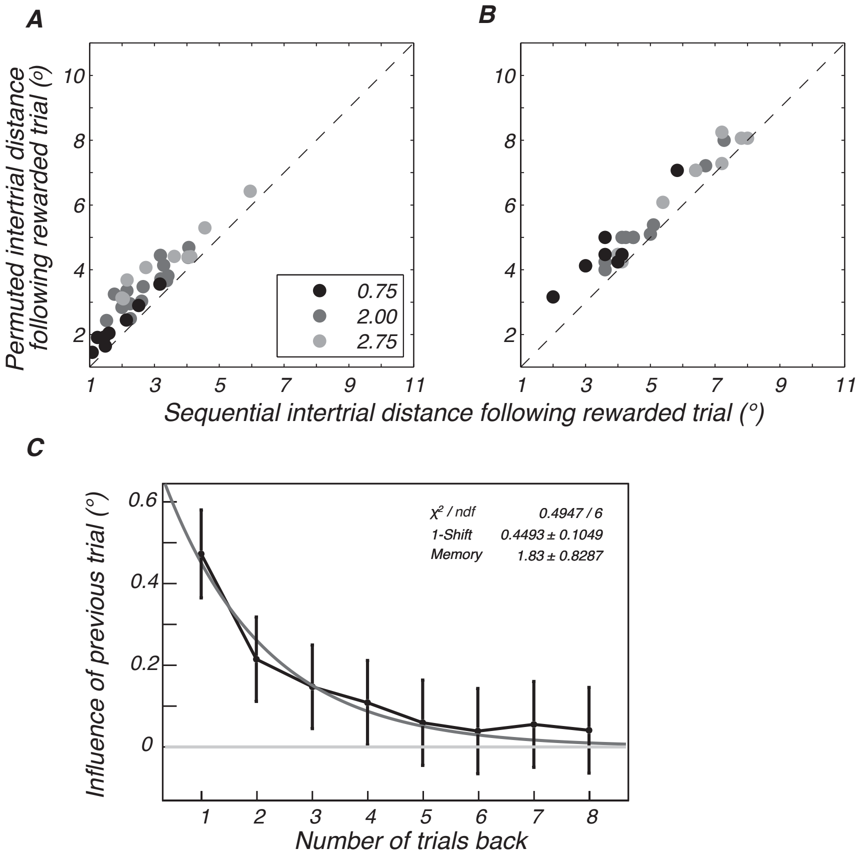


FIGURE 14.4 Sequential effects in the human data and predictions of the RL model. (*A*) For each subject, we plot the mean sequential intertrial distance (the distance between the final fixation on trial *n* and the first fixation on trial *n* + 1 when trial *n* yields a reward) versus the permuted intertrial distance (the distance between the final fixation on a trial and the first fixation of another randomly drawn trial). Each circle denotes a subject, and the circle shade indicates the target-spread condition (black, σ = 0.75; medium gray, σ = 2.00; light gray, σ = 2.75). Consistent with the model prediction (*B*), the sequential intertrial distance is reliably shorter than permuted intertrial distance, as indicated by the points lying above the diagonal. All intertrial distances are larger in the model, reflecting a greater degree of exploration than in the participants, but this mismatch is orthogonal to the sequential effects. (*C*) The effect of previous trials on search in the current trial is plotted as a function of the number of trials back. An exponential fit to the data is shown in light gray.

The influence of previous trials decreases exponentially; the previous two, or possibly three, trials influenced the current trial's saccade choice (Fig. 14.4*C*). This exponential damping of previous trials' influence is approximated by the memoryless case (Snider, 2011), allowing both the RL model and ideal planner to coexist asymptotically.

Bimodal Distribution of Saccade Lengths

Our motivation in designing the hidden target search task was to link the visual search and foraging literatures. Performance in our task had features analogous to those found in the larger context of animal foraging (Fig. 14.5). Although individual trials look like Lévy flights—a mixture

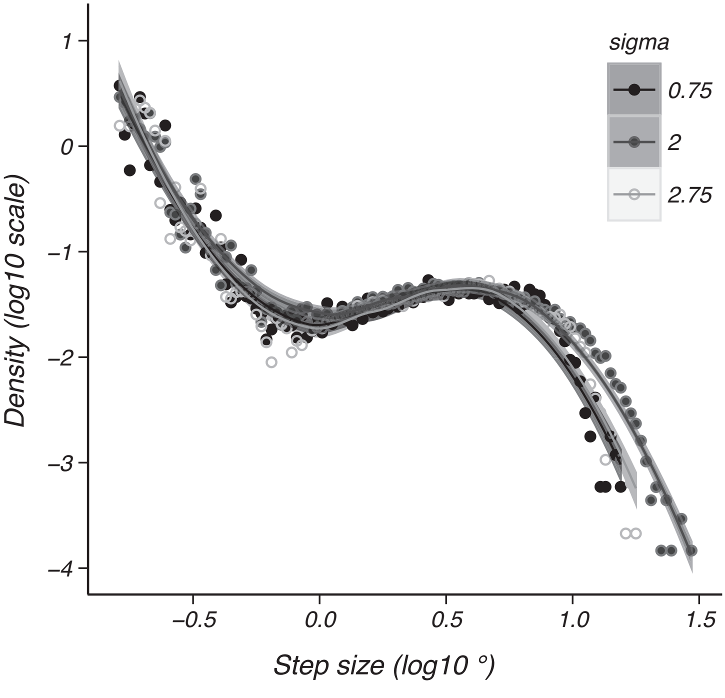


FIGURE 14.5 Length distributions of saccades in the hidden target task. A turning-point algorithm applied to raw eye movement data yields a distribution of step sizes for all participants (*Reinforcement Learning Model* gives details). Very small "fixational" eye movements compose the left side of the plot and large larger saccadic jumps on the right for three different sizes of target distribution. The points and lines (Loess fits with 95 percent confidence interval shading) for each search distribution size all share a similar shape, particularly a bend at step sizes approaching 1° of visual angle.

of fixation and sporadic large excursions that are known to be optimal in some cases of foraging behavior (Schultz et al., 1997; Humphries et al., 2010; James et al., 2011)—the length distribution of all straight-line segments is not Lévy-like, but separates into two distinct length scales like the intermittent search popularized by Bénichou et al. (2005). The shorter length scale, fixations less than about 1°, corresponds to a local power-law search with a very steep exponent, making it a classic random walk that densely samples the local space. That local search is combined with the larger, but rarer, saccades represented by the peaked hump at step sizes larger than 1°. These are the distinct choices from the planned distribution described already (i.e., the guess distribution or value function). The distinctive knee shape in Fig. 14.5 is similar to that found in other demanding visual search tasks (Snider, 2011), as well as intermittent foraging by a wide range of animals (Bénichou et al., 2005; Humphries et al., 2010).

DISCUSSION

Human search performance can be put into the more general context of animal foraging, which has close connections with RL models (Niv et al., 2002) and optimal search theory (Charnov, 1976). The hidden target search task introduced here has allowed us to separate the influence of external cues from internal prior information for seeking rewards in a novel environment (Viswanathan et al., 1999). In our hidden target search task, participants explored a novel environment and quickly learned to align their fixations with the region of space over which invisible targets were probabilistically distributed. After about a dozen trials, the fixation statistics came close to matching those obtained by an ideal-observer theory. This near-match allowed us to cast human performance as optimal memory-free search with perfect knowledge of the target distribution. As a complement to the ideal-observer theory that addresses asymptotic performance, we developed a mechanistic account of trial-to-trial learning from reinforcement. Our RL model characterized the time course of learning, attained an asymptote near ideal-observer performance, and tied the problem of visual search to a broader theory of motivated learning.

Natural Environments

The ideal-observer and reinforcement-learning frameworks provide the foundation for a broader theoretical perspective on saccade choice during natural vision, in which people learn to search in varied contexts for visible targets, where visual features of the scene are clearly essential. In a Bayesian framework, the subjects in our task learned the prior distribution of the hidden targets. In a natural environment, the prior distribution would be combined with visual information to determine the posterior distribution, from which saccadic targets are generated.

Naturalistic environments are nonstationary. For example, an animal foraging for food may exhaust the supply in one neighborhood and have to move on to another. A searcher must be sensitive to such changes in the environment. Sequential dependencies (Fig. 14.4) are a signature of this sensitivity (Fecteau and Munoz, 2003; Wilder et al., 2011; Adams et al., 2012): Recent targets influence subsequent behavior, even after the searcher has seemingly learned the target distribution, as reflected in asymptotic performance. Sequential dependencies were predicted by the RL model, which generated behavior remarkably close to that of the participants as a group, and also captured individual idiosyncrasies (*Reinforcement Learning Model*). Sensitivity to nonstationary environments can explain why our participants and the RL model attained an asymptotic search distribution somewhat further from the target centroid than is predicted by an ideal-observer theory premised on stationarity.

One of the most impressive feats of animal foraging is matching behavior. Herrnstein's matching law (Herrnstein, 1961) describes how foraging animals tend to respond in proportion to the expected value of different patches. Matching behavior has been studied in multiple species from honey bees to humans (Bradshaw et al., 1976; Greggers and Mauelshagen, 1997; Lau and Glimcher, 2005; Gallistel et al., 2007). However, many of these laboratory studies effectively remove the spatial element of foraging from the task by looking at different intervals of reinforcement on two levers or buttons; in this setting, animals quickly detect changes in reinforcement intervals (Mark and Gallistel, 1994) and the motor effort in switching between spatial patches has been examined (Baum, 1982). In nature, foraging is spatially extended, and the hidden-target search paradigm could serve as an effective environment for examining an explicitly spatial foraging task in the context of matching behavior. For example, a version of our hidden-target search paradigm with a bimodal distribution could explore changeover behavior and motor effort by varying the sizes of the two distributions and distance between them (Baum, 1982).

Neural Basis of Search

The neurobiology of eye movement behavior offers an alternative perspective on the similarities of visual search behavior and foraging. The question of where to look next has been explored neurophysiologically, and cells in several regions of the macaque brain seem to carry signatures of task components required for successful visual search. The lateral interparietal (LIP) area and the superior colliculus (SC) are two brain regions that contain a priority map representing locations of relevant stimuli that could serve as the target of the next saccade. Recordings in macaque area LIP and the SC have shown that this priority map integrates information from both external ("bottom-up") and internal ("top-down") signals in visual search tasks (Fecteau and Munoz, 2006; Bisley and Goldberg, 2010).

Recently, Bisley and coworkers (Mirpour et al., 2009) have used a foraging-like visual search task to show that area LIP cells differentiated between targets and distracters and kept a running estimate of likely saccade goal payoffs. Area LIP neurons integrate information from different foraging-relevant modalities to encode the value associated with a movement to a particular target (Platt and Glimcher, 1999; Klein et al., 2008). The neural mechanisms serving patch stay-leave foraging decisions have recently been characterized in a simplified visual choice task (Hayden et al., 2011), providing a scheme for investigations of precisely how prior information and other task demands mix with visual information available in the scene. Subthreshold microstimulation in area LIP (Mirpour et al., 2010) or the SC (Carello and Krauzlis, 2004) also biases the selection saccades toward the target in the stimulated field. Taken together, these results suggest that area LIP and the SC might be neural substrates mediating the map of likely next saccade locations in our task, akin to the value map in our RL model.

We asked how subjects learn to choose valuable targets in a novel environment. Recent neurophysiological experiments in the basal ganglia provide some suggestions on how prior information is encoded for use in choosing the most valuable saccade target in a complex environment (Nakahara and Hikosaka, 2012). Hikosaka and coworkers (Yasuda et al., 2012) have identified signals related to recently learned, and still labile, value information for saccade targets in the head of the caudate nucleus and more stable value information in the tail of the caudate and substantia nigra, pars reticulata. Because the cells carrying this stable value information seem to project preferentially to the SC, these signals are well placed to influence saccade choices through a fast and evolutionarily conserved circuit for controlling orienting behavior. These results provide a neurophysiological basis for understanding how experience is learned and consolidated in the service of the saccades we make to gather information about our environment about three times each second.

CONCLUSIONS

In our eye-movement search task, subjects learned to choose saccade goals based on prior experience of reward that is divorced from specific visual features in a novel scene. The resulting search performance was well described by an RL model similar to that used previously to examine both foraging animal behavior and neuronal firing of dopaminergic cells.

In addition, the search performance approached the theoretical optimum for performance on this task. By characterizing how prior experience guides eye movement choice in novel contexts and integrating it with both model and theory, we have created a framework for considering how prior experience guides saccade choice during natural vision. The primate oculomotor system has been well studied, which will make it possible to uncover the neural mechanisms underlying the learning and performance of the hidden-target task, which may be shared with other search behaviors.

METHODS

We defined a spatial region of an image as salient by associating it with reward to examine how participants used their prior experience of finding targets to direct future saccades. We took advantage of the fact that the goal of saccadic eye movements is to obtain information about the world and asked human participants to "conduct an eye movement search to find a rewarded target location as quickly as possible." Participants were also told that they would learn more about the rewarded targets as the session progressed and that they should try to find the rewarded target location as quickly as possible. The rewarded targets had no visual representation on the screen and were thus invisible to the subject. The display screen was the same on each trial within a session and provided no information about the target location. The location and the spread of the rewarded target distribution were varied with each session.

Each trial began with a central fixation cross on a neutral gray screen with mean luminance of 36.1 cd/m^2 (Fig. 14.1). The search screen spanned the central 25.6° of the subject's view while seated with his or her head immobilized by a bite bar.

Participants initiated each trial with a button press indicating that they were fixating the central cross. The same neutral gray screen served as the search screen after 300 ms of fixation of the cross. Once the fixation cross disappeared, participants had 20 seconds to find the rewarded location for that trial before the fixation screen returned. On each trial an invisible target was drawn from a predefined distribution of possible targets. The shape of the distribution was Gaussian with the center at an integer number of degrees from the fixation region (usually ±6° in x and y) and spread held fixed over each experimental session. The targets only occurred at integer values of the Gaussian. The probability associated with a rewarded target location varied between 4 percent and 0.1 percent and was given by the spread of the distribution (0.75°, 2°, and 2.75° SD). When a subject's gaze landed within 2° of the target in both the x and y directions, a reward tone marked the successful end of the trial. For the target to be "found," fixation (monitored in real time as detailed below) needed to remain steady within the target window for at least 50 ms. This duration ensured that the target was never found simply by sweeping through during a saccade. If at the end of 20 seconds the target was not found, the trial ended with no tone and a fixation cross appeared indicating the beginning of a new trial.

Trial timing and data collection were managed by the TEMPO software system (Reflective Computing) and interfaced with the stimulus display using an extension of the Psychophysics Toolbox (Brainard, 1997) running under MATLAB (MathWorks). Eye movement data were obtained using a video-based eye tracker (ISCAN), sampled at 240 Hz for humans. Eye data were calibrated by having the participants look at stimuli at known locations. Eye movements were analyzed offline in MATLAB. We detected saccades and blinks by using a conservative velocity threshold (40°/s with a 5-ms shoulder after each saccade) after differentiating the eye position signals. Periods of steady fixation during each trial were then marked and extracted for further analyses. Eye positions off of the search screen were discounted from analysis. Visual inspection of individual trials confirmed that the marked periods of fixation were indeed free from saccades or blinks.

Turning Points

In addition to saccades identified by speed criteria, the eye tracking data were processed to estimate the step-size distribution of all eye movements, even within a fixation. To that end, blinks were first removed by removing samples off the screen. Next, we considered the data points three at a time, $\mathbf{x}_{t-1}$, $\mathbf{x}_t$, and $\mathbf{x}_{t+1}$, where $\mathbf{x}$ are the 2D data points and t indexes the time samples, to construct two segments of the eye track $\mathbf{a} = \mathbf{x}_{t-1} - \mathbf{x}_t$ and $\mathbf{b} = \mathbf{x}_t - \mathbf{x}_{t+1}$. We then tested whether the cosine of the angle between these two was greater or less than 0.95. If the cosine was greater than 0.95, then the center point, $\mathbf{x}_t$, was marked as a "turning" point. In addition, some of the large steps slowly curved and this introduced extraneous points (i.e., dividing a long step into two short steps). To overcome this problem, we took advantage of the fact that two long steps almost never occur one after the other without a dense fixation region in between, and any point with no neighbors within 0.5° was assumed to be extraneous and was removed. This resulted in points at which the eye made a significant deviation from ballistic motion and was used to generate the step size distributions in Fig. 14.5.

ACKNOWLEDGMENTS

We thank Krista Kornylo and Natalie Dill for technical assistance. This work was supported in part by National Science Foundation (NSF) Grant SBE 0542013 to the Temporal Dynamics of Learning Center, an NSF Science of Learning Center grant (to L.C., J.S., M.C.M., and T.J.S.), a Blasker Rose-Miah grant from the San Diego Foundation (to L.C.), Office of Naval Research Multidisciplinary University Research Initiative Award N00014-10-1-0072 (to J.S. and T.J.S.), and Howard Hughes Medical Institute (T.J.S.).

15

Impact of Contour on Aesthetic Judgments and Approach-Avoidance Decisions in Architecture

OSHIN VARTANIAN,[*§§] GORKA NAVARRETE,[†]
ANJAN CHATTERJEE,[‡] LARS BRORSON FICH,[§]
HELMUT LEDER,[‖] CRISTIÁN MODROÑO,[#]
MARCOS NADAL,[‖] NICOLAI ROSTRUP,[**] AND
MARTIN SKOV[††‡‡]

On average, we urban dwellers spend about 90 percent of our time indoors, and share the intuition that the physical features of the places we live and work in influence how we feel and act. However, there is surprisingly little research on how architecture impacts behavior, much less on how it influences brain function. To begin closing this gap, we conducted a functional magnetic resonance imaging study to examine how systematic variation in contour impacts aesthetic judgments and approach-avoidance decisions, outcome measures of interest to both architects and users of spaces alike. As predicted, participants were more likely to judge spaces as beautiful if they were curvilinear than if they

---

[*] Department of Psychology, University of Toronto-Scarborough, Toronto, ON, Canada M1C 1A4; [†] Laboratory of Cognitive and Social Neuroscience (LaNCyS), UDP-INECO Foundation Core on Neuroscience (UIFCoN), Universidad Diego Portales, Santiago, Chile; [‡] Department of Neurology, University of Pennsylvania, Philadelphia, PA 19104; [§] Department of Architecture, Design, and Media Technology, University of Aalborg, DK-9000 Aalborg, Denmark; [‖] Faculty of Psychology and Cognitive Science Research Platform, University of Vienna, 1010 Vienna, Austria; [#] Department of Physiology, Universidad de La Laguna, La Laguna, 38071 Santa Cruz de Tenerife, Spain; [**] The Royal Danish Academy of Fine Arts, Schools of Architecture, Design, and Conservation, School of Architecture, DK-1435 Copenhagen, Denmark; [††] Danish Research Centre for Magnetic Resonance, Copenhagen University Hospital Hvidovre, DK-2650 Copenhagen, Denmark; and [‡‡] Decision Neuroscience Research Group, Department of Marketing, Copenhagen Business School, DK-2000 Copenhagen, Denmark.
[§§] To whom correspondence should be addressed. E-mail: oshinv1@mac.com.

were rectilinear. Neuroanatomically, when contemplating beauty, curvilinear contour activated the anterior cingulate cortex exclusively, a region strongly responsive to the reward properties and emotional salience of objects. Complementing this finding, pleasantness—the valence dimension of the affect circumplex—accounted for nearly 60 percent of the variance in beauty ratings. Furthermore, activation in a distributed brain network known to underlie the aesthetic evaluation of different types of visual stimuli covaried with beauty ratings. In contrast, contour did not affect approach-avoidance decisions, although curvilinear spaces activated the visual cortex. The results suggest that the well-established effect of contour on aesthetic preference can be extended to architecture. Furthermore, the combination of our behavioral and neural evidence underscores the role of emotion in our preference for curvilinear objects in this domain.

On average, Americans spend approximately 90 percent of their time indoors (Klepeis et al., 2001), and there is evidence to suggest that a similar pattern exists worldwide (Ott, 1989). Coupled with our intuition that the physical features of the built environments in which we live and work influence our psychological states, one would expect to find a large empirical literature linking variations in physical features of architecture to psychological states. However, despite some evidence supporting the impact of specific physical architectural features (e.g., building facades and height) on perceptions and preferences (Stamps, 1999; Lindal and Hartig, 2013), there is surprisingly little systematic research on this relationship. One reason for this gap in research could be methodological. Arguably, built environments in their common form do not reduce to a few easily manipulated variables in a laboratory. This limitation partly explains the heavy emphasis on case studies in architecture (Jones and Canniffe, 2007). However, some architects might also be skeptical about the extent to which empirical data gathered by behavioral scientists can be used to optimize the planning, designing, and building of spaces (Weber, 2012). This study represents an attempt to overcome these methodological and principal/philosophical constraints by establishing an empirically driven dialogue between architecture and psychology via neuroscience.

Specifically, we argue that neuroscientific data have an important role to play in bridging the conceptual gap between architecture and psychology by elucidating some of the underlying mechanisms that explain how systematic variations in architectural features lead to behavioral outcomes. This argument is bolstered by current knowledge about the neural underpinnings of basic mental processes that underlie our responses to architecture, including visual perception, spatial navigation, and memory (Sternberg and Wilson, 2006). Thus, coupled with a burgeoning literature on neuroaesthetics—the field devoted to the study of neural systems that underlie aesthetic judgments and preference formations (Skov and Vartanian, 2009; Chatterjee, 2011)—there exists the tantalizing possibility that our intuitions about how we feel and act in built environments can be linked to systematic variations in physical features of those environments. In turn, such evidence could be used to optimize the design of spaces, and possibly improve health (Goldstein, 2006).

Because this must be considered an exploratory study, an important objective was narrowing the potentially very large number of physical features that could be manipulated within the context of architecture down to a manageable set. For the purposes of the present study, our key variable of interest was the contour of architectural spaces. We selected contour because historically architects have consistently considered it to be an important physical feature in planning, designing, and building spaces (Le Corbusier, 1948). Furthermore, the selection of contour was empirically motivated because a number of previous studies have demonstrated that it affects aesthetic judgments. Specifically, early psychological investigations going back almost 100 years examined the effect of contour on feelings (Lundholm, 1921; Poffenberger and Barrows, 1924; Hevner, 1935). In the spirit of early empiricists, experimenters manipulated contour using simple stimuli, such as lines or abstract displays composed of curves or angles. The results of these early studies, confirmed later using typography (Kastl and Child, 1968), converged to show that curvilinear forms are experienced as softer and more pleasant, whereas angular forms are experienced as harder and more serious.

Modern researchers have extended the focus of those early studies to also include preferences. The results have demonstrated consistently that people typically prefer curvilinear to rectilinear objects, be they geometric forms, household objects, furniture, or car interiors (Leder and Carbon, 2005; Bar and Neta, 2006; Dazkir and Read, 2012), and that this effect persists even when controlling for symmetry, prototypicality, and balance (Silvia and Barona, 2009). Furthermore, much like the earlier studies, contemporary studies have shown that curvature elicits pleasant emotions (Leder and Carbon, 2005; Dazkir and Read, 2012). This finding is important because it suggests that the impact of contour on judgment in the form of greater preference for curvilinear objects might be driven by an affective response to curvature. Interestingly, a similar conclusion was drawn over a century ago by the psychologist Kate Gordon, who stated that "curves are in general felt to be more beautiful than straight lines. They are more graceful and pliable, and avoid the harshness of some straight lines" (Gordon, 1909). Note in Gordon's definition not only the observation of a preference for curvilinear forms, but also their grounding in feelings. We aimed to measure this affective response in architecture using both behavioral and neural methods.

In terms of behavior, we focused on aesthetic judgments and approach-avoidance decisions, the selection of which was based on two reasons. First, both outcomes are of interest to architects and users of spaces alike. Second, from an evolutionary perspective, there is reason to believe that the environmental signals that give rise to aesthetic judgments might be borne out of those that regulate biologically more fundamental behaviors, such as approach-avoidance decisions. This idea is based on what the geologist Jay Appleton called "habitat theory," according to which the aesthetic satisfaction one derives from contemplating a natural landscape is proportional to the extent to which its physical features signal environmental conditions favorable or unfavorable to survival (Appleton, 1975/1996). Similar ideas have been voiced elsewhere (Nasar, 1988; Sagan and Druyan, 1992; Kellert and Wilson, 1993), grounded in the argument that our relationship with our natural environment is influenced by our evolutionary history. As Appleton said eloquently, "Habitat theory postulates that aesthetic pleasure in landscape derives from the observer experiencing an environment favorable to the satisfaction of his biological needs." He further added that, "The point at which we always seem to run against a brick wall is in understanding more precisely how the actual ingredients of landscape operate on the aesthetic sense" (Appleton, 1975/1996).

Essentially, in habitat theory not only do we see a clear link between aesthetic judgments and assessments that are more fundamental to survival, but also a mechanism that describes this relationship.

Extending Appleton's landscape-based theory to built environments, the architect Grant Hildebrand has proposed that an analogous argument can be put forth regarding our relationships with constructed spaces (Hildebrand, 1999). Specifically, Hildebrand has argued that given our relatively recent shift to built environments, it is likely that features that evolved to regulate our relationships with our natural habitats continue to exert their influence on our interactions with constructed spaces (Kaplan, 1987, 1992). This theory suggests that in the context of constructed spaces one can explore the degree of overlap between observers' behavioral and neural responses when asked to make aesthetic judgments and approach-avoidance decisions. Furthermore, we believe that contour might be one of the "actual ingredients" (Appleton, 1975/1996) that operates on our aesthetic sense and decisions to approach certain built environments and to avoid others.

Aside from contour, we also introduced ceiling height and openness as two control variables into our design. We opted to explicitly control for them within each level of contour because some evidence exists that they can influence cognition and emotion in the context of architecture (Franz et al., 2005; Meyers-Levy and Zhu, 2007). These aspects were not entered as independent variables of focal interest in the present study because previous empirical evidence linking them specifically to our two outcome measures is absent or limited.

Our study consisted of presenting participants in a functional MRI (fMRI) scanner with photographs of interior spaces that varied in contour (Fig. 15.1). The study was presented in two runs, administered counterbalanced across participants. In the beauty-judgment run, participants were instructed to respond "beautiful" or "not beautiful" upon viewing each stimulus. In the approach-avoidance run, participants were instructed to respond "enter" or "exit" upon viewing each stimulus, to indicate whether this was a space they would like to enter or leave. We hypothesized that spaces with curvilinear contours would more likely elicit "beautiful" judgments in the beauty judgment run and "enter" decisions in the approach-avoidance run, than spaces with rectilinear contours. This result would extend earlier findings regarding preferences for curved objects to the domain of architecture, and determine the extent to which aesthetic judgments and approach decisions (as a function of contour) are correlated. In addition, following the completion of fMRI scans, we collected "beauty" and "pleasantness" ratings for all stimuli, enabling us to conduct parametric analyses to further probe the link between brain activation and aesthetic assessment.

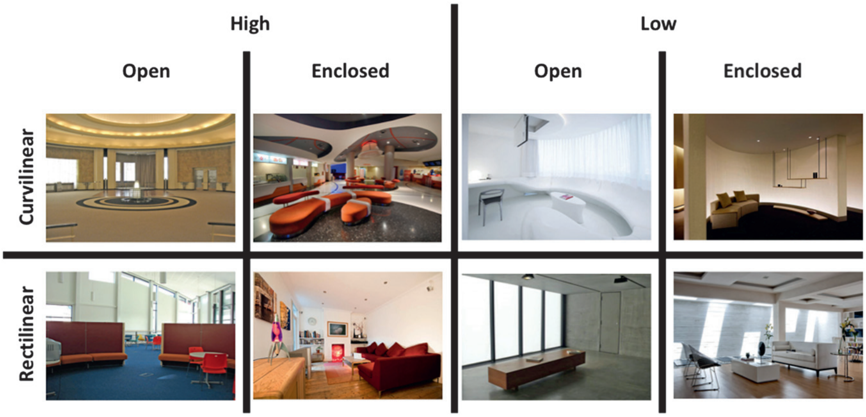


FIGURE 15.1 Examples of stimuli used in the study. The focal aim of the study involved a comparison of contour (i.e., curvilinear vs. rectilinear spaces), although we also controlled for ceiling height (high, low) and openness (open, enclosed) within our two conditions of interest (*Methods*).

At a neurobiological level, we made dissociable predictions for beauty judgments and approach-avoidance decisions. Regarding the former, a large body of literature in neuroaesthetics has demonstrated that aesthetic judgments activate a distributed neural network (Nadal et al., 2008), including the brain's reward and affective circuitry (Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Ishai, 2007; Chatterjee et al., 2009; Di Dio and Gallese, 2009; Ishizu and Zeki, 2011). Indeed, based on the results of the largest meta-analysis of neuroimaging studies of aesthetic appraisal to date, S. Brown et al. (2011) defined a "core circuit for aesthetic processing." Not unlike what has been proposed for the experience of core affect in emotion (Barrett and Wager, 2006; Barrett et al., 2007), this circuit includes four structures: orbitofrontal cortex (OFC), basal ganglia, anterior insula, and cingulate cortex. Each structure has a specific role: OFC's role in reward processing is well established (Kringelbach, 2005). Here, the role underlies the perception of the sensory and reward-based qualities of objects. The anterior insula represents bodily responses in the form of inputs from the interoceptive cortex. The anterior cingulate cortex (ACC), given its strong resting state connectivity with both the OFC and the anterior insula, is proposed to underlie emotional salience monitoring (Taylor et al., 2009). Finally, basal ganglia's role involves processing hedonic information (Berridge and Kringelbach, 2008). Because previous behavioral studies have demonstrated that curvature elicits pleasant emotions (Leder and Carbon, 2005; Dazkir and Read, 2012), we hypothesized that compared with viewing rectilinear spaces, viewing curvilinear spaces would activate structures coextensive with the brain's reward and emotions networks, with specific interest in the regions highlighted in Brown et al.'s meta-analysis of aesthetic appraisal. In turn, we hypothesized that the reverse contrast (i.e., rectilinear-curvilinear) would activate the amygdala. This specific prediction was derived from an earlier fMRI study in which it was shown that viewing rectilinear everyday objects activated the amygdala, suggesting that sharpness might serve as an early warning signal for potential danger (Bar and Neta, 2007).

Regarding approach-avoidance decisions, two distinct bodies of evidence informed our predictions. First, the neural systems for approach-avoidance motivations have been shown to be lateralized: approach motivations are lateralized predominantly to the left hemisphere, whereas avoidance emotions are lateralized predominantly to the right hemisphere (Murphy et al., 2003; Rutherford and Lindell, 2011). Furthermore, electrical stimulation of different regions of the brain can unconditionally elicit approach and avoidance behavior (Olds and Fobes, 1981; Shizgal, 1997; Panksepp, 1998; Knutson and Greer, 2008). For example, electrical stimulation of brain regions that receive projections from midbrain dopamine neurons—including the nucleus accumbens as well as mesial prefrontal cortex—elicits approach behavior. In turn, electrical stimulation of the anterior insula and basolateral amygdala elicits avoidance behavior. Aside from this evidence on the motivational bases of approach-avoidance behavior, contemplating approach or avoidance might also activate brain regions implicated in motor imagery or planning of voluntary motor movement, as the person considers entering or exiting the space (Decety, 1996; Crammond, 1997; Deiber et al., 1998; Grush, 2004; Hanakawa et al., 2008). We therefore hypothesized that compared with viewing rectilinear spaces, viewing curvilinear spaces would activate networks associated with approach motivation or regions implicated in motor imagery or execution. In addition, we hypothesized that the reverse contrast (i.e., rectilinear-curvilinear) would activate networks associated with avoidance motivation.

RESULTS

Behavioral

We analyzed the effect of contour on beauty judgments and approach-avoidance decisions made by participants during the scanning session separately. A Wilcoxon Signed Ranks Test demonstrated that contour had a significant effect on beauty judgments, $Z = -2.13$, $P < 0.05$. Specifically, participants were more likely to judge spaces as beautiful if they had curvilinear rather than rectilinear contours (Fig. 15.2). In contrast, contour had no effect on approach-avoidance decisions, $Z = -1.27$, $P = 0.21$ (Fig. 15.2).

Following the completion of fMRI scanning, participants were presented with all of the stimuli that they had viewed in the scanner once again, and asked to rate each stimulus on pleasantness (using a five-point scale with anchors “very unpleasant” and “very pleasant”) and on beauty (using a five-point scale with anchors “very ugly” and “very beautiful”). Specifically for the stimuli that had been presented in the beauty judgment run, pleasantness ratings (collected outside of the scanner) predicted beauty ratings (collected outside of the scanner), $\beta = 0.73$, $P < 0.001$ (Fig. 15.3). In fact, pleasantness ratings accounted for 58 percent of the observed variance in beauty ratings. We then ran a binary logistic regression where we regressed beauty judgments obtained inside the scanner (i.e., “beautiful” or “not beautiful”) onto pleasantness ratings collected outside of the scanner. Pleasantness was once again a significant predictor of beauty judgment, $\beta = -1.30$, $P < 0.001$. Finally, because we obtained pleasantness ratings for all stimuli (and not just those that were presented in the beauty judgment run), we also ran a binary logistic regression where we regressed approach-avoidance deci-

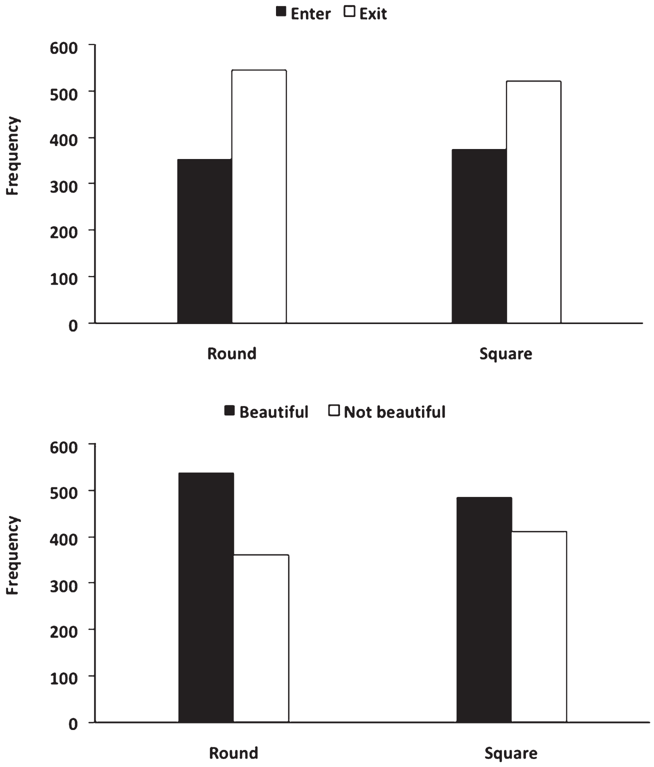


FIGURE 15.2 Effect of curvilinear and rectilinear spaces on beauty judgments and approach-avoidance decisions. The y axis represents the sum of responses.

sions obtained inside the scanner (i.e., "enter" or "exit") onto pleasantness ratings collected outside of the scanner. Pleasantness was a significant predictor of approach-avoidance decisions, $\beta = -1.13$, $P < 0.001$.

Although we had no a priori prediction about response latency, we nevertheless explored the effect of contour on reaction time involving beauty judgments and approach-avoidance decisions. We conducted this analysis because when rating facial attractiveness, people tend to view more attractive faces for longer periods of time (Quinsey et al., 1996; Shimojo et al., 2003). Our results demonstrated that participants viewed spaces that they opted to "enter" for longer periods compared with spaces that they opted to "exit," $t(17) = 2.60$, $P < 0.05$ (Fig. 15.4). In contrast, there was no difference in reaction time related to judging a space as "beautiful" or "not beautiful," $t(17) = -0.84$, $P = 0.41$. In addition, contour had no effect on reaction time in the context of beauty judgments

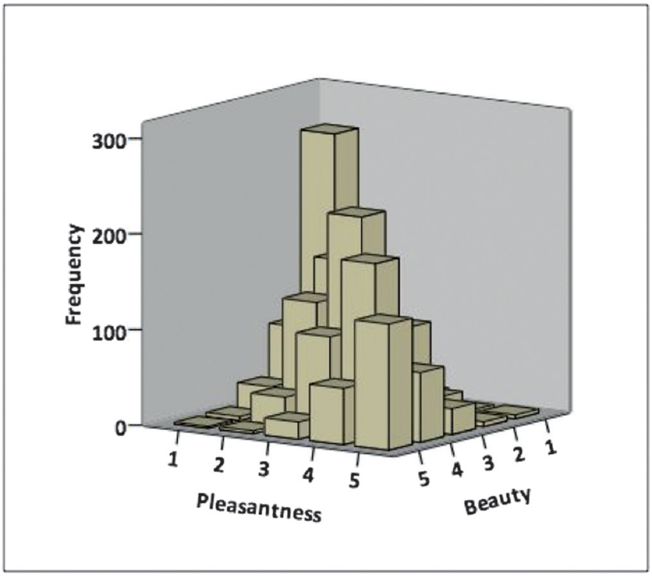


FIGURE 15.3 Pleasantness ratings predict beauty ratings. The *y* axis represents the sum of responses.

FIGURE 15.4 Effect of choice on response latency for beauty judgments and approach-avoidance decisions.

[$t(17) = -0.72$, $P = 0.48$] or approach-avoidance decisions [$t(17) = 1.29$, $P = 0.21$].

Neural

To analyze the fMRI data, we contrasted conditions of interest corresponding to each level of contour by assigning values of 1 and –1 to the regressors of interest, and 0 to all other regressors (*Methods*). For the beauty judgment run, the contrast of curvilinear-rectilinear spaces revealed significant activation in ACC exclusively ($Z = 3.54$, $x = -6$, $y = 42$, $z = -6$, $k = 11$) (Fig. 15.5). The reverse contrast did not reveal any significant area of activation. To further explore the role of reward and emotion in beauty judgment, we conducted two sets of parametric analyses to investigate the covariation of brain activations in relation to (*i*) beauty ratings and (*ii*) pleasantness ratings (both collected outside of the scanner, see above). The first set of analyses involved first-order polynomial expansions exploring linear relationships. The results demonstrated that activation in a distributed network including the frontopolar cortex, superior frontal gyrus, globus pallidus, precuneus, parahippocampus, and the middle occipital gyrus covaried in relation to beauty ratings (Table 15.1). In addition, activation in precuneus, middle frontal gyrus, and ACC covaried in relation to pleasantness ratings (Table 15.1). In our second set

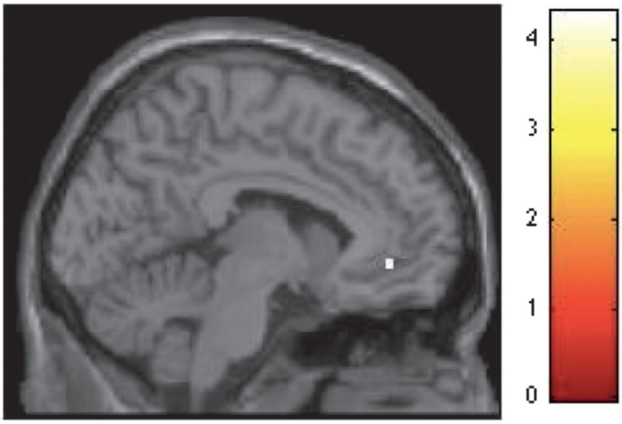


FIGURE 15.5 Curvilinear spaces activate the anterior cingulate cortex in beauty judgments. SPM rendered into standard stereotactic space and superimposed on to sagittal MRI in standard space. Bar represents magnitude of *t*-score.[NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

TABLE 15.1 Regions Activated in the Parametric Analyses Involving Postscan Beauty and Pleasantness Ratings Collected in Relation to the Beauty Run

Parameter	Structure	BA	*x*	*y*	*z*	*z* score	*k*
Beauty	Frontopolar cortex	10	−14	64	−2	3.68	74
	Superior frontal gyrus	6	−26	22	60	3.68	44
	Globus pallidus	—	16	−4	−6	3.66	99
	Precuneus	7	−28	−74	46	3.48	127
	Parahippocampus	27	−26	−32	−2	3.32	35
	Middle occipital gyrus	19	−42	−78	14	3.31	32
	Middle occipital gyrus	19	−30	−86	16	3.30	23
Pleasantness	Precuneus	7	−14	−68	50	3.85	36
	Middle frontal gyrus	9/46	34	42	10	3.77	32
	Middle frontal gyrus	9/46	−38	30	14	3.35	71
	Anterior cingulate cortex	32	−18	44	12	3.42	17

NOTE: BA, Brodmann area; *k*, cluster size. The coordinates are reported in MNI space.

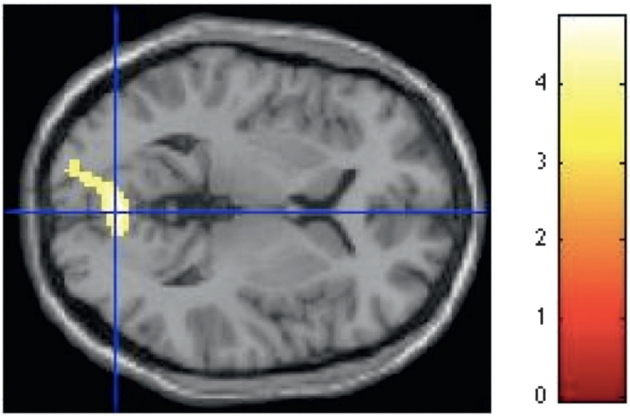


FIGURE 15.6 Curvilinear spaces activate the lingual gyrus and calcarine in approach-avoidance decisions. SPM rendered into standard stereotactic space and superimposed on to transverse MRI in standard space. Bar represents magnitude of *t*-score.[NOTE: Figure can be viewed in color in the PDF version of this volume on the National Academies Press website, www.nap.edu/catalog.php?record_id18573.]

of analyses we explored second-order polynomial expansions but failed to find any evidence for nonlinear relationships between brain activations and beauty or pleasantness ratings.

For the approach-avoidance run, the contrast of curvilinear-rectilinear contours revealed significant activation in a single cluster ($k = 340$) in the visual cortex that included left lingual gyrus ($Z = 3.83$, $x = -20$, $y = -94$, $z = 8$), as well as two regions within the right calcarine ($Z = 3.71$, $x = 2$, $y = -76$, $z = -4$ and $Z = 3.65$, $x = 10$, $y = -74$, $z = -2$) (Fig. 15.6).

Finally, to test Appleton's theory, we conducted a conjunction analysis involving the "beautiful–not beautiful" contrast and the "enter-exit" contrast (*Methods*). In other words, we examined whether judging a space as beautiful activates the same neural system as deciding to enter a space. This conjunction analysis did not reveal any area of significant activation.

DISCUSSION

Our results demonstrated that participants were more likely to judge curvilinear than rectilinear spaces as beautiful (Fig. 15.2). In addition, this effect is likely driven by pleasantness, the valence dimension of the affect circumplex (Russell, 2003) (Fig. 15.4). These results are consistent with evidence from previous studies establishing a preference for curved objects ranging from simple lines to furniture and car interiors (Gordon, 1909; Lundholm, 1921; Poffenberger and Barrows, 1924; Hevner, 1935; Kastl and Child, 1968; Leder and Carbon, 2005; Bar and Neta, 2006; Silvia and Barona, 2009; Dazkir and Read, 2012) and the grounding of that preference in affect (Leder and Carbon, 2005; Dazkir and Read, 2012), and extend them to the domain of architecture. Neuroanatomically, our results demonstrated that judging the beauty of curvilinear spaces was associated exclusively with an increase in ACC activity over and above judging the beauty of rectilinear spaces (Fig. 15.5). As discussed earlier, ACC is part of S. Brown et al.'s (2011) core circuit for aesthetic processing, and its activation here is consistent with the wealth of behavioral data that point to the involvement of emotion and reward in preference for curved objects. Lesion and neuroimaging studies have demonstrated the contribution of ACC to reward and emotional processing (Kringelbach and Rolls, 2004; Liu et al., 2011), as have recent functional connectivity studies based on neuroanatomical parcellation, confirming its role in affective processing (Yu et al., 2011). Along with its rich interconnections with the adjacent OFC (Kringelbach and Rolls, 2004), the ACC is hypothesized to form a functional network underlying sensory consumatory behavior (Van Hoesen et al., 1993). In combination, our results suggest that judgment of beauty for curvilinear spaces is underpinned by emotion and reward, consistent with the role that emotion is known to play in aesthetic experience (Leder et al., 2004).

Interestingly, contrary to expectation, we did not observe activation in the amygdala for the reverse contrast (i.e., rectilinear-curvilinear). This finding suggests that in architecture, sharp contour might not serve as an early warning signal for potential danger as it might elsewhere, an observation that would be consistent with the amygdala's well-established role in fear conditioning (LeDoux, 1998; Phelps, 2006). However, a closer examination of the context within which our data were collected and our analytic method might provide additional explanations for the lack of activation observed in the amygdala. In terms of the former, our daily experiences provide us with ample exposure to rectilinear spaces. Arguably, through conditioning, sharp contours might have lost their value as signals for threat within built environments, for example through mere exposure (Marks and Dar, 2000). Recently, Leder et al. (2011) provided support for the role of context in moderating the effect of contour on preference. Specifically, the authors used positive (e.g., cake, chocolate) and negative (e.g., snake, bomb) stimuli to examine if emotional valence modulates preferences for curved objects. The authors found a preference for curved objects if the context was positive, but not if it was negative. A cross-cultural approach would appear to provide one avenue by which the role of past experience as a moderator of amygdala activation in response to architectural stimuli could be investigated.

From a methodological perspective, amygdala activation in response to rectilinear stimuli (Bar and Neta, 2007) has been observed with very brief presentation times (85 ms). In contrast, our participants viewed each stimulus for 3,000 ms. It is possible that a longer exposure duration might have triggered additional cognitive processing that served to depress the initial, rapid response in the amygdala frequently observed in relation to fearful stimuli (LeDoux, 1998). In addition, there is also evidence to suggest that the amygdala exhibits a nonlinear response profile in relation to facial beauty by responding maximally to extremely attractive and unattractive faces, and relatively less so to faces of average attractiveness (Winston et al., 2007). Insofar as judgment of beauty tracks variations in contour, this finding would suggest that activation in the amygdala could be maximal in relation to maximally curvilinear and maximally rectilinear spaces, although our data do not allow us to examine activation in the amygdala in response to gradations of contour. Future studies in which degree-of-curvature is manipulated systematically could certainly address this possibility.

In addition to the above categorical contrasts involving beauty judgment, we also conducted two parametric analyses involving beauty and pleasantness ratings collected outside of the scanner. The results demonstrated that in the beauty judgment run, brain activation within two distributed networks covaried linearly with beauty and pleasantness ratings (Table 15.1). Importantly, the activation pattern in relation to beauty ratings consisted of structures known to contribute to aesthetic assessments of visual objects. For example, the frontopolar (BA 10) region has been shown to be activated when subjects are instructed to judge the beauty of geometric patterns (Jacobsen et al., 2006), consistent with its more general role in evaluative judgments involving one's thoughts and feelings (Zysset et al., 2002; Christoff et al., 2003). In addition, activations in the parahippocampus, middle occipital gyrus, precuneus, and superior frontal gyrus have been observed in previous studies involving aesthetic assessments of paintings, sculptures, and scenes (Vartanian and Goel, 2004; Di Dio et al., 2007; Yue et al., 2007; Fairhall and Ishai, 2008; Vessel et al., 2012). Interestingly, the structures activated in relation to pleasantness, including the middle frontal gyrus, precuneus, and ACC, have also been shown to be activated for aesthetic assessments of paintings (Vartanian and Goel, 2004; Vessel et al., 2012). The results from the parametric analyses of beauty and pleasantness ratings suggest that in the context of judging beauty in architecture these two variables activate largely dissociable aspects of the same common network that underlies aesthetic assessment of visual stimuli.

In contrast to its effect on beauty judgments, contour had no effect on approach-avoidance decisions (Fig. 15.2). There could be a number of reasons for this result. First, the risk associated with judging a space as beautiful is less than the risk associated with the decision to enter that space, however hypothetical. It is therefore possible that the computation underlying approach and avoidance decisions is weighted differently as a function of this hypothetical risk than judgments of beauty. Consistent with this interpretation, whereas a decision to enter a space was associated with significantly higher response latency than a decision to exit a space, there was no difference in reaction time as a function of response in the beauty judgment condition (Fig. 15.4).

Second, it is also possible that our design might have lacked the degree of fidelity necessary to simulate approach-avoidance decisions that determine behavioral choices in real-life settings. As such, the task would not have fully engaged the decision maker, resulting in a null effect for contour. Methodologically, we opted to use a binary response format for both beauty judgments and approach-avoidance decisions to make comparisons between the two runs possible. As a consequence, our design could not incorporate tasks that, when used in isolation, would appear more ecologically valid for investigating approach-avoidance behavior, such as a visual navigation task.

Finally, the observed behavioral dissociation between beauty judgment and approach-avoidance decisions could also reflect a difference between the impact of contour on "liking" versus "wanting," well established in the neuroscience of reward (Berridge, 1995). In other words, contour may have a genuinely stronger effect on like or dislike for curvilinear spaces than it has on a desire to actually enter or exit these spaces. However, this observed dissociation must be interpreted with some care in light of previous evidence suggesting that in the context of architecture, there may in fact be a close correlation between aesthetic judgments and approach decisions. Specifically, Ritterfeld and Cupchik (1996) instructed their participants to rate photographs of interior spaces on semantic, structural, and connotative dimensions. Their results demonstrated that a willingness to live in a space was determined most strongly by the beauty rating assigned to that space. Also note that in the present study, pleasantness ratings predicted not only beauty judgments but also approach decisions. Taken together, our results suggest that although contour affected aesthetic judgments and approach-avoidance decisions differently, the two outcome measures might nevertheless be influenced by some of the same underlying mechanisms.

When participants made approach-avoidance decisions, the curvilinear-rectilinear contrast activated the visual cortex (Fig. 15.6). We did not observe the predicted activations in areas known to be involved in planning voluntary motor movement. Also notable is the bilateral activation observed in the visual cortex. Indeed, 59 percent of all decisions made in the approach run involved decisions to "exit" spaces ($P < 0.001$, Binomial Test) (Fig. 15.2), based on which one would predict relatively greater involvement of the right hemisphere as a reflection of avoidance motivation (Rutherford and Lindell, 2011; Murphy et al., 2003). As alluded to above, the observed pattern could be attributable to the specific task used in the present study, given that it might have not have engaged processes that motivate approach-avoidance sufficiently.

In his now classic book *The Experience of Landscape*, the geologist Jay Appleton (1975/1996) defined the problem by asking "What is it that we like about landscape, and why do we like it?" In the book, Appleton attempted to reestablish what he perceived to be the lost link in modern society between preferences for certain landscapes and the latter's ability to satisfy the biological and survival needs of humans. By extending habitat theory to built environments and focusing on contour, we asked whether curvilinear spaces would affect beauty judgments and approach decisions in similar ways, and whether the neural systems underlying judgments of "beautiful" and decisions to "enter" a space would overlap. Although the evidence presented here suggests that they might not overlap, we have also noted limitations in our design that suggest further experimentation is necessary to more definitively determine the degree of overlap between their neural bases. Of course our observation could simply be a function of context. Specifically, built environments and landscapes might not be comparable in the extent to which they promote an evaluation of their ingredients for biological survival. Based on this argument, manipulating contour in the context of landscapes might impact approach decisions and their neural correlates differently than what was observed for built environments here.

Critical to understanding the role of context in the perceptual analysis of visual scenes of interiors, are studies of how recruitment of specific structures differs between experts in architecture and laypeople in this process. A number of studies have already begun to address this issue. For example, it has been shown that among architects, neural activation in the OFC and subcallosal cingulate gyrus was higher when assessing the aesthetic value of buildings compared with nonarchitects (Kirk et al., 2009), suggesting that expertise moderates the neural representation of value in the reward network. Furthermore, compared with nonarchitecture students, architecture students recruit fewer brain structures for encoding and detecting building stimuli (Wiesmann and Ishai, 2011), suggesting that their expertise might confer an advantage in terms of neural efficiency in processing domain-specific content. These studies serve to connect studies of expertise in architecture to the broader literature on expertise in empirical aesthetics (Hekkert and van Wieringen, 1996; Müller et al., 2010; Vartanian and Kaufman, 2013). This area would appear to be fertile ground for future research.

CONCLUSION

Long ago, Le Corbusier (1948) opined that "The business of Architecture is to establish emotional relationships by means of raw materials." Le Corbusier was deeply aware of the knowledge that architecture drew from science and engineering toward achieving this goal, mediated as it was by how architectural forms "work physiologically upon our senses." This awareness suggests that neuroaesthetics lies close to the kernel of modern architecture. Given our increasing propensity to spend time indoors (Klepeis et al., 2001), our results suggest that a systematic evaluation of how the physical features of built environments affect human behavior, emotion, and brain function is both timely and within reach. Not only is there the prospect that this interdisciplinary enterprise could lead to the design of more pleasant work and life spaces (Goldstein, 2006; Sternberg and Wilson, 2006), but these data could also shed light on perhaps a more fundamental question: Why it is that we have come to prefer the places that we do?

METHODS

Participants

The participants provided written informed consent under the guidance of the The Universidad de La Laguna REB board–El Comité de Ética de la Investigación y de Bienestar Animal (CEIBA). We recruited 18 (12 females, 6 males) neurologically healthy participants (M = 23.39 years, SD = 4.49) with normal or corrected-to-normal vision. All participants were right handed, as determined by a standard questionnaire (M = 74.72, SD = 19.29) (Oldfield, 1971).

Materials

The stimuli for this study consisted of 200 photographs of architectural spaces (Fig. 15.1). Half of the photographs were used in the beauty judgment run and the other half for the approach-avoidance run. The stimuli were culled from larger architectural image databases available to L.B.F. at the Department of Architecture, Design, and Media Technology in University of Aalborg, Denmark, and to N.R. at The Royal Danish Academy of Fine Arts, Schools of Architecture, Design and Conservation, School of Architecture. Half of the spaces were designated rectilinear and the other half curvilinear. Within each level of contour we also controlled for ceiling height and openness. In other words, within each of the curvilinear and rectilinear sets we included 25 open high-ceiling images, 25 closed high-ceiling images, 25 open low-ceiling images, and 25 closed low-ceiling images. L.B.F. and N.R. reached interrater consensus for the inclusion of each image in the final set. All images were standardized in terms of size and resolution. This procedure was adopted because no available dataset of architectural stimuli existed that provided 100 rectilinear and 100 curvilinear images, balanced for ceiling height and openness. To obtain the stimulus set please contact O.V.

Procedures

In the course of structural MRI acquisition, participants were familiarized with the task via exposure to trials involving beauty judgments and approach-avoidance decisions. During fMRI scanning the beauty judgment and approach-avoidance runs were administered in counterbalanced order across participants. The task was presented using E-Prime. Each trial within the runs had identical structure: it began with a fixation point "X" presented for 1,000 ms, followed by a stimulus presented for 3,000 ms (during which a response was collected), followed by variable intertrial interval (ITI). The average duration of ITI across all trials was 4,000 ms (selected randomly without replacement from a finite bin varying among 3,000, 4,000, 6,000, and 7,000 ms). Immediately after exiting the fMRI scanner, participants rated all stimuli on pleasantness (using a five-point scale with anchors "very unpleasant" and "very pleasant") and on beauty (using a five-point scale with anchors "very ugly" and "very beautiful").

fMRI Acquisition

A 3-Tesla MR scanner with an eight-channel head coil (Signa Excite HD, 16.0 software; General Electric) was used to acquire T1 anatomical volume images (1.0 × 1.0 × 1.0-mm voxels). For functional imaging, T2*-weighted gradient echo spiral-in/out acquisitions were used to produce 35 contiguous 4-mm-thick axial slices [repetition time (TR) = 2,000 ms; echo time (TE) = 21.4 ms; flip angle (FA) = 90°; field of view (FOV) = 260 mm; 64 × 64 matrix; voxel dimensions = 4 × 4 × 4.0 mm], positioned to cover the whole brain. The first 10 volumes were discarded to allow for T1 equilibration effects. The number of volumes acquired was 430 (+10 dummies).

fMRI Analysis

Data were analyzed using Statistical Parametric Mapping (SPM8). Head movement was less than 2 mm in all cases. We implemented slice timing to correct for temporal differences between slices within the same volume, using the first slice within each volume as the reference slice. All functional volumes were spatially realigned to the first volume of the first run. A mean image created from realigned volumes was spatially normalized to the Montreal Neurological Institute (MNI) echo planar imaging brain template using nonlinear basis functions. The derived spatial transformation was applied to the realigned T2* volumes, and spatially smoothed with an 8-mm full-width at half-maximum isotropic Gaussian kernel. Time series across each voxel were high-pass filtered with a cutoff of 128 seconds, using cosine functions to remove section-specific low-frequency drifts in the blood-oxygen level-dependent (BOLD) signal. Condition effects at each voxel were estimated according to the general linear model and regionally specific effects compared using linear contrasts. The BOLD signal was modeled as a boxcar, convolved with a canonical hemodynamic response function. Each contrast produced a statistical parametric map consisting of voxels where the z-statistic was significant at $P < 0.001$. We adopted a combination of voxel-level and cluster-size correction to control against false positives. Specifically, using a random-effects analysis, we reported activations that survived whole-brain voxel-level intensity threshold of $P < 0.001$, and a minimum cluster size of 10 voxels, uncorrected for multiple comparisons. Previous analyses have demonstrated that this combination adequately controls against false positives for both 2D and 3D volumes (Forman et al., 1995; Lieberman and Cunningham, 2009).

We conducted three sets of analyses. The first analysis was a test of our focal hypothesis, and consisted of comparing curvilinear to rectilinear trials, separately for beauty judgment and approach-avoidance runs. The second analysis geared toward testing Appleton's theory was based on a conjunction analysis involving the beautiful–not beautiful contrast and the enter-exit contrast. To ensure that (*i*) both analyses were run based on the same design matrix and (*ii*) explicitly included our control variables, within each run we created 16 regressors corresponding to a crossing of four variables: contour (rectilinear, curvilinear) × ceiling height (high, low) × openness (open, enclosed) × response (enter-exit or beautiful–not beautiful). Our two focal analyses were conducted by assigning weights of “1” or “–1” to the relevant regressors. Although incorporated into the design, motor response and ITI were modeled out of the analyses by assigning null weights to their respective regressors. Our third analyses were parametric and involved first-order polynomial expansions exploring linear relationships as well as second-order polynomial expansions exploring nonlinear relationships in relation to beauty and pleasantness ratings (collected outside of the scanner).

In addition to the aforementioned two focal analyses, for the beautiful–not beautiful contrast we also used small volume correction in SPM8 to conduct region-of-interest analyses by creating spheres with a 15-mm radius around the principal activation-likelihood estimation foci extracted in a recent meta-analysis of studies of visual aesthetics [supplemental table 3 in Brown S et al. (2011)]. We were particularly interested in exploring activations in the anterior insula, the amygdala, and specific structures in the basal ganglia. This region-of-interest exploration did not yield additional areas of activation.

ACKNOWLEDGMENTS

This work was supported by the following: Ministerio de Ciencia a innovación Grant TIN2011-28146, 2011 and Ministerio Industrio, Turismo y Comercio, Avanza Grant TSI-020100-2010-346 under the direction of Jose Luis Gonzalez-Mora; and was supported in part by Servicio de Resonancia Magnética para Investigaciones Biomédicas de la Universidad de La Laguna. The MRI and behavioral data have been deposited in http://figshare.com.

16

Dynamics of Brain Networks in the Aesthetic Appreciation

CAMILO J. CELA-CONDE,*§ JUAN GARCÍA-PRIETO,†
JOSÉ J. RAMASCO,‡ CLAUDIO R. MIRASSO,‡
RICARDO BAJO,† ENRIC MUNAR,* ALBERT FLEXAS,*
FRANCISCO DEL-POZO,† AND FERNANDO MAESTÚ†

Neuroimage experiments have been essential for identifying active brain networks. During cognitive tasks as in, e.g., aesthetic appreciation, such networks include regions that belong to the default mode network (DMN). Theoretically, DMN activity should be interrupted during cognitive tasks demanding attention, as is the case for aesthetic appreciation. Analyzing the functional connectivity dynamics along three temporal windows and two conditions, beautiful and not beautiful stimuli, here we report experimental support for the hypothesis that aesthetic appreciation relies on the activation of two different networks, an initial aesthetic network and a delayed aesthetic network, engaged within distinct time frames. Activation of the DMN might correspond mainly to the delayed aesthetic network. We discuss adaptive and evolutionary explanations for the relationships existing between the DMN and aesthetic networks and offer unique inputs to debates on the mind/brain interaction.

---

*Evocog Group, Instituto de Física Interdisciplinar y Sistemas Complejos (IFISC), Universidad de las Islas Baleares y Consejo Superior de Investigaciones Científicas, 07122 Palma de Mallorca, Spain; †Centro de Tecnología Biomédica, Universidad Politécnica y Universidad Complutense, 28223 Madrid, Spain; and ‡IFISC, 07122 Palma de Mallorca, Spain. §To whom correspondence should be addressed. E-mail: cjcela@atlas.com.es.

Since the appearance of the first neuroimaging articles on aesthetics (Cela-Conde et al., 2004; Kawabata and Zeki, 2004; Vartanian and Goel, 2004), a considerable number of studies have drawn a complex picture of the neural processes underlying people's aesthetic preference for visual and auditory stimuli. Many brain regions seem to be relevant for aesthetic appreciation. However, three sets of regions are often reported in the experimental results—those related to (*i*) reward/pleasure and emotion, (*ii*) judgment/decision making, and (*iii*) perception.

Most experiments have aimed at identifying brain regions whose activity varies with the aesthetic experience. Some studies, however, like Jacobsen et al. (2006) and Vessel et al. (2012), have reported brain activity in terms of putative networks, pointing to a network consisting of medial parts of frontal cortex (FMC), precuneus (PCUN), and posterior cingulate cortex (PCC), among other regions. These interconnected regions partly match the default mode network (DMN), corresponding to a baseline state of the human brain in awake but resting conditions (resting state) (Raichle et al., 2001).

BRAIN CONNECTIVITY RELATED TO DMN

The argument that a brain network exists lies in the assumption that some kind of connectivity exists between the areas involved. Following von der Malsburg and Schneider (1986), connectivity is associated with the presumable synchronization of neuronal assemblies—synchronous "firing." Distributed local networks of neurons would, eventually, be transiently linked by reciprocal dynamic connections (Varela et al., 2001).

"Functional connectivity" (Friston et al., 1993, 1995) is defined as the statistically temporal dependency of neuronal activation patterns of anatomically separated brain regions (van den Heuvel and Hulshoff Pol, 2010). To uncover such dependency, temporal series of activation/deactivation of hypothetically synchronized brain regions must be compared. Such temporal series can be obtained, for instance, by detecting changes in blood oxygen content (blood oxygen level dependent signals) (Ogawa et al., 1990) due to neural activity.

Raichle et al. (2001), using positron emission tomography (PET), were able to identify the DMN, subsequently confirmed with functional magnetic resonance imaging (fMRI) (Greicius et al., 2003). Several variables affect DMN activity, such as age, experience, and disease (Raichle et al., 2001). Despite this variability, resting-state studies using different subjects, different methods, and different types of acquisition protocols have consistently reported that the DMN consists at least of the precuneus, medial frontal, inferior parietal, and medial temporal areas (van den Heuvel and Hulshoff Pol, 2010). The breadth of the DMN has been extended to include ventral anterior cingulate cortex, bilateral inferior parietal cortex, left inferolateral temporal cortex (Greicius et al., 2004), and even the hippocampus (Greicius et al., 2004; Rosazza and Minati, 2011).

Although, as we will see later, some relationships between DMN and executive tasks—particularly involving working memory—exist, the activity of the DMN is curtailed when participants perform attention-demanding, goal-directed activities (Raichle et al., 2001; Greicius et al., 2003; Fox et al., 2005). Tasks asked by Jacobsen et al. (2006) and Vessel et al. (2012) of their participants required cognitive processes that rely on attentional resources. Consequently, the engagement of the DMN during aesthetic appreciation seems surprising.

PROCESSES RELATED TO AESTHETIC APPRECIATION

In neuroaesthetic experiments, the tasks usually required from participants involve at least the processes of (*i*) viewing stimuli, (*ii*) appreciating their aesthetic qualities, (*iii*) rating their value, and (*iv*) formulating a response. These cognitive processes seem not to occur simultaneously. By means of electroencephalography (EEG), Jacobsen et al. reported that descriptive judgments of symmetry are performed faster than evaluative appreciation of their beauty (Jacobsen and Höfel, 2003). In turn, Locher et al. (2007, p. 55), drawing from behavioral experiments and semantic judgments, interpreted that perception of art "begins with the rapid generation of a gist reaction followed by scrutiny of pictorial features." Similarly, Winkielman and Cacioppo (2001) held that beautiful objects, at least, elicit positive emotions before subjects make overt judgments. In a different domain, Haidt (2001) proposed the existence in moral judgments of a quick, unconscious, and automatic evaluation (moral intuition), followed by a posterior reasoning process in which subjects search for justification of their intuitive judgment (moral reasoning). Although Haidt's model is grounded in behavioral experiments, this is particularly interesting because several authors—including Jacobsen et al. (2006)—have posited the eventual existence of brain mechanisms shared by aesthetic and moral judgments (Agnati et al., 2007; Tsukiura and Cabeza, 2011; Zaidel and Nadal, 2011; Avram et al., 2012). Thus, coincidence between moral and aesthetic brain networks might occur.

Regarding aesthetic perception, the following null hypotheses can be expressed:

(*i*) An initial, general appraisal of the aesthetic qualities, consisting of the perception of a visual stimulus as "beautiful" or "not beautiful," is performed very quickly. The neural correlates of such aesthetic appreciation constitute a network. We call this general process "aesthetic appreciation *sensu stricto*" and the network it relies on the "initial aesthetic network."

(*ii*) Particular appraisals of detailed aspects of beauty, such as gauging the extent to which the stimulus is moving, whether it is interesting or original, how to rate it, the reasons for considering it attractive, and so forth, are performed later. We call these detailed processes "aesthetic appreciation *sensu lato*." Putative networks formed by the neural correlates of such detailed aspects might be reduced to just one: the "delayed aesthetic network."

To which network would the DMN correspond: initial, delayed, both, or none? To give an answer, it is necessary to empirically determine the brain networks involved in aesthetic appreciation, as well as the time frame in which they are active. Once this has been clarified, the possible coincidence between the DMN and one or more aesthetic networks can be ascertained.

EXPERIMENT ON BRAIN CONNECTIVITY DURING AESTHETIC APPRECIATION

Our null hypotheses refer to cognitive processes taking place in a short timescale, compared with the relatively stable condition of subjects' brain activity during the resting state. Some studies have focused on the dynamic changes in brain networks, using fMRI (Bassett et al., 2011), but, when the whole brain is considered, their time windows cover several seconds. Therefore, to test our hypotheses we are forced to use higher temporal-resolution techniques.

With a temporal resolution of milliseconds, magnetoencephalography (MEG), which detects changes in the magnetic fields generated by the postsynaptic activity of neurons, is one of such techniques. By means of MEG, we have obtained temporal series of brain activity for 24 participants during the resting state and during aesthetic appreciation of visual stimuli. Four hundred stimuli were successively projected and participants decided whether each stimulus was beautiful or not beautiful.

The MEG signals were split into three time windows and two evaluative conditions. Artifact-free time windows of 500 ms before stimuli projection were manually extracted for further connectivity analysis, constituting time window (TW0). After each stimulus onset, 1,500-ms artifact-free epochs were divided into two additional time windows: TW1, 250–750 ms; and TW2, 1,000–1,500 ms (Fig. 16.1, *Upper*). The length of the windows was determined by taking into account the time span in which brain activity can reach frontal areas during aesthetic appreciation (Cela-Conde et al., 2004). Before 250 ms, cognitive processes related to aesthetic appreciation

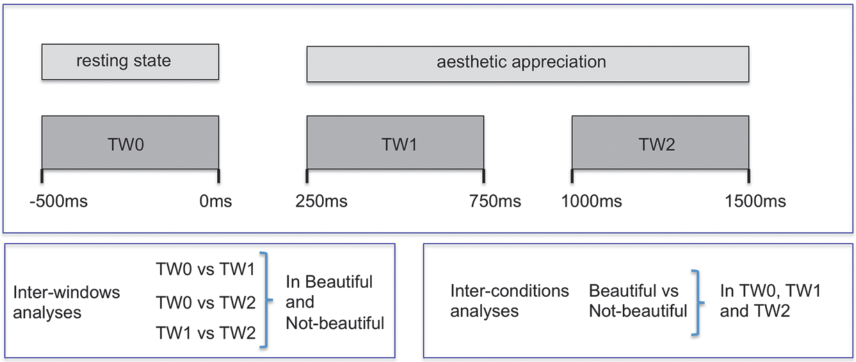


FIGURE 16.1 Temporal windows, conditions, and comparative analyses used in our experiment.

rely mostly on visual-processing occipital areas (Mormann, 2000). In turn, MEG signals corresponding to the participants' stimuli appreciation were grouped, constituting the beautiful and not beautiful conditions.

Two different comparative strategies were carried out. Interwindows comparisons evaluated differences in connectivity between temporal windows along each condition (Fig. 16.1, *Lower Left*). Interconditions comparisons evaluated differences in connectivity between beautiful and not beautiful stimuli in each temporal window (Fig. 16.1, *Lower Right*). We estimated the synchronization of temporal series in the beta band by means of Pearson's correlation coefficient and phase locking value (PLV) (Pereda et al., 2005; Wang et al., 2012). In all cases, $P < 0.05$.

RESULTS

Our analyses measure phase synchronization and amplitude correlation between time traces of activation of MEG sensors. In our case, connectivity is expressed by a bounded [0–1] weight, related to the amount of channelwise synchronization. We infer functional connectivity from these measures. Thus, "connectivity" and "synchronization" can be taken here as equivalent concepts from the point of view of brain communication, despite the lack of information about the anatomical connectivity between neuronal regions and their precise localization. Although correlation takes into account the amplitude of a signal, phase synchronization can be observed even in the absence of amplitude synchronization.

TABLE 16.1 Number of Sensors (*S*) and Links (*L*) More Synchronized in the Interwindows Comparisons at $P < 0.05$

	Beautiful		Not Beautiful	
Windows	*S*	*L*	*S*	*L*
TW0 > TW1	117	1,012	98	695
TW1 > TW0	58	310	58	328
TW0 > TW2	13	8	23	15
TW2 > TW0	0	0	0	0
TW1 > TW2	51	282	63	389
TW2 > TW1	112	1,087	83	431

Interwindows Analyses

Differences in synchronization appear in Table 16.1.

TW0 vs. TW1

Compared with TW1, TW0 shows more synchronized pairs of MEG sensors in both conditions (Table 16.1). The higher TW0 connectivity extends contralaterally from anterior occipital to anterior parietal, linking both hemispheres (Fig. 16.2, *Upper*).

In turn, TW1 > TW0 show similar numbers for both conditions (Table 16.1), with the higher TW1 connectivity placed in occipital regions (Fig. 16.2, *Lower*).

TW0 vs. TW2

Connectivity differences are fewer in TW0 > TW2 compared with the TW0 > TW1 case (Table 16.1). TW2 > TW0 does not show any difference (Table 16.1).

TW1 vs. TW2

TW1 > TW2 connectivity is more apparent in the not beautiful stimuli (Table 16.1). The higher TW1 synchronization appears in occipital–parietal links under both conditions. Moreover, in the not beautiful condition it extends from the occipital and parietal to the orbitofrontal region (Fig. 16.3, *Upper Right*).

TW2 > TW1 synchronization reveals the opposite trend: The number of links and sensors that are more activated is higher for the beautiful

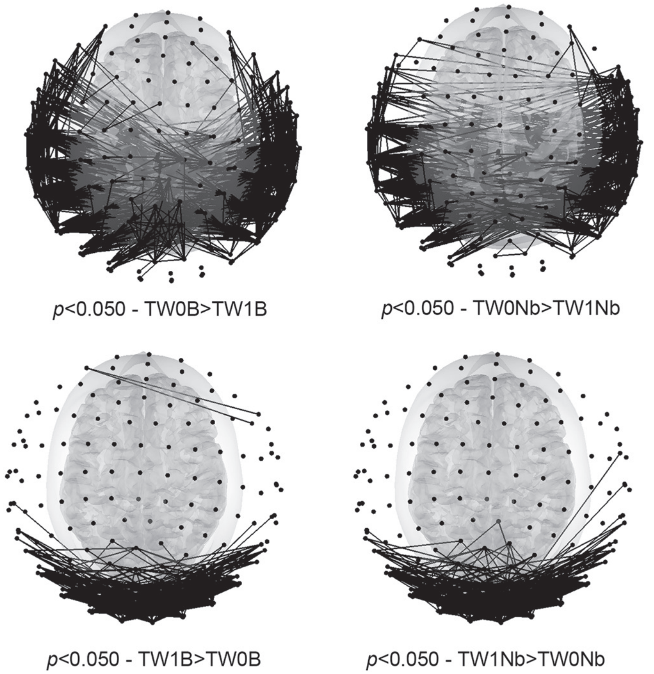


FIGURE 16.2 Differences of synchronization between TW0 and TW1. (*Left*) Under the beautiful condition (brain regions more connected before stimuli qualified as beautiful by participants). (*Right*) Under the not beautiful condition. (*Upper*) TW0 > TW1 synchronization. (*Lower*) TW1 > TW0 synchronization.

condition (Table 16.1). Also, the pattern of synchronization differs. TW2 > TW1 bilaterally reveals higher synchronization shared along parietal to temporal regions. In the beautiful condition, it is more medially and frontally placed. In the not beautiful condition, apart from being reduced, it is more laterally placed (Fig. 16.3, *Lower*).

Interconditions Analyses

Differences in synchronization appear in Table 16.2.

TW0

Intercondition comparisons show minimal significant differences either in beautiful > not beautiful or in the opposite case (Table 16.2).

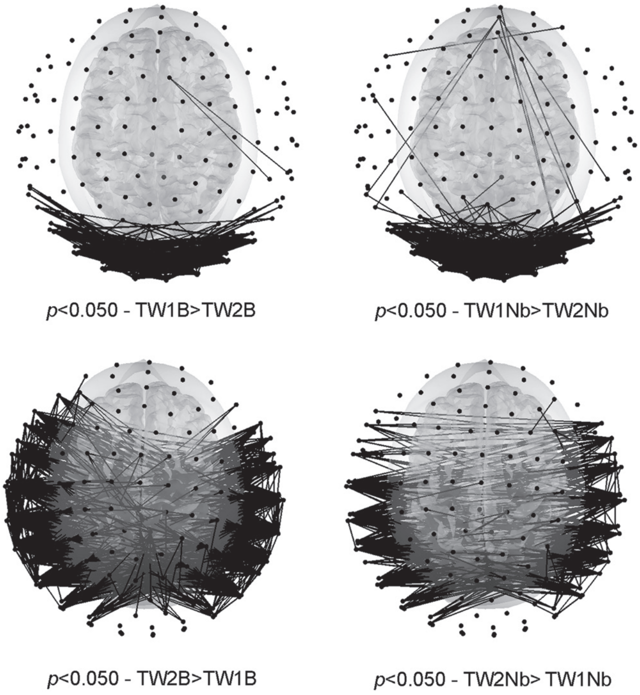
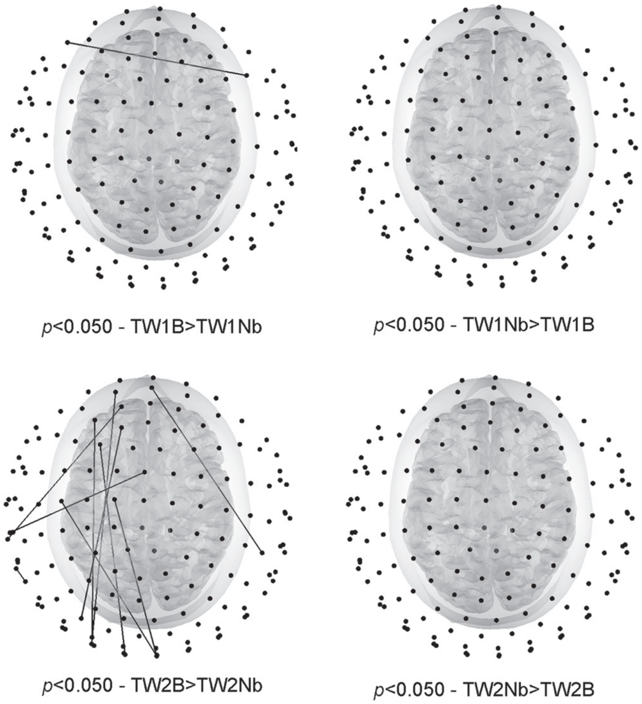


FIGURE 16.3 Synchronization in TW1 and TW2 under beautiful (*Left*) and not beautiful (*Right*) conditions.

TABLE 16.2 Number of Sensors and Links More Synchronized in the Intercondition Comparisons at $P < 0.05$

	Beautiful > Not Beautiful		Not Beautiful > Beautiful	
Windows	Sensors	Links	Sensors	Links
TW0	6	3	0	0
TW1	2	1	0	0
TW2	19	10	0	0



p<0.050 - TW1B>TW1Nb

p<0.050 - TW1Nb>TW1B

p<0.050 - TW2B>TW2Nb

p<0.050 - TW2Nb>TW2B

FIGURE 16.4 Intercondition differences in synchronization at TW1 and TW2. (*Left*) Higher synchronization for the beautiful condition. (*Right*) Higher synchronization for the not beautiful condition.

TW1

Also, intercondition comparisons show minimal significant differences either in beautiful > not beautiful or in the opposite case (Table 16.2).

TW2

In TW2, not beautiful > beautiful does not manifest differences either. On the contrary, beautiful > not beautiful analysis shows 19 sensors more connected (Table 16.2), with links extending from occipital and parietal to frontal regions in the left hemisphere (Fig. 16.4, *Lower*).

DISCUSSION

If we compare interwindow and interconditions analyses, the most conspicuous difference appears in the number of sensors and links implied (Tables 16.1 and 16.2 and Figs. 16.3 and 16.4). Interwindows differences affect extended networks in all cases, whereas interconditions differences are few. This is an expected outcome. Interwindows analyses refer to the dynamics of a cognitive process, that of appreciating beauty, which, as our hypotheses hold, may suffer considerable changes along the different time windows. This means that distinct brain networks will be activated in each case, leading to strong differences in connectivity. In turn, interconditions analyses refer, in the same time window, to the process of appreciation of beauty. Differences will appear only after reaching its result, beautiful or not beautiful, implying subtle changes in connectivity because most of the cognitive resources are the same when an object is considered beautiful or not beautiful.

Resting-State Issue

Both recent experience and consolidated abilities leave memory traces that affect the resting-state brain networks (Waites et al., 2005; Rosazza and Minati, 2011). This is particularly important regarding the specific conditions of TW0, taken as the resting state of our experiment. Participants were quickly aware of the upcoming cognitive task to be performed, on the grounds of their recent experience. Moreover, they were soon habituated to the task of judging the beauty of stimuli. Thus, probably our participants had a TW0 network organization biased by the cognitive tasks to be developed.

However, our subjects could not anticipate the condition of the incoming picture. Thus, TW0 synchronization should be similar under beautiful and not beautiful stimuli. Interconditions analysis for TW0 indicates this coincident synchronization (Table 16.2). The few random differences that appear (Table 16.2) can be attributed to statistical fluctuations caused by the small number of sampled individuals.

Fig. 16.2, *Upper* shows in sagittal view how TW0 is more connected than TW1 mainly in occipital, temporal, and parietal areas. In turn, interwindows TW0 > TW1 analysis manifests a curtailing of the resting-state connectivity during TW1, affecting both conditions (Table 16.1). As is well known, the DMN fades when attentional tasks, such as seeing the projected stimuli, are performed. Our results support this curtailing in TW1.

Brain network differences present in the TW0 to TW1 dynamics disappear when TW0 is compared with TW2 (Table 16.1). This result indicates that the brain networks active during the resting state and diminished in

TW1 are somehow reestablished in TW2. We will come back to this point when discussing the delayed aesthetic network.

Twofold Model of Aesthetic Appreciation

TW1, compared with TW2, shows a different pattern of synchronization under beautiful and not beautiful conditions (Fig. 16.3). The results, thus, support our hypothesis about the existence of distinct cognitive events taking place at different time spans—what we call aesthetic appreciation *sensu stricto* and aesthetic appreciation *sensu lato* processes. Identification of such processes highlights the existence of a dynamical structure embedded within the whole episode of aesthetic appreciation. Also, a distinct network is related to each process—initial aesthetic network/aesthetic appreciation *sensu stricto* vs. delayed aesthetic network/aesthetic appreciation *sensu lato.* This twofold model of aesthetic appreciation is probably the main achievement of our work.

Initial Aesthetic Network

Comparisons between TW0 and TW1 reflect, under both conditions of beauty, that the brain connectivity present in the resting state is substituted during aesthetic appreciation *sensu stricto* by a network that mainly connects occipital regions: the initial aesthetic network. The task of identifying cognitive processes related to these network dynamics is not easy. Compared with TW2, TW1 synchronization is higher in the not beautiful case (Table 16.1). It includes links extending from occipital to frontal regions, particularly the orbitofrontal cortex (OFC) (Fig. 16.3, *Upper Right*). The activation of OFC has been related to not beautiful stimuli appreciation (Munar et al., 2012), so the lack of frontal synchronization in the beautiful condition in the TW1 > TW2 comparison may suggest that beautiful stimuli do not activate OFC during TW1. However, this conclusion would lie in a misunderstanding. As we have already mentioned, our analyses are grounded in comparisons of connectivity, so equally synchronized regions do not yield differences. An OFC equally connected in TW1 and TW2 will not appear in the comparison between these windows. To check the eventually distinct degree of synchronization in OFC—or any other area—before beautiful vs. not beautiful stimuli we must use the interconditions analysis.

Interconditions analyses of synchronization during TW1 give almost no significant difference between beautiful and not beautiful stimuli (Fig. 16.4, *Upper*). This means that, during TW1, all brain regions reached by our analysis—OFC among them—would be equally synchronized in both conditions. TW1 > TW2 connectivity in frontal regions for the not beautiful condition must, then, be grounded on a curtailing during TW2. We can state that the aesthetic appreciation *sensu stricto* (that one corresponding to TW1) implies common, shared cognitive processes regardless of the stimuli beauty or lack of it, giving OFC an important role in the initial aesthetic network.

The activation of OFC has been consistently related to reward and punishment (Bechara et al., 2000; Kringelbach and Rolls, 2004; Nadal et al., 2008). It processes information about the identity and reward value, associating visual stimuli to taste and touch primary reinforcers (Rolls, 2004). However, our concerns refer to its linking paths. OFC, medial prefrontal, and the central nucleus of the amygdala form part of the central autonomic network, which controls appetitive (approach) and aversive (withdraw) behavior (Agnati et al., 2011). Primate OFC receives information about the sight of objects from the temporal lobe cortical visual areas, contributing to stimulus-reinforcement association learning (Rolls, 1999, 2004; Kable and Glimcher, 2009; Rolls and Treves, 2011). As Elliott et al. (2000) stated, the OFC is likely to be activated when the problem of "what to do" before a visual stimulus is best solved by taking into account the likely reward value rather than its identity or location.

Emotional mechanisms related to OFC activation, such as those identified in many neuroaesthetics experiments, could also contribute to the increase of attentional resources, having an important role in decision making (Bechara et al., 2000; Rushworth et al., 2008; Kable and Glimcher, 2009). S. Brown et al. (2011) have pointed out that aesthetic pleasure is an object-related emotion, thus leading to pleasure and repulsion, whereas outcome-related emotion leads to happiness and disappointment. Visual stimuli, such as those normally used in neuroaesthetics, would be examples of "objects," whereas actions used in neuroethics—see Greene et al. (2001), for instance—would constitute "outcomes." Appraisal of objects is strongly associated with OFC (Rushworth et al., 2008), something that is consistent with the idea that this region is "a form of higher-level sensory cortex receiving input from 'what' sensory pathways involved in object processing" (Brown S et al., 2011, p. 251).

Assessment of beauty seems to appear in the dynamic transit from TW1 to TW2, because later latencies manifest—as we will immediately see—differences in synchronization depending on the putative previous results of beauty appreciation. The initial aesthetic network is visible during early latencies (250–750 ms). If this early process follows a parallel with Haidt's moral intuition, it would be performed automatically, in an unconscious manner, although easily accessible to consciousness.

Delayed Aesthetic Network

TW2 > TW1 connectivity is reflected by the pattern and number of sensors/links synchronized under the beautiful and not beautiful conditions, showing important differences between each case (Table 16.1). The scope and meaning of these differences are better understood by means of the interconditions analyses for TW2. Table 16.2 and Fig. 16.4, *Lower,* show TW2 beautiful > not beautiful connectivity. The inverse not beautiful > beautiful synchronization gives no result (Table 16.2). Moreover, it does not appear at any level of significance between $P < 0.01$ and $P < 0.1$. These results support our second hypothesis of existence of a delayed aesthetic network that is active only during the aesthetic appreciation *sensu lato* of beautiful stimuli. Fig. 16.5 shows the delayed aesthetic network under different perspectives.

The delayed aesthetic network consists of synchronized activity mainly present along left regions. Medial occipital, lateral occipital, lateral posterior parietal, medial parietal, medial frontal, and prefrontal in the left hemisphere are linked in it. It is important to underline that (*i*) we are focusing on MEG sensors connectivity, and (*ii*) just sensors more synchronized in the beautiful condition, compared with the not beautiful one, are identified.

Keeping in mind these limitations, relationships between the delayed aesthetic network and regions previously reported as active during the aesthetic appreciation can be stated. Many examples of activation in frontal, parietal, and occipital regions exist. However, few studies on func-

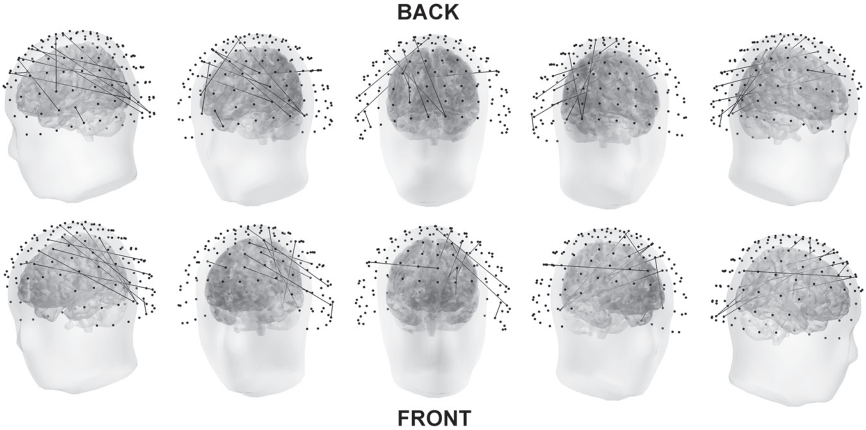


FIGURE 16.5 Delayed aesthetic network in the intercondition (TW2, beautiful > not beautiful) analysis.

tional connectivity during aesthetic appreciation have been carried out, thus far. S. Brown et al. (2011, p. 256) proposed a model of aesthetic processing consisting of "interaction between interoceptive and exteroceptive processing via recurrent connectivity between anterior insula and OFC," pointing out that this circuit "is in no way restricted to aesthetic processing, but may be related to all cognitive processes that involve viscerality . . . . We propose that recurrent connectivity between the anterior insula and the OFC can mediate . . . the assignment of valence to objects." Thus, Brown et al.'s model would better correspond to the initial aesthetic network, where, incidentally, as we have seen, OFC has an important role. Similar patterns of functional connectivity along the reward circuit were offered by Tsukiura and Cabeza (2011), Lacey et al. (2011), and Faivre et al. (2012). Lacking more accurate dynamic studies, all these works seem to cover aesthetic appreciation *sensu stricto* processes, in which resting-state synchronization is greatly diminished. What happens with the putative coincidence of the DMN with aesthetic networks?

DMN Role in Aesthetic Appreciation

As we have seen, the dynamic scenario during the aesthetic appreciation implies a late recovering, during TW2, of the TW0 brain synchronization. The DMN would thus coincide with some of the networks active during this late episode.

Under TW2 > TW1 comparison, beautiful and not beautiful conditions share a bilateral synchronization linking lateral regions along frontal–parietal–temporal–occipital areas (Fig. 16.3, *Lower*). In turn, the differences of synchronization in favor of beautiful stimuli seem to affect mainly medial parts of the brain. These differences are better shown in the TW2 intercondition analysis (Figs. 16.4, *Lower* and 16.5). On the basis of the combined interconditions and interwindows analyses, it seems that, despite the moderate spatial accuracy of MEG signals at the sensors level, the delayed aesthetic network matches frontal, parietal, and temporal medial parts belonging to the DMN (Figs. 16.3 and 16.4). Moreover, this coincidence takes place only in TW2, and only under the beautiful condition. Fig. 16.6 shows in different perspectives more synchronized networks in TW2 vs. TW1 for each condition.

An intriguing question affects the recovering of part of the TW0 connectivity during TW2 when not beautiful stimuli are involved. As we have mentioned, in TW2 > TW1 comparison both conditions share a higher synchronization that is bilaterally expressed along temporal–parietal–occipital links (Fig. 16.3, *Lower*). This pattern matches the similar bilateral synchronization during TW0 (Fig. 16.2, *Upper*). These TW0 and

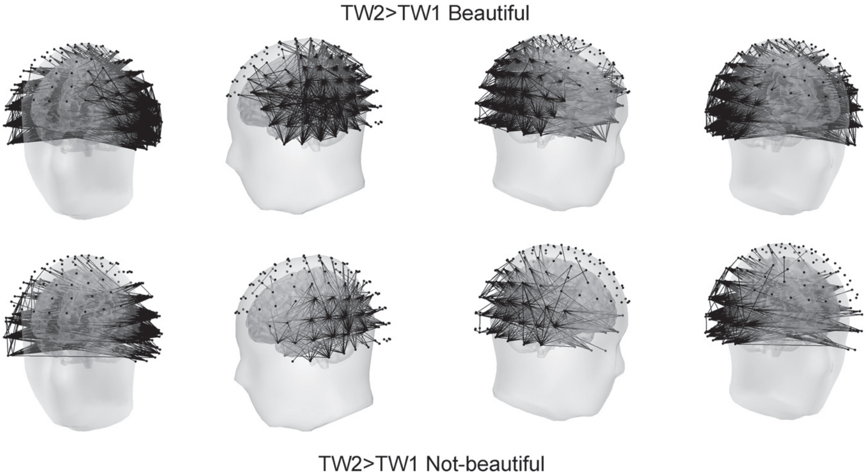


FIGURE 16.6 TW2 > TW1 synchronization in beautiful (*Upper*) and not beautiful (*Lower*) conditions.

TW2 highly connected regions, due to their lateral position, should have scarce relationship with the medially placed DMN.

According to He et al. (2009), during the resting state the brain functional network consists not only of the DMN. Also, four other modules are active. Among them, module III mainly includes lateral parts of frontal and parietal regions, being involved in attention processing (He et al., 2009).

Two different networks related to attention have been indicated as relevant to guide conduct before stimuli of special importance. A dorsal frontoparietal network in the right hemisphere maintains endogenous signals based on expectation of seeing an object at a particular location, linking relevant stimuli to responses (Corbetta et al., 2008). A second system, the ventral frontoparietal network, responds along with the dorsal network when behaviorally relevant objects or targets are detected. This second network disappears when attention is focused, to prevent distraction, but is reactivated during reorienting events such as those needed by the unexpected appearance of objects (Corbetta et al., 2008). These kinds of tasks, also engaged in aesthetic appreciation, would be responsible for the activation of a putative reorienting network during TW2, shared by both beautiful and not beautiful conditions (Fig. 16.7). However, due to the lack of spatial accuracy of MEG at the sensor level, its coincidence with He et al.'s (2009) module III is tentative.

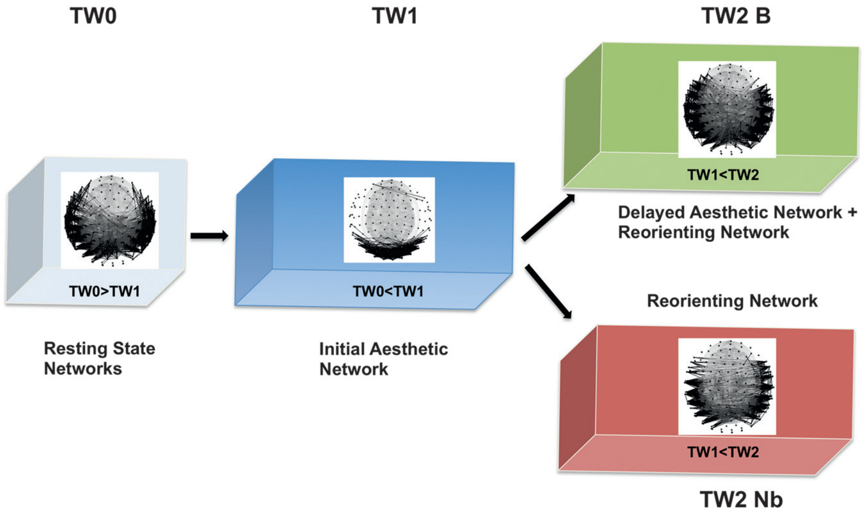


FIGURE 16.7 Dynamics in the appreciation of beauty. TW0 networks (illustrated by the TW0 > TW1 comparison) fade during TW1, being substituted by a similar network shared by beautiful and not beautiful conditions (illustrated by the TW1 > TW0 comparison under the beautiful condition). During TW2, not beautiful stimuli activate a bilateral reorienting network, whereas beautiful stimuli add the delayed aesthetic network, more medially placed (in each condition, TW2 networks are illustrated by TW2 > TW1 comparison).

Activation of the DMN has been proposed to occur during moral decision making (Greene et al., 2004; Amodio and Frith, 2006; Reniers et al., 2012), thus supporting the existence of brain mechanisms shared between moral and aesthetic appreciation *sensu stricto.* These common resources would strengthen the links between our hypotheses and Haidt's (2001) model of moral processes. Early episodes (moral judgment and aesthetic appreciation *sensu stricto*) do seem to have common features. However, the later moral reasoning, with its role as a self-justifying device, differs from our delayed aesthetic appreciation *sensu lato*. The latter seems to be quicker, not having any justificatory purpose. In actual fact, to decide to what point brain networks active during moral reasoning and aesthetic appreciation *sensu lato* are equivalent we would need to get both brain connectivity and its dynamics in moral judgment processes. Although some results on the presence of brain networks during moral reasoning exist (Xue et al., 2013), their dynamic analyses are currently lacking.

Adaptive Issues

It is well established that the brain is a metabolically expensive organ. In the awake resting state, the brain consumes 20% of the total oxygen in the body, despite that it represents only 2 percent of body weight (Gusnard et al., 2001). To explain evolutionary changes in the brain, costs/ benefits ratios should be clarified (Aiello and Wheeler, 1995). Thus, the adaptive advantages of any brain activity must be explained. What might the adaptive value of aesthetic appreciation be?

It has been held that aesthetics could be just an exaptation (Kaplan, 1987). Focusing on positive-valence aesthetic appraisals, S. Brown et al. (2011, p. 257) argued that "[aesthetic processing] evolved first for the appraisal of objects of survival advantage, such as food sources, and was later co-opted in humans for the experience of artworks for the satisfaction of social needs." Obviously, this hypothesis is difficult to test—although it seems reasonably sound when trying to relate aesthetic appreciation to the adaptive advantages of emotions. However, the way in which this exaptation occurred still remains unexplained. The DMN–aesthetic appreciation link might help to justify it.

Raichle et al. (2001, p. 681) posited that the function of the first region of the DMN, formed by the posterior cingulate cortex and adjacent precuneus, was to "continuously gather information about the world around, and possibly within us." Regarding the second region of the DMN, the medial prefrontal cortex would reflect "a dynamic interplay between ongoing cognitive processes and the emotional state of the subject [playing a role] in the integration of emotional and cognitive processes" (Raichle et al., 2001, p. 682). Both functional capacities of the DMN seem adaptive enough to justify its metabolic costs. A different question is that of explaining how this link between the DMN and aesthetic appreciation appeared or, in other words, what characteristic of the DMN might lead to the sudden experiences of a picture's or a landscape's beauty.

An added function of the DMN relates it with "mind wandering" processes. Mind wandering refers to images, thoughts, voices, and feelings that the brain spontaneously produces in the absence of external stimuli [stimulus-independent thought (SIT)] (Mason et al., 2007). This SIT is what we might call the mind talking with itself.

SIT could be a by-product of a general ability to manage concurrent mental tasks, acquired during human evolution (Mason et al., 2007). Nevertheless, Mason et al. (2007) offered two possible explanations for the functional meaning of mind wandering. SIT would enable subjects to maintain an optimal level of arousal, as well as adding coherence to one's past and present experience.

DMN Activation During Executive Tasks

Remembering the past and imagining the future are processes that activate the DMN (Schacter and Addis, 2007). In principle, mental simulations of the future are decoupled from achieving a particular goal, something that fits well with the fact that the DMN decreases its activity during attentional or executive tasks. However, when subjects are presented with imaginary scenarios in which they need to solve specific problems, some coactivity between the DMN and executive regions appears (Gerlach et al., 2011). It seems that simulating how to solve a problem in the future allows "task-positive network regions to be coactive with default network regions without suppressing the contribution of either network" (Gerlach et al., 2011, p. 1823). To do so, the DMN seems to cover two seemingly contrasting functions: spontaneous cognition and monitoring the environment. They need not be mutually exclusive, because they "represent complementary instances of conscious experiences occurring during idle moments of daily life" (Mantini and Vanduffel, 2013, p. 76). There is a growing body of evidence showing the complex relationships existing between inner thought and the processing of external events. It shows that traditional dichotomies, such as on-task vs. off-task, goal-free vs. goal-directed, or mind wandering vs. mental target are inadequate to describe some processes of thought.

This seems to be the case of aesthetic appreciation.

Aesthetic appreciation is not an example of stimulus-independent thinking. Except when recalling past experiences or imaging objects or places, detecting beauty depends on external stimuli. However, aesthetic appreciation might be a by-product of the capacity for mind wandering. Mind wandering is a general, extended process of perception neither guided by any goal nor directed to any particular aspect. A close-to-mind-wandering capacity for assigning beauty or ugliness to visual stimuli could thus lead to continuous and fast processes of aesthetic appreciation. The combination of EEG and fMRI (Kounios and Beeman, 2009) allows us to relate the sudden comprehension that accompanies solving a problem or a perceptual ambiguity—known as the "Aha! moment"—with the culmination of a series of cognitive events starting at the resting state. Regarding aesthetic appreciation, our current study suggests that the appreciation of beauty might also be an Aha! moment, the sudden result of a complex process to which the DMN and other networks contribute.

Aesthetic appreciation processes can be reached even if no previous purpose to evaluate beauty exists. The human capacity for aesthetic appreciation could be tentatively described as something like seeing the world continuously, in a not-oriented way, with an unconscious capacity for perceiving beauty that can almost instantaneously become conscious, constituting an Aha! moment. Everyday life perception of images and the ability to contemplate objects as likely to be seen as beautiful are different orientations that can lead to distinct cognitive processes (Cupchik et al., 2009). Nevertheless, we can posit that the Aha! moment also appears under experimental conditions when stimuli to be judged in aesthetic terms are expected to be seen. Natural and experimental conditions refer to processes that must rest on the same phylogenetically fixed cognitive mechanisms of appreciation of beauty, which include cooperation of the DMN with other perceptual, decisional, and emotional networks. On the grounds of our results, the Aha! moment would have a place when the results of aesthetic appreciation *sensu stricto* become conscious. If the DMN helps in this achievement, the Aha! moment might constitute an early episode during aesthetic appreciation *sensu lato,* i.e., in TW2. The first consideration that subjects perform, at the beginning of TW2, could be the awareness of the actual beauty or ugliness of stimuli.

The eventual relationship of this aesthetic Aha! moment with other episodes, such as that of problem solving, cannot be determined thus far. The cognitive processes related to problem solving and beauty appreciation seem very different from each other. Therefore, different brain networks might be implied. Nevertheless, once again, we need further studies of other Aha! synchronization dynamics to be able to check their eventual coincidence against the aesthetic networks identified by us.

Pathologic Alterations

Aesthetic appreciation compound complexity is supported by pathologic alterations of cognition. The DMN decreases its resting-state activity in patients with Alzheimer's disease (Greicius et al., 2004; Zhou et al., 2010; Bai et al., 2011). Crucial components of the DMN are damaged, impairing cognitive tasks related with explicit memory. Despite this, patients with Alzheimer's disease are still able to enjoy the aesthetic qualities of objects and express their aesthetic preference in a consistent manner, indicated by highly similar ordering at different moments in time of representational, quasi-representational, and abstract picture cards, according to their preference (Halpern et al., 2008). Halpern et al.'s (2008) results show that patients with Alzheimer's disease are well aware of their personal, intrinsic appreciation of beauty and that they are also able to communicate its content. This fact implies that such patients (*i*) appreciate beauty in pictures, (*ii*) can compare pictures according to their beauty, and (*iii*) can order them consequently. The process affects not only aesthetic appreciation *sensu stricto*. Ranking the beauty of each stimulus, comparing them all, rating them, and reporting their response form part of aesthetic appreciation *sensu lato* and are realized in a stable manner over time. The capacity for appreciating beauty despite the impairment of DMN components supports the idea that aesthetic appreciation is achieved by means of a quite general coactivity of distinct networks across the brain. Although patients with Alzheimer's disease would probably have an altered experience of beauty, they keep enough cognitive resources to reach the aesthetic appreciation even in advanced stages of the illness (Graham et al., 2013).

Comparative Synthesis

Combining the previous results obtained with our current MEG results, the following panorama appears:

(*i*) A fast aesthetic appreciative perception (aesthetic appreciation *sensu stricto*) is formed within the 250- to 750-ms time window (TW1), activating the initial aesthetic network.

(*ii*) Further cognitive processes—aesthetic appreciation *sensu lato*—are subsequently performed within the 1,000- to 1,500-ms time window (TW2), relying on the delayed aesthetic network.

(*iii*) The initial aesthetic network is involved in both conditions (beautiful and not beautiful), OFC having an important role in it.

(*iv*) The delayed aesthetic network is composed of more synchronized links in the beautiful condition. It can be posited that matching with the DMN occurs only then, during the aesthetic appreciation *sensu lato.*

(*v*) Initial and delayed aesthetic networks appear to be clearly separated in our analysis. However, this might be a result of the time-windows distribution. Because we have considered TW0, TW1, and TW2 to be separated by 250-ms time spans, an eventual gradual transition from the aesthetic appreciation *sensu stricto* to the aesthetic appreciation *sensu lato* would be hidden by the lack of information corresponding to the temporal borders. To decide the gradual or abrupt character of the transition, precisely identifying the Aha! moment event, more accurate analyses should be carried out.

Hard Problem

The internal but stimulus-dependent visual appreciation of beauty is a subjective experience, what philosophers call a "*quale*." How far have we come in understanding how the brain produces this mental result?

The soft problem of the mind/brain issue (Crick and Koch, 1990), consisting in our case of the localization of brain areas active when subjects gauge the beauty of a visual object, has already been clarified many times under different tasks and experimental conditions.

Combining results of fMRI, MEG, and behavioral studies, we seem to have begun scratching the surface of the hard problem (Crick and Koch, 2003), that is, the way in which the experience of beauty could dynamically arise from the actions of the brain. This point has been only partly solved, thus far. It seems that the structure of the *quale*, consisting of a description of mental processes, can be accessed by means of scientific procedures regarding brain connectivity and its flow along time. Hopefully, we have offered some genuine inputs into the dynamics of aesthetic appreciation. However, for the time being, the content of the *quale*—that is, the eventual result of beauty, or its absence, as an inner sensation—is still out of our reach. Many personal circumstances, from previous experiences to character traits, plus health, age, and maybe sex, as well as cultural and historical particularities of each subject and epoch, surely contribute to the Aha! experience of appreciating beauty.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their important suggestions to improve the article. This work was supported by the following projects of the Spanish Government: Ministerio de Economía y Competitividad and Fondo Europeo de Desarrollo Regional FFI2010-20759 and FIS2012-30634; and Ministerio de Ciencia e Innovación FIS2007-60327. Also, we thank the support of the Comunidad Autonoma de les Illes Balears.

References

Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland T, Jr, Sapolsky RM (2003) Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm Behav* 43(1):67–82.

Acharya VV, Richardson M, Van Nieuwerburgh S, White LJ (2011) *Guaranteed to Fail* (Princeton Univ Press, Princeton, NJ).

Açık A, Sarwary A, Schultze-Kraft R, Onat S, König P (2010) Developmental changes in natural viewing behavior: Bottom-up and top-down differences between children, young adults and older adults. *Front Psychol* 1:207.

Adams GK, Watson KK, Pearson J, Platt ML (2012) Neuroethology of decision-making. *Curr Opin Neurobiol* 22(6):982–989.

Addis DR, Wong AT, Schacter DL (2007) Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45(7):1363–1377.

Adkins-Regan E (2005) *Hormones and Animal Social Behavior* (Princeton Univ Press, Princeton, NJ).

Adolphs R (2003) Cognitive neuroscience of human social behaviour. *Nat Rev Neurosci* 4(3):165–178.

Agnati LF, Agnati A, Mora F, Fuxe K (2007) Does the human brain have unique genetically determined networks coding logical and ethical principles and aesthetics? From Plato to novel mirror networks. *Brain Res Brain Res Rev* 55(1):68–77.

Agnati LF, Barlow PW, Baluška F, Tonin P, Guescini M, Leo G, Fuxe K (2011) A new theoretical approach to the functional meaning of sleep and dreaming in humans based on the maintenance of "predictive psychic homeostasis." *Commun Integr Biol* 4(6):1–16.

Aguirre GK, Zarahn E, D'Esposito M (1998) Neural components of topographical representation. *Proc Natl Acad Sci USA* 95(3):839–846.

Aiello LC, Wheeler P (1995) The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr Anthropol* 36(2):199–221.

Akirav I, Richter-Levin G (1999) Biphasic modulation of hippocampal plasticity by behavioral stress and basolateral amygdala stimulation in the rat. *J Neurosci* 19(23):10530–10535.

Alkire MT, Hudetz AG, Tononi G (2008) Consciousness and anesthesia. *Science* 322(5903): 876–880.

Allen EA, Erhardt EB, Damaraju E, Gruner W, Segall JM, Silva RF, Havlicek M, Rachakonda S, Fries J, Kalyanam R, Michael AM, Caprihan A, Turner JA, Eichele T, Adelsheim S, Bryan AD, Bustillo J, Clark VP, Feldstein Ewing SW, Filbey F, Ford CC, Hutchison K, Jung RE, Kiehl KA, Kodituwakku P, Komesu YM, Mayer AR, Pearlson GD, Phillips JP, Sadek JR, Stevens M, Teuscher U, Thoma RJ, Calhoun VD (2011) A baseline for the multivariate comparison of resting-state networks. *Front Syst Neurosci* 5(2):1–23.

Allen TA, Fortin NJ (2013). Reply to Rattenborg and Martinez-Gonzalez: Fundamental and divergent aspects of the neurobiology of episodic memory. *Proc Natl Acad Sci USA* 110(40):E3742.

Allen TA, Furtak SC, Brown TH (2007) Single-unit responses to 22 kHz ultrasonic vocalizations in rat perirhinal cortex. *Behav Brain Res* 182(2):327–336.

Allman JM (1999) *Evolving Brains* (Scientific American Library, New York).

Amaral DG, Witter MP (1989) The three-dimensional organization of the hippocampal formation: A review of anatomical data. *Neuroscience* 31(3):571–591.

Amemori K, Graybiel AM (2012) Localized microstimulation of primate pregenual cingulate cortex induces negative decision-making. *Nat Neurosci* 15(5):776–785.

Amodio DM, Frith CD (2006) Meeting of minds: The medial frontal cortex and social cognition. *Nat Rev Neurosci* 7(4):268–277.

Amsterdam B (1972) Mirror self-image reactions before age two. *Dev Psychobiol* 5(4): 297–305.

Anderson AK, Yamaguchi Y, Grabski W, Lacka D (2006) Emotional memories are not all created equal: Evidence for selective memory enhancement. *Learn Mem* 13(6):711–718.

Anderson JR, Gallup GG, Jr (2011) Do rhesus monkeys recognize themselves in mirrors? *Am J Primatol* 73(7):603–606.

Anderson SA, Classey JD, Condé F, Lund JS, Lewis DA (1995) Synchronous development of pyramidal neuron dendritic spines and parvalbumin-immunoreactive chandelier neuron axon terminals in layer III of monkey prefrontal cortex. *Neuroscience* 67(1):7–22.

Andreoni J, Bernheim BD (2009) Social image and the 50–50 norm: A theoretical and experimental analysis of audience effects. *Econometrica* 77(5):1607–1636.

Andreoni J, Petrie R (2004) Public goods experiments without confidentiality: A glimpse into fund-raising. *J Public Econ* 88(7):1605–1623.

Apperly IA (2012) What is "theory of mind"? Concepts, cognitive processes and individual differences. *Q J Exp Psychol (Hove)* 65(5):825–839.

Appleton J (1975/1996) *The Experience of Landscape* (John Wiley & Sons, New York).

Arai T, Watanabe T, Nagaro T, Matsuo S (1981) Blood-brain barrier impairment after cardiac resuscitation. *Crit Care Med* 9(6):444–448.

Araujo C, Kowler E, Pavel M (2001) Eye movements during visual search: The costs of choosing the optimal path. *Vision Res* 41(25–26):3613–3625.

Aron A, Fisher H, Mashek DJ, Strong G, Li H, Brown LL (2005) Reward, motivation, and emotion systems associated with early-stage intense romantic love. *J Neurophysiol* 94(1):327–337.

Aru J, Bachmann T, Singer W, Melloni L (2012) Distilling the neural correlates of consciousness. *Neurosci Biobehav Rev* 36(2):737–746.

Arum R, Roksa J (2010) *Academically Adrift* (Univ of Chicago Press, Chicago).

Ashraf N, Bandiera O, Jack K (2012) No Margin, No Mission? A Field Experiment on Incentives for Pro-social Tasks. Harvard Business School Working Papers. Available at www.hbs.edu/faculty/Pages/download.aspx?name=12-008.pdf. Accessed April 20, 2013.

Atoji Y, Wild JM (2004) Fiber connections of the hippocampal formation and septum and subdivisions of the hippocampal formation in the pigeon as revealed by tract tracing and kainic acid lesions. *J Comp Neurol* 475(3):426–461.

Atoji Y, Wild JM (2006) Anatomy of the avian hippocampal formation. *Rev Neurosci* 17(1-2): 3–15.

Averbeck BB (2010) Oxytocin and the salience of social cues. *Proc Natl Acad Sci USA* 107(20): 9033–9034.

Avise, JC, Ayala FJ, eds (2007) *In the Light of Evolution. Volume I: Adaptation and Complex Design* (National Academies Press, Washington, DC).

Avise JC, Ayala FJ, eds (2009) *In the Light of Evolution. Volume III: Two Centuries of Darwin* (National Academies Press, Washington, DC).

Avise JC, Ayala FJ, eds (2010) *In the Light of Evolution. Volume IV: The Human Condition* (National Academies Press, Washington, DC).

Avise JC, Hubbell SP, Ayala FJ, eds (2008) *In the Light of Evolution. Volume II: Biodiversity and Extinction* (National Academies Press, Washington, DC).

Avram M, Gutyrchik E, Bao Y, Pöppel E, Reiser M, Blautzik J (2012) Neurofunctional correlates of aesthetic and moral judgments. *Neurosci Lett* 534:128–132.

Axelrod R (1984) *The Evolution of Cooperation* (Basic Books, New York).

Ayala F (2012) Foreword. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 49-74.

Ayotte J, Peretz I, Hyde K (2002) Congenital amusia: A group study of adults afflicted with a music-specific disorder. *Brain* 125(Pt 2):238–251.

Ayres I, Raseman S, Shih A (2009) Evidence from Two Large Field Experiments That Peer Comparison Feedback Can Reduce Residential Energy Usage. NBER Working Paper No. 15386 (National Bureau of Economic Research, Cambridge, MA).

Azzi JC, Sirigu A, Duhamel JR (2012) Modulation of value representation by social context in the primate orbitofrontal cortex. *Proc Natl Acad Sci USA* 109(6):2126–2131.

Baars BJ (2002) The conscious access hypothesis: Origins and recent evidence. *Trends Cogn Sci* 6(1):47–52.

Baars BJ (2003) The double life of B. F. Skinner. *J Conscious Stud* 10(1):5–25.

Baars BJ (2005) Subjective experience is probably not limited to humans: The evidence from neurobiology and behavior. *Conscious Cogn* 14(1):7–21.

Babb S, Crystal J (2005) Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learn Motiv* 36:177–189.

Babb SJ, Crystal JD (2006) Episodic-like memory in the rat. *Curr Biol* 16(13):1317–1321.

Bachevalier J, Brickson M, Hagger C (1993) Limbic-dependent recognition memory in monkeys develops early in infancy. *Neuroreport* 4(1):77–80.

Bacon F (2000) *The New Organon,* eds Jardine L, Silverthorne M (Cambridge Univ Press, Cambridge, UK).

Bai F, Watson DR, Shi Y, Wang Y, Yue C, Teng Y, Wu D, Yuan Y, Zhang Z (2011) Specifically progressive deficits of brain functional marker in amnestic type mild cognitive impairment. *PLoS ONE* 6(9):e24271.

Baird B, Smallwood J, Mrazek MD, Kam JW, Franklin MS, Schooler JW (2012) Inspired by distraction: Mind wandering facilitates creative incubation. *Psychol Sci* 23(10):1117–1122.

Balkin TJ, Braun AR, Wesensten NJ, Jeffries K, Varga M, Baldwin P, Belenky G, Herscovitch P (2002) The process of awakening: A PET study of regional brain activity patterns mediating the re-establishment of alertness and consciousness. *Brain* 125(Pt 10):2308–2319.

Baluch F, Itti L (2011) Mechanisms of top-down attention. *Trends Neurosci* 34(4):210–224.

Banta Lavenex P, Lavenex P (2009) Spatial memory and the monkey hippocampus: Not all space is created equal. *Hippocampus* 19(1):8–19.

Bar M, Neta M (2006) Humans prefer curved visual objects. *Psychol Sci* 17(8):645–648.

Bar M, Neta M (2007) Visual elements of subjective preference modulate amygdala activation. *Neuropsychologia* 45(10):2191–2200.

Barefoot JC, Grønbaek M, Jensen G, Schnohr P, Prescott E (2005) Social network diversity and risks of ischemic heart disease and total mortality: Findings from the Copenhagen City Heart Study. *Am J Epidemiol* 161(10):960–967.

Baron RA, Markman GD (2003) Beyond social capital: The role of entrepreneurs' social competence in their financial success. *J Bus Venturing* 18(1):41–60.

Baron-Cohen S (2012) *The Science of Evil* (Basic Books, New York).

Barrett LF, Wager T (2006) The structure of emotion: Evidence from the neuroimaging of emotion. *Curr Dir Psychol Sci* 15(2):79–85.

Barrett LF, Mesquita B, Ochsner KN, Gross JJ (2007) The experience of emotion. *Annu Rev Psychol* 58:373–403.

Barth J, Call J (2006) Tracking the displacement of objects: A series of tasks with great apes and young children. *J Exp Psychol* 32:239–252.

Barton BH (2010) *The Lawyer-Judge Bias in the American Legal System* (Cambridge Univ Press, New York).

Barton RA, Capellini I (2011) Maternal investment, life histories, and the costs of brain growth in mammals. *Proc Natl Acad Sci USA* 108(15):6169–6174.

Bartz JA, Zaki J, Bolger N, Ochsner KN (2011) Social effects of oxytocin in humans: Context and person matter. *Trends Cogn Sci* 15(7):301–309.

Bass DI, Partain KN, Manns JR (2012) Event-specific enhancement of memory via brief electrical stimulation to the basolateral complex of the amygdala in rats. *Behav Neurosci* 126(1):204–208.

Bassett DS, Wymbs NF, Porter MA, Mucha PJ, Carlson JM, Grafton ST (2011) Dynamic reconfiguration of human brain networks during learning. *Proc Natl Acad Sci USA* 108(18):7641–7646.

Bateson M, Nettle D, Roberts G (2006) Cues of being watched enhance cooperation in a real-world setting. *Biol Lett* 2(3):412–414.

Batson CD (2012) The empathy-altruism hypothesis. In *Empathy: From Bench to Bedside*, ed Decety J (MIT Press, Cambridge, MA), pp 41–54.

Baum WM (1982) Choice, changeover, and travel. *J Exp Anal Behav* 38(1):35–49.

Bayer HM, Glimcher PW (2005) Midbrain dopamine neurons encode a quantitative reward prediction error signal. *Neuron* 47(1):129–141.

Bayley PJ, Frascino JC, Squire LR (2005) Robust habit learning in the absence of awareness and independent of the medial temporal lobe. *Nature* 436(7050):550–553.

Bechara A, Damasio H, Damasio AR (2000) Emotion, decision making and the orbitofrontal cortex. *Cereb Cortex* 10(3):295–307.

Becker GM, DeGroot MH, Marschak J (1964) Measuring utility by a single-response sequential method. *Behav Sci* 9(3):226–232.

Beehner J, Bergman T, Cheney D, Seyfarth R, Whitten P (2005) The effect of new alpha males on female stress in free-ranging baboons. *Anim Behav* 69(5):1211–1221.

Belin D, Everitt BJ (2008) Cocaine seeking habits depend upon dopamine-dependent serial connectivity linking the ventral with the dorsal striatum. *Neuron* 57(3):432–441.

Belin V, Moos F (1986) Paired recordings from supraoptic and paraventricular oxytocin cells in suckled rats: Recruitment and synchronization. *J Physiol* 377:369–390.

Ben-Ami Bartal I, Decety J, Mason P (2011) Empathy and pro-social behavior in rats. *Science* 334(6061):1427–1430.

Bendor D, Wang X (2005) The neuronal representation of pitch in primate auditory cortex. *Nature* 436(7054):1161–1165.

Bénichou O, Coppey M, Moreau M, Suet P-H, Voituriez R (2005) Optimal search strategies for hidden targets. *Phys Rev Lett* 94(19):198101–198104.

Bergado JA, Rojas Y, Capdevila V, González O, Almaguer-Melian W (2006) Stimulation of the basolateral amygdala improves the acquisition of a motor skill. *Restor Neurol Neurosci* 24(2):115–121.

Berger U (2011) Learning to cooperate via indirect reciprocity. *Games Econ Behav* 72(1):30–37.

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. *Science* 302(5648):1234–1236.

Berkman LF (2000) Social support, social networks, social cohesion and health. *Soc Work Health Care* 31(2):3–14.

Berlau DJ, McGaugh JL (2006) Enhancement of extinction memory consolidation: The role of the noradrenergic and GABAergic systems within the basolateral amygdala. *Neurobiol Learn Mem* 86(2):123–132.

Bernecker S (2010) *Memory* (Oxford Univ Press, Oxford).

Berridge KC (1995) Food reward: Brain substrates of wanting and liking. *Neurosci Biobehav Rev* 20(1):1–25.

Berridge KC, Kringelbach ML (2008) Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology (Berl)* 199(3):457–480.

Bertrand M, Karlan D, Mullainathan S, Shafir E, Zinman J (2010) What's advertising content worth? Evidence from a consumer credit marketing field experiment. *Q J Econ* 125(1):263–306.

Bharucha J (1994) Tonality and expectation. In *Musical Perceptions,* ed Aiello R (Oxford Univ Press, Oxford), pp 213–239.

Bianchi S, Stimpson CD, Bauernfeind AL, Schapiro SJ, Baze WB, McArthur MJ, Bronson E, Hopkins WD, Semendeferi K, Jacobs B, Hof PR, Sherwood CC (2012) Dendritic morphology of pyramidal neurons in the chimpanzee neocortex: Regional specializations and comparison to humans. *Cereb Cortex* 23(10):2429–2436.

Biederman I, Vessel E (2006) Perceptual pleasure and the brain. *Am Sci* 94:249–255.

Bilalić M, McLeod P, Gobet F (2008) Why good thoughts block better ones: The mechanism of the pernicious Einstellung (set) effect. *Cognition* 108(3):652–661.

Bingman VP, Sharp PE (2006) Neuronal implementation of hippocampal-mediated spatial behavior: A comparative evolutionary perspective. *Behav Cogn Neurosci Rev* 5(2):80–91.

Birnholz JC (1981) The development of human fetal eye movement patterns. *Science* 213(4508):679–681.

Bisley JW, Goldberg ME (2010) Attention, intention, and priority in the parietal lobe. *Annu Rev Neurosci* 33:1–21.

Block N (2007) Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behav Brain Sci* 30(5–6):481–499.

Blood AJ, Zatorre RJ (2001) Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc Natl Acad Sci USA* 98(20):11818–11823.

Bloss EB, Janssen WG, Ohm DT, Yuk FJ, Wadsworth S, Saardi KM, McEwen BS, Morrison JH (2011) Evidence for reduced experience-dependent dendritic spine plasticity in the aging prefrontal cortex. *J Neurosci* 31(21):7831–7839.

Blumenfeld H (2011) Epilepsy and the consciousness system: Transient vegetative state? *Neurol Clin* 29(4):801–823.

Blumenfeld H (2012) Impaired consciousness in epilepsy. *Lancet Neurol* 11(9):814–826.

Blumstein DT, Patton ML, Saltzman W (2006) Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett* 2(1):29–32.

Bohannon JN, 3rd (1988) Flashbulb memories for the space shuttle disaster: A tale of two theories. *Cognition* 29(2):179–196.

Boileau I, Dagher A, Leyton M, Gunn RN, Baker GB, Diksic M, Benkelfat C (2006) Modeling sensitization to stimulants in humans: An [^{11}C]raclopride/positron emission tomography study in healthy men. *Arch Gen Psychiatry* 63(12):1386–1395.

Bolton GE, Katok E, Zwick R (1998) Dictator game giving: Rules of fairness versus acts of kindness. *Int J Game Theory* 27:269–299.

Bolton GE, Katok E, Ockenfels A (2005) Cooperation among strangers with limited information about reputation. *J Public Econ* 89(8):1457–1468.

Boly M, Balteau E, Schnakers C, Degueldre C, Moonen G, Luxen A, Phillips C, Peigneux P, Maquet P, Laureys S (2007) Baseline brain activity fluctuations predict somatosensory perception in humans. *Proc Natl Acad Sci USA* 104(29):12187–12192.

Bonhomme VL, Boveroux P, Brichant JF, Laureys S, Boly M (2012) Neural correlates of consciousness during general anesthesia using functional magnetic resonance imaging (fMRI). *Arch Ital Biol* 150(2–3):155–163.

Borges JL (1944) Funes el memorioso. In *Ficciones,* ed Kerrigan A, trans Bonner A (1962) (Grove Press, New York).

Bose M, Muñoz-Llancao P, Roychowdhury S, Nichols JA, Jakkamsetti V, Porter B, Byrapureddy R, Salgado H, Kilgard MP, Aboitiz F, Dagnino-Subiabre A, Atzori M (2010) Effect of the environment on the dendritic morphology of the rat auditory cortex. *Synapse* 64(2):97–110.

Botvinick MM, Wang J, Cowan E, Roy S, Bastianen C, Mayo JP, Houk JC (2009) An analysis of immediate serial recall performance in a macaque. *Anim Cogn* 12(5):671–678.

Box GEP, Draper NR (1987) *Empirical Model-Building and Response Surfaces* (John Wiley & Sons, New York).

Boyd R, Richerson PJ, Henrich J (2011) The cultural niche: Why social learning is essential for human adaptation. *Proc Natl Acad Sci USA* 108(Suppl 2):10918–10925.

Bradshaw CM, Szabadi E, Bevan P (1976) Behavior of humans in variable-interval schedules of reinforcement. *J Exp Anal Behav* 26(2):135–141.

Brainard DH (1997) The Psychophysics Toolbox. *Spat Vis* 10(4):433–436.

Brandt H, Sigmund K (2006) The good, the bad and the discriminator—errors in direct and indirect reciprocity. *J Theor Biol* 239(2):183–194.

Bräuer J, Call J (2011) The magic cup: Great apes and domestic dogs (*Canis familiaris*) individuate objects according to their properties. *J Comp Psychol* 125(3):353–361.

Bräuer J, Call J, Tomasello M (2006) Are apes really inequity averse? *Proc Biol Sci* 273(1605): 3123–3128.

Bräuer J, Call J, Tomasello M (2009) Are apes inequity averse? New data on the token-exchange paradigm. *Am J Primatol* 71(2):175–181.

Breen RA, McGaugh JL (1961) Facilitation of maze learning with posttrial injections of picrotoxin. *J Comp Physiol Psychol* 54:498–501.

Breithaupt F (2012) Empathy does provide rational support for decisions. But is it the right decision? *Emot Rev* 4(1):96–97.

Brennan PA, Kendrick KM (2006) Mammalian social odours: Attraction and individual recognition. *Philos Trans R Soc Lond B Biol Sci* 361(1476):2061–2078.

Brent LJN, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson AG, Skene JH, Platt ML (2013) Genetic origins of social networks in rhesus macaques. *Sci Rep* 3:1042.

Brin D (2012) Self-addiction and self-righteousness. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 77–84.

Broglio C, Gó**mez A, Durán E, Ocaña FM, Jiménez-Moya F, Rodríguez F, Salas C (2005) Hall**marks of a common forebrain vertebrate plan: Specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Res Bull* 66(4–6):277–281.

Brosnan M, Ashwin C, Gamble T (2011) Greater empathizing and reduced systemizing in people who show a jumping to conclusions bias in the general population. *Psychosis* 5(1):1–11.

Brosnan SF (2006) At a crossroads of disciplines. *Soc Justice Res* 19(2):218–227.

Brosnan SF (2010) What do capuchin monkeys tell us about cooperation? In *For the Greater Good of All: Perspectives on Individualism, Society, and Leadership*, eds Forsyth DR, Hoyt CL (Palgrave Macmillan, New York), pp 11–28.

Brosnan SF (2011) A hypothesis of the co-evolution of inequity and cooperation. *Front Neurosci* 5:43.

Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. *Nature* 425(6955):297–299.

Brosnan SF, de Waal FBM (2009) Capuchin monkeys tolerate intermittent unreliability in human experimenters. *International Journal of Primatology* 30:663–674.

Brosnan SF, Schiff HC, de Waal FBM (2005) Tolerance for inequity may increase with social closeness in chimpanzees. *Proc Biol Sci* 272(1560):253–258.

Brosnan SF, Freeman C, de Waal FBM (2006) Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *Am J Primatol* 68(7):713–724.

Brosnan SF, Houser D, Leimgruber K, Xiao E, Chen T, de Waal FBM (2010a) Competing demands of prosociality and equity in monkeys. *Evol Hum Behav* 31(4):279–288.

Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Schapiro SJ (2010b) Mechanisms underlying the response to inequity in chimpanzees, *Pan troglodytes*. *Anim Behav* 79(6):1229–1237.

Brosnan SF, Flemming TE, Talbot C, Mayo L, Stoinski TS (2011) Responses to inequity in orangutans. *Folia Primatol (Basel)* 82:56–70.

Brosnan SF, Beran MJ, Parrish A, Price SA, Wilson BJ (2013) Comparative approaches to studying strategy: Towards an evolutionary account of primate decision-making. *Evol Psychol* 11(3):606–627.

Brown EN, Lydic R, Schiff ND (2010) General anesthesia, sleep, and coma. *N Engl J Med* 363(27):2638–2650.

Brown EN, Purdon PL, Van Dort CJ (2011) General anesthesia and altered states of arousal: A systems neuroscience analysis. *Annu Rev Neurosci* 34:601–628.

Brown MW, Aggleton JP (2001) Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nat Rev Neurosci* 2(1):51–61.

Brown R, Kulik J (1977) Flashbulb memories. *Cognition* 5(1):73–99.

Brown S, Gao X, Tisdelle L, Eickhoff SB, Liotti M (2011) Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. *Neuroimage* 58(1):250–258.

Brown VJ, Bowman EM (2002) Rodent models of prefrontal cortical function. *Trends Neurosci* 25(7):340–343.

Bruce C, Desimone R, Gross CG (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J Neurophysiol* 46(2):369–384.

Brusseau R (2008) Developmental perspectives: Is the fetus conscious? *Int Anesthesiol Clin* 46(3):11–23.

Buckner RL (2010) The role of the hippocampus in prediction and imagination. *Annu Rev Psychol* 61:27–48, C1–C8.

Buckner RL, Andrews-Hanna JR, Schacter DL (2008) The brain's default network: Anatomy, function, and relevance to disease. *Ann N Y Acad Sci* 1124:1–38.

Bugnyar T (2011) Knower-guesser differentiation in ravens: Others' viewpoints matter. *Proc Biol Sci* 278(1705):634–640.

Buhusi CV, Meck WH (2005) What makes us tick? Functional and neural mechanisms of interval timing. *Nat Rev Neurosci* 6(10):755–765.

Burgess N, Maguire EA, O'Keefe J (2002) The human hippocampus and spatial and episodic memory. *Neuron* 35(4):625–641.

Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proc Natl Acad Sci USA* 104(50):19762–19766.

Burkart JM, Hrdy SB, Van Schaik CP (2009) Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18(5):175–186.

Burmeister SS, Jarvis ED, Fernald RD (2005) Rapid behavioral and genomic responses to social opportunity. *PLoS Biol* 3(11):e363.

Burnham T, Hare B (2007) Engineering human cooperation: Does involuntary neural activation increase public goods contributions? *Hum Nat* 18(2):88–108.

Burton R (2012) Pathological certitude. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 131–137.

Burwell RD (2000) The parahippocampal region: Corticocortical connectivity. *Ann N Y Acad Sci* 911:25–42.

Buswell GT (1935) *How People Look at Pictures: A Study of the Psychology of Perception in Art* (Univ of Chicago Press, Chicago).

Butler AB (2008) Evolution of brains, cognition, and consciousness. *Brain Res Bull* 75 (2–4):442–449, www.sciencedirect.com/science/journal/03619230.

Butler AB, Cotterill RM (2006) Mammalian and avian neuroanatomy and the question of consciousness in birds. *Biol Bull* 211(2):106–127.

Butler AB, Manger PR, Lindahl BI, Arhem P (2005) Evolution of the neural basis of consciousness: A bird-mammal comparison. *Bioessays* 27(9):923–936.

Buttelmann D, Carpenter M, Call J, Tomasello M (2007) Enculturated chimpanzees imitate rationally. *Dev Sci* 10(4):F31–F38.

Buzsáki G, Moser EI (2013) Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nat Neurosci* 16(2):130–138.

Byrne R, Whiten A (1989) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Oxford Science, Oxford).

Cabeza R, St. Jacques P (2007) Functional neuroimaging of autobiographical memory. *Trends Cogn Sci* 11(5):219–227.

Cáceres M, Suwyn C, Maddox M, Thomas JW, Preuss TM (2007) Increased cortical expression of two synaptogenic thrombospondins in human brain evolution. *Cereb Cortex* 17(10):2312–2321.

Cacioppo JT, Tassinary LG, Berntson GG, eds (2007) *Handbook of Psychophysiology* (Cambridge Univ Press, New York).

Cahill L, Alkire MT (2003) Epinephrine enhancement of human memory consolidation: Interaction with arousal at encoding. *Neurobiol Learn Mem* 79(2):194–198.

Cahill L, Prins B, Weber M, McGaugh JL (1994) β-adrenergic activation and memory for emotional events. *Nature* 371(6499):702–704.

Cahill L, Haier RJ, Fallon J, Alkire MT, Tang C, Keator D, Wu J, McGaugh JL (1996) Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proc Natl Acad Sci USA* 93(15):8016–8021.

Cahill L, Gorski L, Le K (2003) Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. *Learn Mem* 10(4):270–274.

Camerer C (2003) *Behavioral Game Theory: Experiments in Strategic Interaction* (Russell Sage Foundation; Princeton Univ Press, Princeton, NJ).

Campbell MW, de Waal FB (2011) Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS ONE* 6(4):e18283.

Canli T, Lesch KP (2007) Long story short: The serotonin transporter in emotion regulation and social cognition. *Nat Neurosci* 10(9):1103–1109.

Canli T, Zhao Z, Brewer J, Gabrieli JD, Cahill L (2000) Event-related activation in the human amygdala associates with later memory for individual emotional experience. *J Neurosci* 20(19):RC99.

Canli T, Desmond JE, Zhao Z, Gabrieli JD (2002) Sex differences in the neural basis of emotional memories. *Proc Natl Acad Sci USA* 99(16):10789–10794.

Canli T, Congdon E, Constable RT, Lesch KP (2008) Additive effects of serotonin transporter and tryptophan hydroxylase-2 gene variation on neural correlates of affective processing. *Biol Psychol* 79(1):118–125.

Capitanio JP (2011) Individual differences in emotionality: Social temperament and health. *Am J Primatol* 73(6):507–515.

Cardinal RN, Parkinson JA, Hall J, Everitt BJ (2002) Emotion and motivation: The role of the amygdala, ventral striatum, and prefrontal cortex. *Neurosci Biobehav Rev* 26(3):321–352.

Carello CD, Krauzlis RJ (2004) Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron* 43(4):575–583.

Carlton DW, Perloff JM (1994) *Modem Industrial Organization* (HarperCollins, New York).

Carmichael ST, Price JL (1995a) Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. *J Comp Neurol* 363(4):615–641.

Carmichael ST, Price JL (1995b) Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *J Comp Neurol* 363(4):642–664.

Carmichael ST, Price JL (1996) Connectional networks within the orbital and medial prefrontal cortex of macaque monkeys. *J Comp Neurol* 371(2):179–207.

Carpenter M, Tomasello M (2006) Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Soc Dev* 4(3):217–237.

Carter CS, Grippo AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW (2008) Oxytocin, vasopressin and sociality. *Prog Brain Res* 170:331–336.

Caspi A, Sugden K, Moffitt TE, Taylor A, Craig IW, Harrington H, McClay J, Mill J, Martin J, Braithwaite A, Poulton R (2003) Influence of life stress on depression: Moderation by a polymorphism in the 5-HTT gene. *Science* 301(5631):386–389.

Castelhano MS, Heaven C (2010) The relative contribution of scene context and target features to visual search in scenes. *Atten Percept Psychophys* 72(5):1283–1297.

Castelhano MS, Heaven C (2011) Scene context influences without scene gist: Eye movements guided by spatial associations in visual search. *Psychon Bull Rev* 18(5):890–896.

Castelhano MS, Mack ML, Henderson JM (2009) Viewing task influences eye movement control during active scene perception. *J Vis* 9(3):1–15.

Catchpole CK, Slater PJB (1995) *Bird Song: Biological Themes and Variations* (Cambridge Univ Press, Cambridge).

Cauchard L, Boogert N, Lefebvre L, Dubois F, Doligez B (2013) Problem-solving performance correlates with reproductive success in a wild bird population. *Anim Behav* 85(1):19–26.

Cela-Conde CJ, Ayala FJ (2007) *Human Evolution: Trails from the Past* (Oxford University Press, Oxford).

Cela-Conde CJ, Marty G, Maestú F, Ortiz T, Munar E, Fernández A, Roca M, Rosselló J, Quesney F (2004) Activation of the prefrontal cortex in the human visual aesthetic perception. *Proc Natl Acad Sci USA* 101(16):6321–6325.

Chagnon NA (2013) *Noble Savages* (Simon & Schuster, New York).

Chalmers D (1996) *The Conscious Mind: In Search of a Fundamental Theory* (Oxford Univ Press, New York).

Chang I (1998) *The Rape of Nanking* (Penguin, New York).

Chang J, Halliday J (2005) *Mao* (Jonathan Cape, London).

Chang SW, Winecoff AA, Platt ML (2011) Vicarious reinforcement in rhesus macaques (*Macaca mulatta*). *Front Neurosci* 5:27.

Chang SW, Barter JW, Ebitz RB, Watson KK, Platt ML (2012) Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (*Macaca mulatta*). *Proc Natl Acad Sci USA* 109(3):959–964.

Chang SW, Gariépy J-F, Platt ML (2013) Neuronal reference frames for social decisions in primate frontal cortex. *Nat Neurosci* 16(2):243–250.

Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9(2): 129–136.

Chartrand TL, Bargh JA (1999) The chameleon effect: The perception-behavior link and social interaction. *J Pers Soc Psychol* 76(6):893–910.

Chatterjee A (2011) Neuroaesthetics: A coming of age story. *J Cogn Neurosci* 23(1):53–62.

Chatterjee A, Thomas A, Smith SE, Aguirre GK (2009) The neural response to facial attractiveness. *Neuropsychology* 23(2):135–143.

Chavez CM, McGaugh JL, Weinberger NM (2009) The basolateral amygdala modulates specific sensory memory representations in the cerebral cortex. *Neurobiol Learn Mem* 91(4):382–392.

Chavez CM, McGaugh JL, Weinberger NM (2012) Amygdala strengthening of cortical memory representations. In *The Amygdala—A Discrete Multitasking Manager,* ed Ferry B (In Tech, Rijeka, Croatia). Available at http://www.intechopen.com/books/the-amygdala-a-discrete-multitasking-manager/amygdala-strengthening-of-cortical-memory-representations.

Chavez CM, McGaugh JL, Weinberger NM (2013) Activation of the basolateral amygdala induces long-term enhancement of specific memory representations in the cerebral cortex. *Neurobiol Learn Mem* 101:8–18.

Chen GL, Novak MA, Hakim S, Xie Z, Miller GM (2006) Tryptophan hydroxylase-2 gene polymorphisms in rhesus monkeys: Association with hypothalamic-pituitary-adrenal axis function and in vitro gene expression. *Mol Psychiatry* 11(10):914–928.

Cheney DL (2011) Extent and limits of cooperation in animals. *Proc Natl Acad Sci USA* 108(Suppl 2):10902–10909.

Cheney DL, Seyfarth RM (1997) Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Anim Behav* 54(2):409–418.

Cheney D, Seyfarth R (2007) *Baboon Metaphysics: The Evolution of a Social Mind* (Univ of Chicago Press, Chicago).

Cheney D, Seyfarth R, Silk J (1995) The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Anim Behav* 50(1):249–257.

Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM (2010) Contingent cooperation between wild female baboons. *Proc Natl Acad Sci USA* 107(21):9562–9566.

Chib VS, Rangel A, Shimojo S, O'Doherty JP (2009) Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. *J Neurosci* 29(39):12315–12320.

Chiesa A, Serretti A (2009) Mindfulness-based stress reduction for stress management in healthy people: A review and meta-analysis. *J Altern Complement Med* 15(5):593–600.

Cho MM, DeVries AC, Williams JR, Carter CS (1999) The effects of oxytocin and vasopressin on partner preferences in male and female prairie voles (*Microtus ochrogaster*). *Behav Neurosci* 113(5):1071–1079.

Choi J-K, Ahn TK (2013) Strategic reward and altruistic punishment support cooperation in a public goods game experiment. *J Econ Psychol* 35:17–30.

Choi JK, Bowles S (2007) The coevolution of parochial altruism and war. *Science* 318(5850):636–640.

Chooi W-T, Thompson L (2012) Working memory training does not improve intelligence in healthy young adults. *Intelligence* 40:531–542.

Christianson S-A (1992) *Handbook of Emotion and Memory: Current Research and Theory* (Lawrence Erlbaum Associates, Hillsdale, NJ).

Christoff K, Ream JM, Geddes LP, Gabrieli JD (2003) Evaluating self-generated information: Anterior prefrontal contributions to human cognition. *Behav Neurosci* 117(6):1161–1168.

Chugani HT, Phelps ME, Mazziotta JC (1987) Positron emission tomography study of human brain functional development. *Ann Neurol* 22(4):487–497.

Chun MM, Jiang Y (1998) Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognit Psychol* 36(1):28–71.

Chupka MW, Earle R, Fox-Penner P, Hledik R (2008) *Transforming America's Power Industry: The Investment Challenge 2010–2030* (The Edison Foundation, Washington, DC).

Churchland PS (2011; 2012) *Braintrust: What Neuroscience Tells Us About Morality* (Princeton Univ Press, Princeton, NJ).

Churchland PS (2012) *Braintrust: What Neuroscience Tells Us About Morality* (Princeton Univ Press, Princeton, NJ).

Cikara M, Fiske ST (2011) Bounded empathy: Neural responses to outgroup targets' (mis) fortunes. *J Cogn Neurosci* 23(12):3791–3803.

Clark KB, Smith DC, Hassert DL, Browning RA, Naritoku DK, Jensen RA (1998) Posttraining electrical stimulation of vagal afferents with concomitant vagal efferent inactivation enhances memory storage processes in the rat. *Neurobiol Learn Mem* 70(3):364–373.

Clark KB, Naritoku DK, Smith DC, Browning RA, Jensen RA (1999) Enhanced recognition memory following vagus nerve stimulation in human subjects. *Nat Neurosci* 2(1):94–98.

Clark RE, Martin SJ (2005) Interrogating rodents regarding their object and spatial memory. *Curr Opin Neurobiol* 15(5):593–598.

Clark RE, Squire LR (2010) An animal model of recognition memory and medial temporal lobe amnesia: History and current issues. *Neuropsychologia* 48(8):2234–2244.

Clark RE, Zola SM, Squire LR (2000) Impaired recognition memory in rats after damage to the hippocampus. *J Neurosci* 20(23):8853–8860.

Clark RE, West AN, Zola SM, Squire LR (2001) Rats with lesions of the hippocampus are impaired on the delayed nonmatching-to-sample task. *Hippocampus* 11(2):176–186.

Clayton EC, Williams CL (2000) Adrenergic activation of the nucleus tractus solitarius potentiates amygdala norepinephrine release and enhances retention performance in emotionally arousing and spatial memory tasks. *Behav Brain Res* 112(1–2):151–158.

Clayton NS, Dickinson A (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395(6699):272–274.

Clayton NS, Dickinson A (1999) Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *J Exp Psychol Anim Behav Process* 25(1):82–91.

Clayton NS, Griffiths DP, Emery NJ, Dickinson A (2001) Elements of episodic-like memory in animals. *Philos Trans R Soc Lond B Biol Sci* 356(1413):1483–1491.

Clayton NS, Bussey TJ, Dickinson A (2003a) Can animals recall the past and plan for the future? *Nat Rev Neurosci* 4(8):685–691.

Clayton NS, Yu KS, Dickinson A (2003b) Interacting cache memories: Evidence for flexible memory use by western scrub-jays (*Aphelocoma californica*). *J Exp Psychol Anim Behav Process* 29(1):14–22.

Cohen NJ, Squire LR (1980) Preserved learning and retention of pattern-analyzing skill in amnesia: Dissociation of knowing how and knowing that. *Science* 210(4466):207–210.

Cohen S (2004) Social relationships and health. *Am Psychol* 59(8):676–684.

Cole EF, Morand-Ferron J, Hinks AE, Quinn JL (2012) Cognitive ability influences reproductive life history variation in the wild. *Curr Biol* 22(19):1808–1812.

Cole S, ed (2001) *What's Wrong with Sociology?* (Transaction, New Brunswick, NJ).

Colombo M, Cawley S, Broadbent N (1997) The effects of hippocampal and area parahippocampalis lesions in pigeons. II. Concurrent discrimination and spatial memory. *Q J Exp Psychol B* 50(2):172–189.

Colonnier M, Beaulieu C (1985) An empirical assessment of stereological formulae applied to the counting of synaptic disks in the cerebral cortex. *J Comp Neurol* 231(2):175–179.

Conard NJ, Malina M, Münzel SC (2009) New flutes document the earliest musical tradition in southwestern Germany. *Nature* 460(7256):737–740.

Conway MA (1995) *Flashbulb Memories* (Erlbaum, Brighton, England).

Conway MA, Anderson SJ, Larsen SF, Donnelly CM, McDaniel MA, McClelland AG, Rawles RE, Logie RH (1994) The formation of flashbulb memories. *Mem Cognit* 22(3):326–343.

Coon H, Dunn D, Lainhart J, Miller J, Hamil C, Battaglia A, Tancredi R, Leppert MF, Weiss R, McMahon W (2005) Possible association between autism and variants in the brain-expressed tryptophan hydroxylase gene (*TPH2*). *Am J Med Genet B Neuropsychiatr Genet* 135B(1):42–46.

Corbetta M, Patel G, Shulman GL (2008) The reorienting system of the human brain: From environment to theory of mind. *Neuron* 58(3):306–324.

Corkin S, Amaral DG, González RG, Johnson KA, Hyman BT (1997) H.M.'s medial temporal lobe lesion: Findings from magnetic resonance imaging. *J Neurosci* 17(10):3964–3979.

Cornelissen G, Dewitte S, Warlop L (2011) Are social value orientations expressed automatically? Decision making in the dictator game. *Pers Soc Psychol Bull* 37(8):1080–1090.

Correia SP, Dickinson A, Clayton NS (2007) Western scrub-jays anticipate future needs independently of their current motivational state. *Curr Biol* 17(10):856–861.

Correll RE, Scoville WB (1965) Effects of medial temporal lesions on visual discrimination performance. *J Comp Physiol Psychol* 60(2):175–181.

Costa DL, Kahn ME (2010) Energy Conservation" Nudges" and Environmentalist Ideology: Evidence from a Randomized Residential Electricity Field Experiment. NBER Working Paper No. 15939 (National Bureau of Economic Research, Cambridge, MA).

Cotterill RM (2001) Cooperation of the basal ganglia, cerebellum, sensory cerebrum and hippocampus: Possible implications for cognition, consciousness, intelligence and creativity. *Prog Neurobiol* 64(1):1–33.

Coull JT, Jones ME, Egan TD, Frith CD, Maze M (2004) Attentional effects of nor-adrenaline vary with arousal level: Selective activation of thalamic pulvinar in humans. *Neuroimage* 22(1):315–322.

Cowan N (2001) The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behav Brain Sci* 24(1):87–114, discussion 114–185.

Cowan N, Elliott EM, Scott Saults J, Morey CC, Mattox S, Hismjatullina A, Conway AR (2005) On the capacity of attention: Its estimation and its role in working memory and cognitive aptitudes. *Cognit Psychol* 51 (1):42–100.

Cowan N, AuBuchon AM, Gilchrist AL, Ricker TJ, Saults JS (2011) Age differences in visual working memory capacity: Not based on encoding limitations. *Dev Sci* 14(5):1066–1074.

Craik FIM, Lockhart RS (1972) Levels of processing: A framework for memory research. *J Verbal Learn Verbal Behav* 11:671–684.

Crammond DJ (1997) Motor imagery: Never in your wildest dream. *Trends Neurosci* 20(2): 54–57.

Crick F (1994) *The Astonishing Hypothesis* (Scribner, New York).

Crick F, Koch C (1990) Towards a neurobiological theory of consciousness. *Semin Neurosci* 2:263–275.

Crick F, Koch C (2003) A framework for consciousness. *Nat Neurosci* 6(2):119–126.

Crockford C, Herbinger I, Vigilant L, Boesch C (2004) Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology* 110:221–243.

Crockford C, Wittig RM, Whitten PL, Seyfarth RM, Cheney DL (2008) Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Horm Behav* 53(1):254–265.

Crockford C, Wittig RM, Mundry R, Zuberb**ühler K (2012) Wild chimpanzees inform ignorant** group members of danger. *Curr Biol* 22(2):142–146.

Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbühler K, Deschner T (2013) Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc Biol Sci* 280(1755):20122765.

Cronin KA, Schroeder KKE, Rothwell ES, Silk JB, Snowdon CT (2009) Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *J Comp Psychol* 123(3):231–241.

Cronin KA, Schroeder KKE, Snowdon CT (2010) Prosocial behaviour emerges independent of reciprocity in cottontop tamarins. *Proc Biol Sci* 277(1701):3845–3851.

Crystal JD (2010) Episodic-like memory in animals. *Behav Brain Res* 215(2):235–243.

Cupchik GC, Vartanian O, Crawley A, Mikulis DJ (2009) Viewing artworks: Contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain Cogn* 70(1):84–91.

Curley JP, Jensen CL, Mashoodh R, Champagne FA (2011) Social influences on neurobiology and behavior: Epigenetic effects during development. *Psychoneuroendocrinology* 36(3):352–371.

Cushman F, Young L, Greene JD (2010) Multi-system moral psychology. In *The Moral Psychology Handbook,* ed Doris JM (Oxford Univ Press, New York), pp 47–71.

Damasio A (1994) *Descartes' Error* (G. P. Putnam's Sons, New York).

Damasio A (1999) *The Feeling of What Happens* (Harcourt Brace, New York).

Damasio A (2003) Mental self: The person within. *Nature* 423(6937):227.

Damasio AR, Geschwind N (1984) The neural basis of language. *Annu Rev Neurosci* 7(1): 127–147.

Darlington PJ, Jr (1978) Altruism: Its characteristics and evolution. *Proc Natl Acad Sci USA* 75(1):385–389.

Darwin C (1836-1844) *Notebooks. Geology, Transmutation of Species, Metaphysical Enquiries,* eds Barrett PH, Gautrey PJ, Herbert S, Kohn D, Smith S (Cambridge Univ Press, Cambridge, UK).

Darwin C (1859) *On the Origin of Species* (John Murray, London).

Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex* (John Murray, London).

Darwin CR (1872) *The Expression of the Emotions in Man and Animals* (John Murray, London, UK).

Darwin C (1887) *The Life and Letters of Charles Darwin* (John Murray, London).

Daselaar SM, Porat Y, Huijbers W, Pennartz CM (2010) Modality-specific and modality-independent components of the human imagery system. *Neuroimage* 52(2):677–685.

Dasgupta P (2012) Dark matters: Exploitation as cooperation. *Journal of Theoretical Biology* 299:180–187.

Davidson PS, Drouin H, Kwan D, Moscovitch M, Rosenbaum RS (2012) Memory as social glue: Close interpersonal relationships in amnesic patients. *Front Psychol* 3:531.

Davidson TJ, Kloosterman F, Wilson MA (2009) Hippocampal replay of extended experience. *Neuron* 63(4):497–507.

Day M, Langston RF, Morris RG (2003) Glutamate-receptor-mediated encoding and retrieval of paired-associate learning. *Nature* 424(6945):205–209.

Dazkir SS, Read MA (2012) Furniture forms and their influence on our emotional responses toward interior environments. *Environ Behav* 44(5):722–734.

de Graaf TA, Hsieh PJ, Sack AT (2012) The "correlates" in neural correlates of consciousness. *Neurosci Biobehav Rev* 36(1):191–197.

de Quervain DJ, Fischbacher U, Treyer V, Schellhammer M, Schnyder U, Buck A, Fehr E (2004) The neural basis of altruistic punishment. *Science* 305(5688):1254–1258.

de Waal FBM (1978) Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. *Behaviour* 66:268–312.

de Waal FBM (1991) The chimpanzee's sense of social regularity and its relation to the human sense of justice. *Am Behav Sci* 34(3):335–349.

de Waal FB (2012) The antiquity of empathy. *Science* 336(6083):874–876.

de Waal FBM, Berger ML (2000) Payment for labour in monkeys. *Nature* 404(6778):563.

de Waal FBM, Leimgruber K, Greenberg AR (2008) Giving is self-rewarding for monkeys. *Proc Natl Acad Sci USA* 105(36):13685–13689.

Deacon TW (1997) *The Symbolic Species: The Coevolution of Language and the Brain (*WW Norton & Company, New York).

Deag JM (1977) Aggression and submission in monkey societies. *Anim Behav* 25(2):465–474.

Deaner RO, Khera AV, Platt ML (2005) Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Curr Biol* 15(6):543–548.

Decety J (1996) The neurophysiological basis of motor imagery. *Behav Brain Res* 77(1–2):45–52.

Decety J (2011) The neuroevolution of empathy. *Ann N Y Acad Sci* 1231:35–45.

Decety J, Jackson PL (2004) The functional architecture of human empathy. *Behav Cogn Neurosci Rev* 3(2):71–100.

Decety J, Jeannerod M, Prablanc C (1989) The timing of mentally represented actions. *Behav Brain Res* 34(1–2):35–42.

Decety J, Yang CY, Cheng Y (2010) Physicians down-regulate their pain empathy response: An event-related brain potential study. *Neuroimage* 50(4):1676–1682.

Dehaene S, Sergent C, Changeux JP (2003) A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proc Natl Acad Sci USA* 100(14):8520–8525.

Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C (2006) Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends Cogn Sci* 10(5):204–211.

Deiber MP, Ibañez V, Honda M, Sadato N, Raman R, Hallett M (1998) Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. *Neuroimage* 7(2):73–85.

Delfour F, Marten K (2001) Mirror image processing in three marine mammal species: Killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*) and California sea lions (*Zalophus californianus*). *Behav Processes* 53(3):181–190.

Dennett CD (1991) *Consciousness Explained* (Little, Brown, Boston, MA).

Dennett CD, Hofstadter RD (1981) *The Mind's I: Fantasies and Reflections on the Self and Soul* (Bantam House, New York).

Dennis MY, Nuttle X, Sudmant PH, Antonacci F, Graves TA, Nefedov M, Rosenfeld JA, Sajjadian S, Malig M, Kotkiewicz H, Curry CJ, Shafer S, Shaffer LG, de Jong PJ, Wilson RK, Eichler EE (2012) Evolution of human-specific neural *SRGAP2* genes by incomplete segmental duplication. *Cell* 149(4):912–922.

Denton DA (2005) *The Primordial Emotions: The Dawning of Consciousness* (Oxford Univ Press, Oxford).

Denton DA, McKinley MJ, Farrell M, Egan GF (2009) The role of primordial emotions in the evolutionary origin of consciousness. *Conscious Cogn* 18(2):500–514.

Dere E, Huston JP, De Souza Silva MA (2005) Integrated memory for objects, places, and temporal order: Evidence for episodic-like memory in mice. *Neurobiol Learn Mem* 84(3):214–221.

Derrien T, Johnson R, Bussotti G, Tanzer A, Djebali S, Tilgner H, Guernec G, Martin D, Merkel A, Knowles DG, Lagarde J, Veeravalli L, Ruan X, Ruan Y, Lassmann T, Carninci P, Brown JB, Lipovich L, Gonzalez JM, Thomas M, Davis CA, Shiekhattar R, Gingeras TR, Hubbard TJ, Notredame C, Harrow J, Guigó R (2012) The GENCODE v7 catalog of human long noncoding RNAs: Analysis of their gene structure, evolution, and expression. *Genome Res* 22(9):1775–1789.

Descartes R (1996) *Meditations on First Philosophy,* trans Cottingham J (Cambridge Univ Press, Cambridge, UK).

Deshmukh SS, Johnson JL, Knierim JJ (2012) Perirhinal cortex represents nonspatial, but not spatial, information in rats foraging in the presence of objects: Comparison with lateral entorhinal cortex. *Hippocampus* 22(10):2045–2058.

DeSilva JM (2011) A shift toward birthing relatively large infants early in human evolution. *Proc Natl Acad Sci USA* 108(3):1022–1027.

DeSilva JM, Lesnik JJ (2008) Brain size at birth throughout human evolution: A new method for estimating neonatal brain size in hominins. *J Hum Evol* 55(6):1064–1074.

Desimone R (1991) Face-selective cells in the temporal cortex of monkeys. *J Cogn Neurosci* 3(1):1–8.

Desimone R, Albright TD, Gross CG, Bruce C (1984) Stimulus-selective properties of inferior temporal neurons in the macaque. *J Neurosci* 4(8):2051–2062.

Desmond A (1984) *Archetypes and Ancestors* (Univ of Chicago Press, Chicago).

Devilbiss DM, Page ME, Waterhouse BD (2006) Locus ceruleus regulates sensory encoding by neurons and networks in waking animals. *J Neurosci* 26(39):9860–9872.

Di Dio C, Gallese V (2009) Neuroaesthetics: A review. *Curr Opin Neurobiol* 19:1–6.

Di Dio C, Macaluso E, Rizzolatti G (2007) The golden beauty: Brain response to classical and renaissance sculptures. *PLoS ONE* 2(11):e1201.

Diamond MC, Connor JRJ, Jr (1982) Plasticity of the aging cerebral cortex. *Exp Brain Res* (Suppl 5):36–44.

Dielenberg RA, Carrive P, McGregor IS (2001) The cardiovascular and behavioral response to cat odor in rats: Unconditioned and conditioned effects. *Brain Res* 897(1–2):228–237.

Dindo M, de Waal FBM (2007) Partner effects on food consumption in brown capuchin monkeys. *Am J Primatol* 69(4):448–456.

Dix SL, Aggleton JP (1999) Extending the spontaneous preference test of recognition: Evidence of object-location and object-context recognition. *Behav Brain Res* 99(2):191–200.

Dobzhansky T (1973) Nothing in biology makes sense except in the light of evolution. *Am Biol Teach* 35:125–129.

Doeller CF, Barry C, Burgess N (2010) Evidence for grid cells in a human memory network. *Nature* 463(7281):657–661.

Dolcos F, LaBar KS, Cabeza R (2004) Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron* 42(5):855–863.

Donaldson ZR, Young U (2008) Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322(5903):900–904.

Dornelles A, de Lima MN, Grazziotin M, Presti-Torres J, Garcia VA, Scalco FS, Roesler R, Schröder N (2007) Adrenergic enhancement of consolidation of object recognition memory. *Neurobiol Learn Mem* 88(1):137–142.

Douglas RJ (1967) The hippocampus and behavior. *Psychol Bull* 67(6):416–422.

Doupe AJ, Konishi M (1991) Song-selective auditory circuits in the vocal control system of the zebra finch. *Proc Natl Acad Sci USA* 88(24):11339–11343.

Dreger A (2011) Darkness's descent on the American Anthropological Association. A cautionary tale. *Hum Nat* 22(3):225–246.

Dringenberg HC, Vanderwolf CH (1996) Cholinergic activation of the electrocorticogram: An amygdaloid activating system. *Exp Brain Res* 108(2):285–296.

Dringenberg HC, Saber AJ, Cahill L (2001) Enhanced frontal cortex activation in rats by convergent amygdaloid and noxious sensory signals. *Neuroreport* 12(11):2395–2398.

Dringenberg HC, Kuo MC, Tomaszek S (2004) Stabilization of thalamo-cortical long-term potentiation by the amygdala: Cholinergic and transcription-dependent mechanisms. *Eur J Neurosci* 20(2):557–565.

Dudchenko PA (2004) An overview of the tasks used to test working memory in rodents. *Neurosci Biobehav Rev* 28(7):699–709.

Duff MC, Brown-Schmidt S (2012) The hippocampus and the flexible use and processing of language. *Front Hum Neurosci* 6:69.

Dunbar RI (1995) Neocortex size and group size in primates: A test of the hypothesis. *J Hum Evol* 28(3):287–296.

Dunbar RIM (1998) The social brain hypothesis. *Evolut Anthropol* 6(5):178–190.

Dunbar RIM, Marriott A, Duncan NDC (1997) Human conversational behavior. *Hum Nat* 8(3):231–246.

Duncan CP (1949) The retroactive effect of electroshock on learning. *J Comp Physiol Psychol* 42(1):32–44.

Dutton K (2012) *The Wisdom of Psychopaths* (Farrar, Straus and Giroux, New York).

Eacott MJ, Easton A (2010) Episodic memory in animals: Remembering which occasion. *Neuropsychologia* 48(8):2273–2280.

Eacott MJ, Easton A, Zinkivskay A (2005) Recollection in an episodic-like memory task in the rat. *Learn Mem* 12(3):221–223.

Easterly W (2006) *The White Man's Burden* (Penguin Press, New York).

Ebbinghaus H (1885) *Uber das Gedachtnis* (Drucker and Humblat, Leipzig, Germany).

Edelman GM, Tononi G (2000) *A Universe of Consciousness* (Basic Books, New York).

Edlund JA, Chaumont N, Hintze A, Koch C, Tononi G, Adami C (2011) Integrated information increases with fitness in the evolution of animats. *PLOS Comput Biol* 7(10): e1002236.

Eichenbaum H (2013) Memory on time. *Trends Cogn Sci* 17(2):81–88.

Eichenbaum H, Fortin N (2003) Episodic memory and the hippocampus: It's about time. *Curr Dir Psychol Sci* 12:53–57.

Eichenbaum H, Fortin NJ (2005) Bridging the gap between brain and behavior: Cognitive and neural mechanisms of episodic memory. *J Exp Anal Behav* 84(3):619–629.

Eichenbaum H, Fortin NJ (2009) The neurobiology of memory based predictions. *Philos Trans R Soc Lond B Biol Sci* 364(1521):1183–1191.

Eichenbaum H, Stewart C, Morris RGM (1990) Hippocampal representation in place learning. *J Neurosci* 10(11):3531–3542.

Eichenbaum H, Dudchenko P, Wood E, Shapiro M, Tanila H (1999) The hippocampus, memory, and place cells: Is it spatial memory or a memory space? *Neuron* 23(2):209–226.

Eichenbaum H, Fortin NJ, Ergorul C, Wright SP, Agster KL (2005) Episodic recollection in animals: "If it walks like a duck and quacks like a duck. . ." *Learn Motiv* 36(2):190–207.

Eichenbaum H, Yonelinas AP, Ranganath C (2007) The medial temporal lobe and recognition memory. *Annu Rev Neurosci* 30:123–152.

Eichenbaum H, Fortin N, Sauvage M, Robitsek RJ, Farovik A (2010) An animal model of amnesia that uses receiver operating characteristics (ROC) analysis to distinguish recollection from familiarity deficits in recognition memory. *Neuropsychologia* 48(8):2281–2289.

Eidelson R, Soldz S (2012) Does Comprehensive Soldier Fitness Work: CSF Research Fails the Test. Working Paper No. 1 (Coalition for an Ethical Psychology, Bala Cynwyd, PA).

Eisenberg N, Eggum ND (2009) Empathic responding. *The Social Neuroscience of Empathy*, eds Decety J, Ickes WJ (MIT Press, Cambridge, MA), pp 71–83.

Eisenberg N, Mussen PH (1989) *The Roots of Prosocial Behavior in Children* (Cambridge Univ Press, Cambridge, UK; New York).

Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, Newman EL, Fried I (2003) Cellular networks underlying human spatial navigation. *Nature* 425(6954):184–188.

Eldakar OT, Wilson DS (2008) Selfishness as second-order altruism. *Proc Natl Acad Sci USA* 105(19):6982–6986.

Eliades SJ, Wang X (2008) Neural substrates of vocalization feedback monitoring in primate auditory cortex. *Nature* 453(7198):1102–1106.

Ellingsen T, Herrmann B, Nowak MA, Rand DG, Tarnita CE (2012) Civic Capital in Two Cultures: The Nature of Cooperation in Romania and USA. Available at http://ssrn.com/abstract=2179575. Accessed April 20, 2013.

Elliott R, Dolan RJ, Frith CD (2000) Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cereb Cortex* 10(3):308–317.

Elston GN, Benavides-Piccione R, DeFelipe J (2001) The pyramidal cell in cognition: A comparative study in human and monkey. *J Neurosci* 21(17):RC163.

Elston GN, Oga T, Fujita I (2009) Spinogenesis and pruning scales across functional hierarchies. *J Neurosci* 29(10):3271–3275.

Emery NJ (2000) The eyes have it: The neuroethology, function and evolution of social gaze. *Neurosci Biobehav Rev* 24(6):581–604.

Emery NJ (2006) Cognitive ornithology: The evolution of avian intelligence. *Philos Trans R Soc Lond B Biol Sci* 361(1465):23–43.

Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414(6862):443–446.

Emery NJ, Clayton NS (2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science* 306(5703):1903–1907.

Emery NJ, Clayton NS (2005) Evolution of the avian brain and intelligence. *Curr Biol* 15(23):R946–R950.

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006a) Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc Biol Sci* 273(1587):707–712.

Engh A, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006b) Female hierarchy instability, male immigration, and infanticide increase glucocorticoid levels in female chacma baboons. *Anim Behav* 71(5):1227–1237.

Engh A, Hoffmeier R, Cheney D, Seyfarth R (2006c) Who me? Can baboons infer the target of vocalisations? *Anim Behav* 71(2):381–387.

Engle R (2010) Role of working-memory capacity in cognitive control. *Curr Anthropol* 51: S17–S26.

Ennaceur A, Delacour J (1988) A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. *Behav Brain Res* 31(1):47–59.

Ergorul C, Eichenbaum H (2004) The hippocampus and memory for “what,” “where,” and “when.” *Learn Mem* 11(4):397–405.

Ericsson KA, Kintsch W (1995) Long-term working memory. *Psychol Rev* 102(2):211–245.

Eriksen CW, Yeh Y-Y (1985) Allocation of attention in the visual field. *J Exp Psychol Hum Percept Perform* 11(5):583–597.

Ernest-Jones M, Nettle D, Bateson M (2011) Effects of eye images on everyday cooperative behavior: A field experiment. *Evol Hum Behav* 32(3):172–178.

Evans J (2010) *Thinking Twice* (Oxford Univ Press, Oxford).

Evans J, Frankish K, eds (2009) *In Two Minds: Dual Processes and Beyond* (Oxford Univ Press, Oxford).

Fagan JF, 3rd (1970) Memory in the infant. *J Exp Child Psychol* 9(2):217–226.

Fagot J, De Lillo C (2011) A comparative study of working memory: Immediate serial spatial recall in baboons (*Papio papio*) and humans. *Neuropsychologia* 49(14):3870–3880.

Fahrenfort JJ, Scholte HS, Lamme VA (2008) The spatiotemporal profile of cortical processing leading up to visual perception. *J Vis* 8(1):11–12.

Fairbanks LA, Newman TK, Bailey JN, Jorgensen MJ, Breidenthal SE, Ophoff RA, Comuzzie AG, Martin LJ, Rogers J (2004) Genetic contributions to social impulsivity and aggressiveness in vervet monkeys. *Biol Psychiatry* 55(6):642–647.

Fairhall SL, Ishai A (2008) Neural correlates of object indeterminacy in art compositions. *Conscious Cogn* 17(3):923–932.

Faivre N, Charron S, Roux P, Lehéricy S, Kouider S (2012) Nonconscious emotional processing involves distinct neural pathways for pictures and videos. *Neuropsychologia* 50(14):3736–3744.

Fanselow MS, Lester LS (1988) A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior. In *Evolution and Learning,* eds Bolles RC, Beecher MD (Lawrence Erlbaum, Hillsdale, NJ), pp 185–212.

Fecteau JH, Munoz DP (2003) Exploring the consequences of the previous trial. *Nat Rev Neurosci* 4(6):435–443.

Fecteau JH, Munoz DP (2006) Salience, relevance, and firing: A priority map for target selection. *Trends Cogn Sci* 10(8):382–390.

Federal Energy Regulatory Commission (2011) *Assessment of Demand Response and Advanced Metering: Staff Report* (Federal Energy Regulatory Commission, Washington, DC).

Feeney MC, Roberts WA, Sherry DF (2009) Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Anim Cogn* 12(6):767–777.

Fehr E, Fischbacher U (2003) The nature of human altruism. *Nature* 425(6960):785–791.

Fehr E, Schmidt KM (1999) A theory of fairness, competition, and cooperation. *Q J Econ* 114:817–868.

Feigenson L, Carey S (2005) On the limits of infants' quantification of small object arrays. *Cognition* 97(3):295–313.

Feinberg LM, Allen TA, Ly D, Fortin NJ (2012) Recognition memory for social and non-social odors: Differential effects of neurotoxic lesions to the hippocampus and perirhinal cortex. *Neurobiol Learn Mem* 97(1):7–16.

Ferkin MH, Combs A, delBarco-Trillo J, Pierce AA, Franklin S (2008) Meadow voles, *Microtus pennsylvanicus,* have the capacity to recall the "what," "where," and "when" of a single past event. *Anim Cogn* 11(1):147–159.

Fernald RD (2012) Social control of the brain. *Annu Rev Neurosci* 35:133–151.

Fernandez-Ruiz J, Wang J, Aigner TG, Mishkin M (2001) Visual habit formation in monkeys with neurotoxic lesions of the ventrocaudal neostriatum. *Proc Natl Acad Sci USA* 98(7):4196–4201.

Ferrari PF, Visalberghi E, Paukner A, Fogassi L, Ruggiero A, Suomi SJ (2006) Neonatal imitation in rhesus macaques. *PLoS Biol* 4(9):e302.

Fine C (2006) *A Mind of Its Own* (W. W. Norton, New York).

Fishman YI, Volkov IO, Noh MD, Garell PC, Bakken H, Arezzo JC, Howard MA, Steinschneider M (2001) Consonance and dissonance of musical chords: Neural correlates in auditory cortex of monkeys and humans. *J Neurophysiol* 86(6):2761–2788.

Flack JC, de Waal FBM, Krakauer DC (2005) Social structure, robustness, and policing cost in a cognitively sophisticated species. *Am Nat* 165(5):E126–E139.

Flack JC, Girvan M, de Waal FBM, Krakauer DC (2006) Policing stabilizes construction of social niches in primates. *Nature* 439(7075):426–429.

Fletcher GE (2008) Attending to the outcome of others: Disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *Am J Primatol* 70(9):901–905.

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G (2005) Parietal lobe: From action organization to intention understanding. *Science* 308(5722):662–667.

Fontenot MB, Watson SL, Roberts KA, Miller RW (2007) Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. *Anim Behav* 74(3):487–496.

Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magn Reson Med* 33(5):636–647.

Formisano E, Kim DS, Di Salle F, van de Moortele PF, Ugurbil K, Goebel R (2003) Mirror-symmetric tonotopic maps in human primary auditory cortex. *Neuron* 40(4):859–869.

Fortin NJ, Agster KL, Eichenbaum HB (2002) Critical role of the hippocampus in memory for sequences of events. *Nat Neurosci* 5(5):458–462.

Fortin NJ, Wright SP, Eichenbaum H (2004) Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature* 431 (7005):188–191.

Fowler JH, Dawes CT, Christakis NA (2009) Model of genetic variation in human social networks. *Proc Natl Acad Sci USA* 106(6):1720–1724.

Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human brain is intrinsically organized into dynamic, anti-correlated functional networks. *Proc Natl Acad Sci USA* 102(27):9673–9678.

Frank RH (1988) *Passions Within Reason: The Strategic Role of the Emotions* (W. W. Norton, New York).

Franks NP (2008) General anaesthesia: From molecular targets to neuronal pathways of sleep and arousal. *Nat Rev Neurosci* 9(5):370–386.

Frantz CMP, Janoff-Bulman R (2000) Considering both sides: The limits of perspective taking. *Basic Appl Soc Psych* 22(1):31–42.

Franz G, von der Heyde M, Bülthoff HH (2005) An empirical approach to the experience of architectural space in virtual reality—Exploring relations between features and affective appraisals of rectangular indoor spaces. *Autom Construct* 14(2):165–172.

Freeman HD, Sullivan J, Hopper LM, Talbot CF, Holmes AN, Schultz-Darken N, Williams LE, Brosnan SF (2013). Different responses to reward comparisons by three primate species. *PLoS ONE* 8(10):e76297; doi:10.1371/journal.pone.0076297.

Fried I, Cameron KA, Yashar S, Fong R, Morrow JW (2002) Inhibitory and excitatory responses of single neurons in the human medial temporal lobe during recognition of faces and objects. *Cereb Cortex* 12(6):575–584.

Friederici AD, Rüschemeyer S-A, Hahne A, Fiebach CJ (2003) The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cereb Cortex* 13(2):170–177.

Friedman EB, Sun Y, Moore JT, Hung HT, Meng QC, Perera P, Joiner WJ, Thomas SA, Eckenhoff RG, Sehgal A, Kelz MB (2010) A conserved behavioral state barrier impedes transitions between anesthetic-induced unconsciousness and wakefulness: Evidence for neural inertia. *PLoS ONE* 5(7):e11903.

Friedman EH (2008) *The Myth of the Shiksa* (Church, New York).

Friedman WJ (1993) Memory for the time of past events. *Psychol Bull* 113:44–66.

Friston KJ, Frith CD, Liddle PF, Frackowiak RS (1993) Functional connectivity: The principal-component analysis of large (PET) data sets. *J Cereb Blood Flow Metab* 13(1):5–14.

Friston KJ, Holmes AP, Worsley KJ, Poline JP, Frith CD, Frackowiak RSJ (1995) Statistical parametric maps in functional imaging: A general linear approach. *Hum Brain Mapp* 2(4):189–210.

Fritz J, Mishkin M, Saunders RC (2005) In search of an auditory engram. *Proc Natl Acad Sci USA* 102(26):9359–9364.

Fritz T, Jentschke S, Gosselin N, Sammler D, Peretz I, Turner R, Friederici AD, Koelsch S (2009) Universal recognition of three basic emotions in music. *Curr Biol* 19(7):573–576.

Fu F, Hauert C, Nowak MA, Wang L (2008) Reputation-based partner choice promotes cooperation in social networks. *Phys Rev E Stat Nonlin Soft Matter Phys* 78(2 Pt 2):026117.

Fu X, Giavalisco P, Liu X, Catchpole G, Fu N, Ning ZB, Guo S, Yan Z, Somel M, Pääbo S, Zeng R, Willmitzer L, Khaitovich P (2011) Rapid metabolic evolution in human prefrontal cortex. *Proc Natl Acad Sci USA* 108(15):6181–6186.

Furlong EE, Boose KJ, Boysen ST (2008) Raking it in: The impact of enculturation on chimpanzee tool use. *Anim Cogn* 11(1):83–97.

Furtak SC, Wei S-M, Agster KL, Burwell RD (2007) Functional neuroanatomy of the parahippocampal region in the rat: The perirhinal and postrhinal cortices. *Hippocampus* 17(9):709–722.

Fuster JM (2001) The prefrontal cortex—an update: Time is of the essence. *Neuron* 30(2):319–333.

Fyhn M, Molden S, Witter MP, Moser EI, Moser M-B (2004) Spatial representation in the entorhinal cortex. *Science* 305(5688):1258–1264.

Gaab N, Gaser C, Zaehle T, Jancke L, Schlaug G (2003) Functional anatomy of pitch memory—an fMRI study with sparse temporal sampling. *Neuroimage* 19(4):1417–1426.

Gaffan D (1974) Recognition impaired and association intact in the memory of monkeys after transaction of the fornix. *J Comp Physiol Psychol* 88(6):1100–1109.

Gaffan D (1994) Scene-specific memory for objects: A model of episodic memory impairment in monkeys with fornix transection. *J Cogn Neurosci* 6:305–320.

Gagliardo A, Ioalé **P, Bingman VP (1999) Homing in pigeons: The role of the hippocampal for**mation in the representation of landmarks used for navigation. *J Neurosci* 19(1):311–315.

Gaillard R, Del Cul A, Naccache L, Vinckier F, Cohen L, Dehaene S (2006) Nonconscious semantic processing of emotional words modulates conscious access. *Proc Natl Acad Sci USA* 103(19):7524–7529.

Gaillard R, Cohen L, Adam C, Clemenceau S, Hasboun D, Baulac M, Willer JC, Dehaene S, Naccache L (2007) Subliminal words durably affect neuronal activity. *Neuroreport* 18(15):1527–1531.

Gallagher M, Kapp BS, Pascoe JP, Rapp PR (1981) A neuropharmacology of amygdaloid systems which contribute to learning and memory. In *The Amygdaloid Complex*, ed Ben-Ari Y (Elsevier, Amsterdam), pp 343–354.

Gallistel CR, King AP, Gottlieb D, Balci F, Papachristos EB, Szalecki M, Carbone KS (2007) Is matching innate? *J Exp Anal Behav* 87(2):161–199.

Gallup GG, Jr (1970) Chimpanzees: Self-recognition. *Science* 167(3914):86–87.

Gallup GG, Jr (1985) Do minds exist in species other than our own? *Neurosci Biobehav Rev* 9(4):631–641.

Galvez R, Mesches MH, McGaugh JL (1996) Norepinephrine release in the amygdala in response to footshock stimulation. *Neurobiol Learn Mem* 66(3):253–257.

Ganis G, Keenan JP, Kosslyn SM, Pascual-Leone A (2000) Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cereb Cortex* 10(2):175–180.

Gao T, Scholl BJ, McCarthy G (2012) Dissociating the detection of intentionality from animacy in the right posterior superior temporal sulcus. *J Neurosci* 32(41):14276–14280.

Garrity AG, Pearlson GD, McKiernan K, Lloyd D, Kiehl KA, Calhoun VD (2007) Aberrant “default mode” functional connectivity in schizophrenia. *Am J Psychiatry* 164(3):450–457.

Gazzaley A, Cooney JW, McEvoy K, Knight RT, D’Esposito M (2005) Top-down enhancement and suppression of the magnitude and speed of neural activity. *J Cogn Neurosci* 17(3):507–517.

Geng JJ, Behrmann M (2005) Spatial probability as an attentional cue in visual search. *Percept Psychophys* 67(7):1252–1268.

Gerard RW (1961) The fixation of experience. In *Brain Mechanisms and Learning,* eds Fessard A, Gerard RW, Konorski J (Thomas, Springfield, IL), pp 21–35.

Gerlach KD, Spreng RN, Gilmore AW, Schacter DL (2011) Solving future problems: Default network and executive activity associated with goal-directed mental simulations. *Neuroimage* 55(4):1816–1824.

Ghazanfar AA, Hauser MD (2001) The auditory behaviour of primates: A neuroethological perspective. *Curr Opin Neurobiol* 11(6):712–720.

Giedd JN, Blumenthal J, Jeffries NO, Castellanos FX, Liu H, Zijdenbos A, Paus T, Evans AC, Rapoport JL (1999) Brain development during childhood and adolescence: A longitudinal MRI study. *Nat Neurosci* 2(10):861–863.

Gilbert DT, Wilson TD (2007) Prospection: Experiencing the future. *Science* 317(5843):1351–1354.

Gilbert PE, Kesner RP (2002) Role of the rodent hippocampus in paired-associate learning involving associations between a stimulus and a spatial location. *Behav Neurosci* 116(1):63–71.

Gilbert PE, Kesner RP (2003) Localization of function within the dorsal hippocampus: The role of the CA3 subregion in paired-associate learning. *Behav Neurosci* 117(6):1385–1394.

Gilchrist ID, North A, Hood B (2001) Is visual search really like foraging? *Perception* 30(12):1459–1464.

Gino F, Galinsky AD (2012) Vicarious dishonesty: When psychological closeness creates distance from one’s moral compass. *Organ Behav Hum Decis Process* 119:15–26.

Glimcher PW (2011) Understanding dopamine and reinforcement learning: The dopamine reward prediction error hypothesis. *Proc Natl Acad Sci USA* 108(Suppl 3):15647–15654.

Glore J (1987) *Personal Arts,* Vol 2 (SCR Theatre, Costa Mesa, CA).

Gneezy U, Rustichini A (2000) Pay enough or don't pay at all. *Q J Econ* 115(3):791–810.

Gogtay N, Giedd JN, Lusk L, Hayashi KM, Greenstein D, Vaituzis AC, Nugent TF, 3rd, Herman DH, Clasen LS, Toga AW, Rapoport JL, Thompson PM (2004) Dynamic mapping of human cortical development during childhood through early adulthood. *Proc Natl Acad Sci USA* 101(21):8174–8179.

Gold PE, McGaugh JL (1977) Hormones and memory. In *Neuropeptide Influences on the Brain and Behavior,* eds Miller LH, Sandman CA, Kastin AJ (Raven, New York), pp 127–143.

Gold PE, Van Buskirk RB (1975) Facilitation of time-dependent memory processes with posttrial epinephrine injections. *Behav Biol* 13(2):145–153.

Gold PE, Van Buskirk R (1978) Posttraining brain norepinephrine concentrations: Correlation with retention performance of avoidance training and with peripheral epinephrine modulation of memory processing. *Behav Biol* 23(4):509–520.

Gold PE, Hankins L, Edwards RM, Chester J, McGaugh JL (1975) Memory interference and facilitation with posttrial amygdala stimulation: Effect on memory varies with footshock level. *Brain Res* 86(3):509–513.

Goldman-Rakic PS (1995) Cellular basis of working memory. *Neuron* 14(3):477–485.

Goldman-Rakic PS (1996) Regional and cellular fractionation of working memory. *Proc Natl Acad Sci USA* 93(24):13473–13480.

Goldman-Rakic PS, Funahashi S, Bruce CJ (1990) Neocortical memory circuits. *Cold Spring Harb Symp Quant Biol* 55:1025–1038.

Goldstein RN (2006) Architectural design and the collaborative research environment. *Cell* 127(2):243–246.

González-Gómez PL, Bozinovic F, Vásquez RA (2011) Elements of episodic-like memory in free-living hummingbirds, energetic consequences. *Anim Behav* 81:1257–1262.

Goodrich BG (2010) We do, therefore we think: Time, motility, and consciousness. *Rev Neurosci* 21(5):331–361.

Gordon K (1909) *Esthetics* (Henry Holt, New York).

Goyal MS, Raichle ME (2013) Gene expression-based modeling of human cortical synaptic density. *Proc Natl Acad Sci USA* 110(16):6571–6576.

Graham D, Stockinger S, Leder H (2013) An island of stability: Art images and natural scenes—but not natural faces—show consistent aesthetic response in Alzheimer's-related dementia. *Front Psychol* 4:107.

Grahn JA, Rowe JB (2009) Feeling the beat: Premotor and striatal interactions in musicians and nonmusicians during beat perception. *J Neurosci* 29(23):7540–7548.

Grant EG, Mackintosh JH (1963) A comparison of the social postures of some common laboratory rodents. *Behaviour* 21(3–4):246–259.

Greene JD, Sommerville RB, Nystrom LE, Darley JM, Cohen JD (2001) An fMRI investigation of emotional engagement in moral judgment. *Science* 293(5537):2105–2108.

Greene JD, Nystrom LE, Engell AD, Darley JM, Cohen JD (2004) The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44(2):389–400.

Greene MR, Liu T, Wolfe JM (2012) Reconsidering Yarbus: A failure to predict observers' task from eye movement patterns. *Vision Res* 62:1–8.

Greggers U, Mauelshagen J (1997) Matching behavior of honeybees in a multiple-choice situation: The differential effect of environmental stimuli on the choice process. *Anim Learn Behav* 25(4):458–472.

Greicius MD, Krasnow B, Reiss AL, Menon V (2003) Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proc Natl Acad Sci USA* 100(1):253–258.

Greicius MD, Srivastava G, Reiss AL, Menon V (2004) Default-mode network activity distinguishes Alzheimer's disease from healthy aging: Evidence from functional MRI. *Proc Natl Acad Sci USA* 101(13):4637–4642.

Griffiths TD, Büchel C, Frackowiak RSJ, Patterson RD (1998) Analysis of temporal structure in sound by the human brain. *Nat Neurosci* 1(5):422–427.

Gross CG (1993a) Hippocampus minor and man's place in nature: A case study in the social construction of neuroanatomy. *Hippocampus* 3(4):403–415.

Gross CG (1993b) Huxley versus Owen: The hippocampus minor and evolution. *Trends Neurosci* 16(12):493–498.

Grush R (2004) The emulation theory of representation: Motor control, imagery, and perception. *Behav Brain Sci* 27(3):377–396, discussion 396–442.

Grutzendler J, Kasthuri N, Gan W-B (2002) Long-term dendritic spine stability in the adult cortex. *Nature* 420(6917):812–816.

Guastella AJ, MacLeod C (2012) A critical review of the influence of oxytocin nasal spray on social cognition in humans: Evidence and future directions. *Horm Behav* 61(3):410–418.

Güntürkün O (2005) The avian "prefrontal cortex" and cognition. *Curr Opin Neurobiol* 15(6):686–693.

Gusnard DA, Raichle ME, Raichle ME (2001) Searching for a baseline: Functional imaging and the resting human brain. *Nat Rev Neurosci* 2(10):685–694.

Guth W, Schmittberger R, Schwartze B (1982) An experimental analysis of ultimatum bargaining. *J Econ Behav Organ* 3:367–388.

Gutsell JN, Inzlicht M (2012) Intergroup differences in the sharing of emotive states: Neural evidence of an empathy gap. *Soc Cogn Affect Neurosci* 7(5):596–603.

Guzowski JF, Lyford GL, Stevenson GD, Houston FP, McGaugh JL, Worley PF, Barnes CA (2000) Inhibition of activity-dependent Arc protein expression in the rat hippocampus impairs the maintenance of long-term potentiation and the consolidation of long-term memory. *J Neurosci* 20(11):3993–4001.

Haber SN, Knutson B (2010) The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology* 35(1):4–26.

Haidt J (2001) The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychol Rev* 108(4):814–834.

Haidt J (2012) *The Righteous Mind* (Pantheon Books, New York).

Halabi S, Nadler A (2009) Receiving help. In *The Psychology of Prosocial Behavior,* eds Stürmer S, Snyder M (Wiley-Blackwell, New York), pp 121–138.

Haley KJ, Fessler DMT (2005) Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evol Hum Behav* 26:245–256.

Halpern AR (1988) Mental scanning in auditory imagery for songs. *J Exp Psychol Learn Mem Cogn* 14(3):434–443.

Halpern AR, Ly J, Elkin-Frankston S, O'Connor MG (2008) "I know what I like": Stability of aesthetic preference in Alzheimer's patients. *Brain Cogn* 66(1):65–72.

Hamann SB, Ely TD, Grafton ST, Kilts CD (1999) Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nat Neurosci* 2(3):289–293.

Hamann SB, Ely TD, Hoffman JM, Kilts CD (2002) Ecstasy and agony: Activation of the human amygdala in positive and negative emotion. *Psychol Sci* 13(2):135–141.

Hammond RS, Tull LE, Stackman RW (2004) On the delay-dependent involvement of the hippocampus in object recognition memory. *Neurobiol Learn Mem* 82(1):26–34.

Hampton RR, Shettleworth SJ (1996) Hippocampal lesions impair memory for location but not color in passerine birds. *Behav Neurosci* 110(4):831–835.

Hanakawa T, Dimyan MA, Hallett M (2008) Motor planning, imagery, and execution in the distributed motor network: A time-course study with functional MRI. *Cereb Cortex* 18(12):2775–2788.

Hannesson DK, Howland JG, Phillips AG (2004) Interaction between perirhinal and medial prefrontal cortex is required for temporal order but not recognition memory for objects in rats. *J Neurosci* 24(19):4596–4604.

Hansen S, Bergvall AH, Nyiredi S (1993) Interaction with pups enhances dopamine release in the ventral striatum of maternal rats: A microdialysis study. *Pharmacol Biochem Behav* 45(3):673–676.

Hanus D, Mendes N, Tennie C, Call J (2011) Comparing the performance of apes and human children in the floating peanut task. *PLoS ONE* 6:e19555.

Haque OS, Waytz A (2012) Dehumanization in medicine: Causes, solutions, and functions. *Perspect Psychol Sci* 7(2):176–186.

Hardin G (1968) The tragedy of the commons. The population problem has no technical solution; it requires a fundamental extension in morality. *Science* 162(3859):1243–1248.

Harding RS (1981) An order of omnivores: Nonhuman primate diets in the wild. In *Omnivorous Primates: Gathering and Hunting in Human Evolution,* eds Harding RS, Teleki G (Columbia Univ Press, New York), pp 191–214.

Hariri AR, Holmes A (2006) Genetics of emotional regulation: The role of the serotonin transporter in neural function. *Trends Cogn Sci* 10(4):182–191.

Harrison GW, List JA (2004) Field experiments. *J Econ Lit* 42(4):1009–1055.

Harvey PH, Clutton-Brock TH, Mace GM (1980) Brain size and ecology in small mammals and primates. *Proc Natl Acad Sci USA* 77(7):4387–4389.

Hassabis D, Kumaran D, Vann SD, Maguire EA (2007) Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci USA* 104(5):1726–1731.

Hassert DL, Miyashita T, Williams CL (2004) The effects of peripheral vagal nerve stimulation at a memory-modulating intensity on norepinephrine output in the basolateral amygdala. *Behav Neurosci* 118(1):79–88.

Hatfield E, Walster GW, Berscheid E (1978) *Equity: Theory and Research* (Allyn and Bacon, Boston).

Hatfield T, McGaugh JL (1999) Norepinephrine infused into the basolateral amygdala post-training enhances retention in a spatial water maze task. *Neurobiol Learn Mem* 71(2):232–239.

Hatfield T, Spanis C, McGaugh JL (1999) Response of amygdalar norepinephrine to footshock and GABAergic drugs using in vivo microdialysis and HPLC. *Brain Res* 835(2):340–345.

Hauser MD, McDermott J (2003) The evolution of the music faculty: A comparative perspective. *Nat Neurosci* 6(7):663–668.

Hauser MD, Carey S, Hauser LB (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proc Biol Sci* 267(1445):829–833.

Hayama HR, Drumheller KM, Mastromonaco M, Reist C, Cahill LF, Alkire MT (2012) Event-related functional magnetic resonance imaging of a low dose of dexmedetomidine that impairs long-term memory. *Anesthesiology* 117(5):981–995.

Hayden BY, Parikh PC, Deaner RO, Platt ML (2007) Economic principles motivating social attention in humans. *Proc Biol Sci* 274(1619):1751–1756.

Hayden BY, Pearson JM, Platt ML (2011) Neuronal basis of sequential foraging decisions in a patchy environment. *Nat Neurosci* 14(7):933–939.

Hayes DJ, Greenshaw AJ (2011) 5-HT receptors and reward-related behaviour: A review. *Neurosci Biobehav Rev* 35(6):1419–1449.

Hayhoe M, Ballard D (2005) Eye movements in natural behavior. *Trends Cogn Sci* 9(4):188–194.

Hayne H, Imuta K (2011) Episodic memory in 3- and 4-year-old children. *Dev Psychobiol* 53(3):317–322.

He Y, Wang J, Wang L, Chen ZJ, Yan C, Yang H, Tang H, Zhu C, Gong Q, Zang Y, Evans AC (2009) Uncovering intrinsic modular organization of spontaneous brain activity in humans. *PLoS ONE* 4(4):e5226.

Heavey L, Pring L, Hermelin B (1999) A date to remember: The nature of memory in savant calendrical calculators. *Psychol Med* 29(1):145–160.

Hebb DO (1949) *The Organization of Behavior* (Wiley, New York).

Hecht EE, Patterson R, Barbey AK (2012) What can other animals tell us about human social cognition? An evolutionary perspective on reflective and reflexive processing. *Front Hum Neurosci* 6:224.

Heinrichs M, von Dawans B, Domes G (2009) Oxytocin, vasopressin, and human social behavior. *Front Neuroendocrinol* 30(4):548–557.

Hekkert P, van Wieringen PCW (1996) The impact of level of expertise on the evaluation of original and altered versions of post-impressionistic paintings. *Acta Psychol (Amst)* 94(2):117–131.

Helbing D, Yu W (2009) The outbreak of cooperation among success-driven individuals under noisy conditions. *Proc Natl Acad Sci USA* 106(10):3680–3685.

Helt MS, Eigsti IM, Snyder PJ, Fein DA (2010) Contagious yawning in autistic and typical development. *Child Dev* 81(5):1620–1631.

Henckens MJAG, Hermans EJ, Pu Z, Joëls M, Fernández G (2009) Stressed memories: How acute stress affects memory formation in humans. *J Neurosci* 29(32):10111–10119.

Henrich J, Fehr E, Bowles S, Boyd R, Camerer C, eds (2004) *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies* (Oxford Univ Press, Oxford).

Herholz SC, Lappe C, Knief A, Pantev C (2008) Neural basis of music imagery and the effect of musical expertise. *Eur J Neurosci* 28(11):2352–2360.

Herholz SC, Halpern AR, Zatorre RJ (2012) Neuronal correlates of perception, imagery, and memory for familiar tunes. *J Cogn Neurosci* 24(6):1382–1397.

Hernandez L, Hoebel BG (1988) Food reward and cocaine increase extracellular dopamine in the nucleus accumbens as measured by microdialysis. *Life Sci* 42(18):1705–1712.

Herold C, Palomero-Gallagher N, Hellmann B, Kröner S, Theiss C, Güntürkün O, Zilles K (2011) The receptor architecture of the pigeons’ nidopallium caudolaterale: An avian analogue to the mammalian prefrontal cortex. *Brain Struct Funct* 216(3):239–254.

Herrington TM, Assad JA (2010) Temporal sequence of attentional modulation in the lateral intraparietal area and middle temporal area during rapid covert shifts of attention. *J Neurosci* 30(9):3287–3296.

Herrnstein RJ (1961) Relative and absolute strength of response as a function of frequency of reinforcement. *J Exp Anal Behav* 4:267–272.

Hevner K (1935) Experimental studies of the affective value of colors and lines. *J Appl Psychol* 19(4):385–398.

Higham JP, Heistermann M, Maestripieri D (2013) The endocrinology of male rhesus macaque social and reproductive status: A test of the challenge and social stress hypotheses. *Behav Ecol Sociobiol* 67(1):19–30.

Hildebrand G (1999) *Origins of Architectural Pleasure* (Univ of California Press, Berkeley).

Hill J, Inder T, Neil J, Dierker D, Harwell J, Van Essen D (2010) Similar patterns of cortical expansion during human development and evolution. *Proc Natl Acad Sci USA* 107(29):13135–13140.

Hirschenhauser K, Oliveira RF (2006) Social modulation of androgens in male vertebrates: Meta-analyses of the challenge hypothesis. *Anim Behav* 71(2):265–277.

Hobson JA (2009) REM sleep and dreaming: Towards a theory of protoconsciousness. *Nat Rev Neurosci* 10(11):803–813.

Hoffman EA, Haxby JV (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat Neurosci* 3(1):80–84.

Hoffman ML, Beran MJ, Washburn DA (2009) Memory for “what,” “where,” and “when” information in rhesus monkeys (*Macaca mulatta*). *J Exp Psychol Anim Behav Process* 35(2):143–152.

Hohwy J (2009) The neural correlates of consciousness: New experimental approaches needed? *Conscious Cogn* 18(2):428–438.

Holbrook TL, Galarneau MR, Dye JL, Quinn K, Dougherty AL (2010) Morphine use after combat injury in Iraq and post-traumatic stress disorder. *N Engl J Med* 362(2):110–117.

Holland SM, Smulders TV (2011) Do humans use episodic memory to solve a what-where-when memory task? *Anim Cogn* 14(1):95–102.

Homberg JR, Lesch K-P (2011) Looking on the bright side of serotonin transporter gene variation. *Biol Psychiatry* 69(6):513–519.

Hopper LM, Lambeth SP, Schapiro SJ, Bernacky BJ, Brosnan SF (2013) The ontogeny of social comparisons in rhesus macaques (*Macaca mulatta*). *J Primatol* 2:109.

Horner V, Carter JD, Suchak M, de Waal FBM (2011) Spontaneous prosocial choice by chimpanzees. *Proc Natl Acad Sci USA* 108(33):13847–13851.

Horowitz A (2012) Fair is fine, but more is better: Limits to inequity aversion in the domestic dog. *Soc Justice Res* 25(2):195–212.

Huff NC, Wright-Hardesty KJ, Higgins EA, Matus-Amat P, Rudy JW (2005) Context pre-exposure obscures amygdala modulation of contextual-fear conditioning. *Learn Mem* 12(5):456–460.

Humphries NE, Queiroz N, Dyer JR, Pade NG, Musyl MK, Schaefer KM, Fuller DW, Brunnschweiler JM, Doyle TK, Houghton JD, Hays GC, Jones CS, Noble LR, Wearmouth VJ, Southall EJ, Sims DW (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465(7301):1066–1069.

Hunnius S (2007) The early development of visual attention and its implications for social and cognitive development. *Prog Brain Res* 164:187–209.

Hunt E, Love T (1972) How good can memory be? In *Coding Processes in Human Memory,* eds Melton AW, Martin E (Winston-Wiley, Washington, DC).

Hupbach A, Fieman R (2012) Moderate stress enhances immediate and delayed retrieval of educationally relevant material in healthy young men. *Behav Neurosci* 126(6):819–825.

Huron D (2006) *Sweet Anticipation: Music and the Psychology of Expectaction* (MIT Press, Cambridge, MA).

Hurst LC, Mulhall DJ (1988) Another calendar savant. *Br J Psychiatry* 152:274–277.

Huttenlocher PR, Dabholkar AS (1997) Regional differences in synaptogenesis in human cerebral cortex. *J Comp Neurol* 387(2):167–178.

Huxley L (1900) *Life and Letters of Thomas Henry Huxley* (Macmillan, London).

Huxley TH (1861a) On the brain of *Ateles paniscus*. In *Proceedings of the Scientific Meetings of the Zoological Society of London* (Taylor aand Francis, London), 247–260.

Huxley TH (1861b) On the zoological relations of man with the lower animals. *Natural History Review* 1:67–84.

Huxley TH (1863) *Evidence as to Man's Place in Nature* (Macmillan, London).

Hyde KL, Lerch JP, Zatorre RJ, Griffiths TD, Evans AC, Peretz I (2007) Cortical thickness in congenital amusia: When less is better than more. *J Neurosci* 27(47):13028–13032.

Hyde KL, Peretz I, Zatorre RJ (2008) Evidence for the role of the right auditory cortex in fine pitch resolution. *Neuropsychologia* 46(2):632–639.

Ikegaya Y, Saito H, Abe K (1995) High-frequency stimulation of the basolateral amygdala facilitates the induction of long-term potentiation in the dentate gyrus in vivo. *Neurosci Res* 22(2):203–207.

Imas OA, Ropella KM, Ward BD, Wood JD, Hudetz AG (2005) Volatile anesthetics disrupt frontal-posterior recurrent information transfer at gamma frequencies in rat. *Neurosci Lett* 387(3):145–150.

Inoue S, Matsuzawa T (2007) Working memory of numerals in chimpanzees. *Curr Biol* 17(23):R1004–R1005.

Insausti R (1993) Comparative anatomy of the entorhinal cortex and hippocampus in mammals. *Hippocampus* 3(Spec No):19–26.

Ioannidis JPA (2005) Why most published research findings are false. *PLoS Med* 2(8):e124.

Ishai A (2007) Sex, beauty and the orbitofrontal cortex. *Int J Psychophysiol* 63(2):181–185.

Ishizu T, Zeki S (2011) Toward a brain-based theory of beauty. *PLoS ONE* 6(7):e21852.

Itti L, Koch C (2000) A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Res* 40(10–12):1489–1506.

Izuma K, Saito DN, Sadato N (2008) Processing of social and monetary rewards in the human striatum. *Neuron* 58(2):284–294.

Izumi A (2000) Japanese monkeys perceive sensory consonance of chords. *J Acoust Soc Am* 108(6):3073–3078.

Jacobs B, Scheibel AB (1993) A quantitative dendritic analysis of Wernicke's area in humans. I. Lifespan changes. *J Comp Neurol* 327(1):83–96.

Jacobs B, Driscoll L, Schall M (1997) Life-span dendritic and spine changes in areas 10 and 18 of human cortex: A quantitative Golgi study. *J Comp Neurol* 386(4):661–680.

Jacobs B, Schall M, Prather M, Kapler E, Driscoll L, Baca S, Jacobs J, Ford K, Wainwright M, Treml M (2001) Regional dendritic and spine variation in human cerebral cortex: A quantitative Golgi study. *Cereb Cortex* 11(6):558–571.

Jacobs NS, Allen TA, Nguyen N, Fortin NJ (2013) Critical role of the hippocampus in memory for elapsed time. *J Neurosci* 33(34):13888–13893.

Jacobsen T, Höfel L (2003) Descriptive and evaluative judgment processes: Behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cogn Affect Behav Neurosci* 3(4):289–299.

Jacobsen T, Schubotz RI, Höfel L, Cramon DY (2006) Brain correlates of aesthetic judgment of beauty. *Neuroimage* 29(1):276–285.

Jacquet J, Hauert C, Traulsen A, Milinski M (2011) Shame and honour drive cooperation. *Biol Lett* 7(6):899–901.

Jaeggi SM, Buschkuehl M, Jonides J, Perrig WJ (2008) Improving fluid intelligence with training on working memory. *Proc Natl Acad Sci USA* 105(19):6829–6833.

Jaeggi SM, Buschkuehl M, Jonides J, Shah P (2011) Short- and long-term benefits of cognitive training. *Proc Natl Acad Sci USA* 108(25):10081–10086.

James A, Plank MJ, Edwards AM (2011) Assessing Lévy walks as models of animal foraging. *J R Soc Interface* 8(62):1233–1247.

James W (1890) *Principles of Psychology* (Henry Holt and Company, New York).

Janata P (2012) Acuity of mental representations of pitch. *Ann N Y Acad Sci* 1252(1):214–221.

Janson CH, Brosnan SF (2013). Experiments in primatology: From the lab to the field and back again. In *Primate Ecology and Conservation: A Handbook of Techniques*, eds Blair M, Sterling E, Bynum N (Oxford Univ Press, Oxford, UK), pp 177–194.

Jarvis ED, Güntürkün O, Bruce L, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Striedter G, Wild JM, Ball GF, Dugas-Ford J, Durand SE, Hough GE, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB; Avian Brain Nomenclature Consortium (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 6(2):151–159.

Jeannerod M (2006) *Motor Cognition* (Oxford Univ Press, Oxford).

Jedema HP, Gianaros PJ, Greer PJ, Kerr DD, Liu S, Higley JD, Suomi SJ, Olsen AS, Porter JN, Lopresti BJ, Hariri AR, Bradberry CW (2010) Cognitive impact of genetic variation of the serotonin transporter in primates is associated with differences in brain morphology rather than serotonin neurotransmission. *Mol Psychiatry* 15(5):512–522.

Jellema T, Baker CI, Wicker B, Perrett DI (2000) Neural representation for the perception of the intentionality of actions. *Brain Cogn* 44(2):280–302.

Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc Biol Sci* 273(1589):1013–1021.

Jensen K, Call J, Tomasello M (2007) Chimpanzees are rational maximizers in an ultimatum game. *Science* 318(5847):107–109.

Jing J, Gillette R, Weiss KR (2009) Evolving concepts of arousal: Insights from simple model systems. *Rev Neurosci* 20(5–6):405–427.

Johnson AM, Vernon PA, Feiler AR (2008) Behavioral genetic studies of personality: An introduction and review of the results of 50+ years of research. In *Handbook of Personality Theory and Assessment,* eds Boyle G, Matthews G, Saklofske D (Sage, London), pp 145–173.

Johnson MH, Dziurawiec S, Ellis H, Morton J (1991) Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40(1–2):1–19.

Jones BE (2003) Arousal systems. *Front Biosci* 8:S438–S451.

Jones PB, Canniffe E (2007) *Modern Architecture Through Case Studies 1945–1990* (Architectural Press, Oxford).

Jonides J, Lewis RL, Nee DE, Lustig CA, Berman MG, Moore KS (2008) The mind and brain of short-term memory. *Annu Rev Psychol* 59:193–224.

Jung MW, Qin Y, McNaughton BL, Barnes CA (1998) Firing characteristics of deep layer neurons in prefrontal cortex in rats performing spatial working memory tasks. *Cereb Cortex* 8(5):437–450.

Juslin PN, Sloboda JA (2001) *Music and Emotion: Theory and Research* (Oxford Univ Press, Oxford).

Kaas JH, Hackett TA (2000) Subdivisions of auditory cortex and processing streams in primates. *Proc Natl Acad Sci USA* 97(22):11793–11799.

Kaas JH, Hackett TA, Tramo MJ (1999) Auditory processing in primate cerebral cortex. *Curr Opin Neurobiol* 9(2):164–170.

Kabaso D, Coskren PJ, Henry BI, Hof PR, Wearne SL (2009) The electrotonic structure of pyramidal neurons contributing to prefrontal cortical circuits in macaque monkeys is significantly altered in aging. *Cereb Cortex* 19(10):2248–2268.

Kable JW, Glimcher PW (2009) The neurobiology of decision: Consensus and controversy. *Neuron* 63(6):733–745.

Kahneman D (2011) *Thinking, Fast and Slow* (Farrar, Straus and Giroux, New York).

Kalev A, Dobbin F, Kelly E (2006) Best practices or best guesses? Assessing the efficacy of corporate affirmative action and diversity policies. *Am Sociol Rev* 71(4):589–617.

Kaminski J, Call J, Tomasello M (2008) Chimpanzees know what others know, but not what they believe. *Cognition* 109(2):224–234.

Kandori M (1992) Social norms and community enforcement. *Rev Econ Stud* 59:63–80.

Kane MJ, Hambrick DZ, Conway AR (2005) Working memory capacity and fluid intelligence are strongly related constructs: Comment on Ackerman, Beier, and Boyle (2005). *Psychol Bull* 131(1):66–71, author reply 72–75.

Kaplan S (1987) Aesthetics, affect, and cognition. *Environ Behav* 19(1):3–32.

Kaplan S (1992) Environmental preference in a knowledge-seeking, knowledge-using organism. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture,* eds Barkow JH, Cosmides L, Tooby J (Oxford Univ Press, New York), pp 581–598.

Kapur N, Ellison D, Smith MP, McLellan DL, Burrows EH (1992) Focal retrograde amnesia following bilateral temporal lobe pathology. A neuropsychological and magnetic resonance study. *Brain* 115(Pt 1):73–85.

Karlan D, McConnell MA (2012) *Hey Look at Me: The Effect of Giving Circles on Giving* (National Bureau of Economic Research, Cambridge, MA).

Kart-Teke E, De Souza Silva MA, Huston JP, Dere E (2006) Wistar rats show episodic-like memory for unique experiences. *Neurobiol Learn Mem* 85(2):173–182.

Kastl AJ, Child IL (1968) Emotional meaning of four typographical variables. *J Appl Psychol* 52(6):440–446.

Katz PS (2006) Comparative neurophysiology: An electric convergence in fish. *Curr Biol* 16(9):R327–R330.

Katz PS, Harris-Warrick RM (1999) The evolution of neuronal circuits underlying species-specific behavior. *Curr Opin Neurobiol* 9(5):628–633.

Kawabata H, Zeki S (2004) Neural correlates of beauty. *J Neurophysiol* 91(4):1699–1705.

Keagy J, Savard J-F, Borgia G (2011) Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus. Anim Behav* 81(4):1063–1070.

Keating CF, Keating EG (1982) Visual scan patterns of rhesus monkeys viewing faces. *Perception* 11(2):211–219.

Keenan JP, Gallup GG, Falk D (2003) *The Face in the Mirror: The Search for the Origins of Consciousness* (HarperCollins, New York).

Kellert SR, Wilson EO (1993) *The Biophilia Hypothesis* (Island Press, Washington, DC).

Kemp AH, Guastella AJ (2010) Oxytocin: Prosocial behavior, social salience, or approach-related behavior? *Biol Psychiatry* 67(6):e33–e34; author reply e35.

Kendrick K (1994) Neurobiological correlates of visual and olfactory recognition in sheep. *Behav Processes* 33(1):89–111.

Kennedy PJ, Shapiro ML (2004) Retrieving memories via internal context requires the hippocampus. *J Neurosci* 24(31):6979–6985.

Kensinger EA, Corkin S (2004) Two routes to emotional memory: Distinct neural processes for valence and arousal. *Proc Natl Acad Sci USA* 101(9):3310–3315.

Kensinger EA, Krendl AC, Corkin S (2006) Memories of an emotional and a non-emotional event: Effects of aging and delay interval. *Exp Aging Res* 32(1):23–45.

Kensinger EA, Addis DR, Atapattu RK (2011) Amygdala activity at encoding corresponds with memory vividness and with memory for select episodic details. *Neuropsychologia* 49(4):663–673.

Kesner RP (1998) Neural mediation of memory for time: Role of the hippocampus and medial prefrontal cortex. *Psychon Bull Rev* 5:585–596.

Kesner RP, Ellis ME (1983) Memory consolidation: Brain region and neurotransmitter specificity. *Neurosci Lett* 39(3):295–300.

Kesner RP, Gilbert PE, Barua LA (2002) The role of the hippocampus in memory for the temporal order of a sequence of odors. *Behav Neurosci* 116(2):286–290.

Keverne EB (1999) The vomeronasal organ. *Science* 286(5440):716–720.

Keverne EB (2004) Understanding well-being in the evolutionary context of brain development. *Philos Trans R Soc Lond B Biol Sci* 359(1449):1349–1358.

Killian NJ, Jutras MJ, Buffalo EA (2012) A map of visual space in the primate entorhinal cortex. *Nature* 491(7426):761–764.

Kilpatrick L, Cahill L (2003) Modulation of memory consolidation for olfactory learning by reversible inactivation of the basolateral amygdala. *Behav Neurosci* 117(1):184–188.

Kim J, Delcasso S, Lee I (2011) Neural correlates of object-in-place learning in hippocampus and prefrontal cortex. *J Neurosci* 31(47):16991–17006.

Kimble DP (1963) The effects of bilateral hippocampal lesions in rats. *J Comp Physiol Psychol* 56:273–283.

Kirk U, Skov M, Christensen MS, Nygaard N (2009) Brain correlates of aesthetic expertise: A parametric fMRI study. *Brain Cogn* 69(2):306–315.

Klein JT, Platt ML (2013) Social information signaling by neurons in primate striatum. *Curr Biol* 23(8):691–696.

Klein JT, Deaner RO, Platt ML (2008) Neural correlates of social target value in macaque parietal cortex. *Curr Biol* 18(6):419–424.

Klein JT, Shepherd SV, Platt ML (2009) Social attention and the brain. *Curr Biol* 19(20): R958–R962.

Klein ME, Zatorre RJ (2011) A role for the right superior temporal sulcus in categorical perception of musical chords. *Neuropsychologia* 49(5):878–887.

Klepeis NE, Nelson WC, Ott WR, Robinson JP, Tsang AM, Switzer P, Behar JV, Hern SC, Engelmann WH (2001) The National Human Activity Pattern Survey (NHAPS): A resource for assessing exposure to environmental pollutants. *J Expo Anal Environ Epidemiol* 11(3):231–252.

Knierim JJ, Lee I, Hargreaves EL (2006) Hippocampal place cells: Parallel input streams, subregional processing, and implications for episodic memory. *Hippocampus* 16(9):755–764.

Knudsen EI (2007) Fundamental components of attention. *Annu Rev Neurosci* 30: 57–78.

Knutson B, Cooper JC (2005) Functional magnetic resonance imaging of reward prediction. *Curr Opin Neurol* 18(4):411–417.

Knutson B, Greer SM (2008) Anticipatory affect: Neural correlates and consequences for choice. *Philos Trans R Soc Lond B Biol Sci* 363(1511):3771–3786.

Knutson B, Adams CM, Fong GW, Hommer D (2001) Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J Neurosci* 21(16):RC159.

Koch C (2012) *Consciousness: Confessions of a Romantic Reductionist* (MIT Press, Cambridge, MA).

Koelsch S, Gunter TC, Friederici AD, Schröger E (2000) Brain indices of music processing: "Nonmusicians" are musical. *J Cogn Neurosci* 12(3):520–541.

Koelsch S, Fritz T, von Cramon DY, Müller K, Friederici AD (2006) Investigating emotion with music: An fMRI study. *Hum Brain Mapp* 27(3):239–250.

Koelsch S, Kilches S, Steinbeis N, Schelinski S (2008) Effects of unexpected chords and of performer's expression on brain responses and electrodermal activity. *PLoS ONE* 3(7):e2631.

Koenderink MJ, Uylings HB (1995) Postnatal maturation of layer V pyramidal neuronsin the human prefrontal cortex. A quantitative Golgi analysis. *Brain Res* 678(1–2):233–243.

Kolata S, Light K, Townsend DA, Hale G, Grossman HC, Matzel LD (2005) Variations in working memory capacity predict individual differences in general learning abilities among genetically diverse mice. *Neurobiol Learn Mem* 84(3):241–246.

Kolata S, Light K, Grossman HC, Hale G, Matzel LD (2007) Selective attention is a primary determinant of the relationship between working memory and general learning ability in outbred mice. *Learn Mem* 14(1):22–28.

Kolling N, Behrens TE, Mars RB, Rushworth MF (2012) Neural mechanisms of for aging. *Science* 336(6077):95–98.

Komisaruk BR, Whipple B (2005) Functional MRI of the brain during orgasm in women. *Annu Rev Sex Res* 16:62–86.

Komorowski RW, Manns JR, Eichenbaum H (2009) Robust conjunctive item-place coding by hippocampal neurons parallels learning what happens where. *J Neurosci* 29(31): 9918–9929.

Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E (2005) Oxytocin increases trust in humans. *Nature* 435(7042):673–676.

Kosslyn S (1994) *Image and Brain* (MIT Press, Cambridge, MA).

Kossmeier S, Ariely D, Bracha A (2009) Doing good or doing well? Image motivation and monetary incentives in behaving prosocially. *Am Econ Rev* 99(1):544–555.

Kounios J, Beeman M (2009) The *Aha!* moment. The cognitive neuroscience of insight. *Curr Dir Psychol Sci* 18:210–216.

Kouwenberg A-L, Walsh CJ, Morgan BE, Martin GM (2009) Episodic-like memory in crossbred Yucatan minipigs (*Sus scrofa*). *Appl Anim Behav Sci* 117:165–172.

Kouzakova M, van Baaren R, van Knippenberg A (2010) Lack of behavioral imitation in human interactions enhances salivary cortisol levels. *Horm Behav* 57(4–5):421–426.

Kowalski C, Ommen O, Driller E, Ernstmann N, Wirtz MA, Köhler T, Pfaff H (2010) Burnout in nurses—the relationship between social capital in hospitals and emotional exhaustion. *J Clin Nurs* 19(11–12):1654–1663.

Kringelbach ML (2005) The human orbitofrontal cortex: Linking reward to hedonic experience. *Nat Rev Neurosci* 6(9):691–702.

Kringelbach ML, Rolls ET (2004) The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. *Prog Neurobiol* 72(5):341–372.

Kringelbach M, Vuust P (2009) The pleasure of music. In *Pleasures of the Brain*, eds Kringelbach M, Berridge K (Oxford Univ Press, New York), pp 255–269.

Krivanek J, McGaugh JL (1968) Effects of pentylenetetrazol on memory storage in mice. *Psychopharmacology (Berl)* 12(4):303–321.

Krueger JI, Funder DC (2004) Towards a balanced social psychology: Causes, consequences, and cures for the problem-seeking approach to social behavior and cognition. *Behav Brain Sci* 27(3):313–327, discussion 328–376.

Krugers HJ, Zhou M, Joels M, Kindt M (2011) Regulation of excitatory synapses and fearful memories by stress hormones. *Front Behav Neurosci* 5(2011):62.

Krumhansl CL (1990) *Cognitive Foundations of Musical Pitch* (Oxford Univ Press, New York).

Ku SW, Lee U, Noh GJ, Jun IG, Mashour GA (2011) Preferential inhibition of frontal-to-parietal feedback connectivity is a neurophysiologic correlate of general anesthesia in surgical patients. *PLoS ONE* 6(10):e25155.

Kühn S, Müller BC, van Baaren RB, Wietzker A, Dijksterhuis A, Brass M (2010) Why do I like you when you behave like me? Neural mechanisms mediating positive consequences of observing someone being imitated. *Soc Neurosci* 5(4):384–392.

Kuhn T (1970) *The Structure of Scientific Revolutions*, 2nd Ed (Univ of Chicago Press, Chicago).

Kumaran D, Maguire EA (2006) An unexpected sequence of events: Mismatch detection in the human hippocampus. *PLoS Biol* 4(12):e424.

Kung S-J, Chen JL, Zatorre RJ, Penhune VB (2013) Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. *J Cogn Neurosci* 25(3):401–420.

LaBar KS, Cabeza R (2006) Cognitive neuroscience of emotional memory. *Nat Rev Neurosci* 7(1):54–64.

Lacetera N, Macis M (2010) Social image concerns and prosocial behavior: Field evidence from a nonlinear incentive scheme. *J Econ Behav Organ* 76(2):225–237.

Lacey S, Hagtvedt H, Patrick VM, Anderson A, Stilla R, Deshpande G, Hu X, Sato JR, Reddy S, Sathian K (2011) Art for reward's sake: Visual art recruits the ventral striatum. *Neuroimage* 55(1):420–433.

Lakin JL, Chartrand TL (2003) Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychol Sci* 14(4):334–339.

Lakin J, Jefferis V, Cheng C, Chartrand T (2003) The chameleon effect as social glue: Evidence for the evolutionary significance of nonconscious mimicry. *J Nonverbal Behav* 27(2):145–162.

Lakin JL, Chartrand TL, Arkin RM (2008) I am too just like you: Nonconscious mimicry as an automatic behavioral response to social exclusion. *Psychol Sci* 19(8):816–822.

Lakshminarayanan VR, Santos LR (2008) Capuchin monkeys are sensitive to others' welfare. *Curr Biol* 18(21):R999–R1000.

LaLumiere RT, Buen T-V, McGaugh JL (2003) Post-training intra-basolateral amygdala infusions of norepinephrine enhance consolidation of memory for contextual fear conditioning. *J Neurosci* 23(17):6754–6758.

Lamme VA (2006) Towards a true neural stance on consciousness. *Trends Cogn Sci* 10(11):494–501.

Långsjö JW, Alkire MT, Kaskinoro K, Hayama H, Maksimow A, Kaisti KK, Aalto S, Aantaa R, Jääskeläinen SK, Revonsuo A, Scheinin H (2012) Returning from oblivion: Imaging the neural core of consciousness. *J Neurosci* 32(14):4935–4943.

Large EW, Palmer C (2002) Perceiving temporal regularity in music. *Cogn Sci* 26:1–37.

Lau B, Glimcher PW (2005) Dynamic response-by-response models of matching behavior in rhesus monkeys. *J Exp Anal Behav* 84(3):555–579.

Laureys S (2005) The neural correlate of (un)awareness: Lessons from the vegetative state. *Trends Cogn Sci* 9(12):556–559.

Laureys S, Owen AM, Schiff ND (2004) Brain function in coma, vegetative state, and related disorders. *Lancet Neurol* 3(9):537–546.

Lavenex P, Amaral DG (2000) Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus* 10(4):420–430.

Lawrance J, Bogart C, Burnett M, Bellamy R, Rector K, Fleming SD (2013) How programmers debug, revisited: An information for aging theory perspective. *IEEE Trans Software Engineering* 39(2):197–215.

Le Corbusier (1948) *Towards a New Architecture* (Architectural Press, London, UK).

Leakey LS, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202(4927):7–9.

Leder H, Carbon C (2005) Dimensions in appreciation of car interior design. *Appl Cogn Psychol* 19(5):603–618.

Leder H, Belke B, Oeberst A, Augustin D (2004) A model of aesthetic appreciation and aesthetic judgments. *Br J Psychol* 95(Pt 4):489–508.

Leder H, Tinio PPL, Bar M (2011) Emotional valence modulates the preference for curved objects. *Perception* 40(6):649–655.

LeDoux J (1998) *The Emotional Brain: The Mysterious Underpinnings of Emotional Life* (Touchstone, New York).

Lee D (2008) Game theory and neural basis of social decision making. *Nat Neurosci* 11(4): 404–409.

Lee D, Seo H, Jung MW (2012) Neural basis of reinforcement learning and decision making. *Annu Rev Neurosci* 35:287–308.

Lee U, Kim S, Noh GJ, Choi BM, Hwang E, Mashour GA (2009a) The directionality and functional organization of frontoparietal connectivity during consciousness and anesthesia in humans. *Conscious Cogn* 18(4):1069–1078.

Lee U, Mashour GA, Kim S, Noh GJ, Choi BM (2009b) Propofol induction reduces the capacity for neural information integration: Implications for the mechanism of consciousness and general anesthesia. *Conscious Cogn* 18(1):56–64.

Lee U, Müller M, Noh GJ, Choi B, Mashour GA (2011) Dissociable network properties of anesthetic state transitions. *Anesthesiology* 114(4):872–881.

Lee Y-S, Janata P, Frost C, Hanke M, Granger R (2011) Investigation of melodic contour processing in the brain using multivariate pattern-based fMRI. *Neuroimage* 57(1):293–300.

Lehn H, Steffenach HA, van Strien NM, Veltman DJ, Witter MP, Håberg AK (2009) A specific role of the human hippocampus in recall of temporal sequences. *J Neurosci* 29(11):3475–3484.

Leigh SR (2004) Brain growth, life history, and cognition in primate and human evolution. *Am J Primatol* 62(3):139–164.

Leimar O, Hammerstein P (2001) Evolution of cooperation through indirect reciprocity. *Proc Biol Sci* 268(1468):745–753.

Leino S, Brattico E, Tervaniemi M, Vuust P (2007) Representation of harmony rules in the human brain: Further evidence from event-related potentials. *Brain Res* 1142:169–177.

Lennie P (2003) The cost of cortical computation. *Curr Biol* 13(6):493–497.

Leonard WR, Robertson ML, Snodgrass JJ, Kuzawa CW (2003) Metabolic correlates of hominid brain evolution. *Comp Biochem Physiol A Mol Integr Physiol* 136(1):5–15.

LePort AKR, Mattfeld AT, Dickinson-Anson H, Fallon JH, Stark CE, Kruggel F, Cahill L, McGaugh JL (2012) A behavioral and neuroanatomical investigation of highly superior autobiographical memory. *Neurobiol Learn Mem* 98(1):78–92.

Levin SA (2006) Learning to live in a global commons: Socioeconomic challenges for a sustainable environment. *Ecol Res* 21(3):328–333.

Levine B, Black SE, Cabeza R, Sinden M, Mcintosh AR, Toth JP, Tulving E, Stuss DT (1998) Episodic memory and the self in a case of isolated retrograde amnesia. *Brain* 121(Pt 10):1951–1973.

Levitt SD, List JA (2007) What do laboratory experiments measuring social preferences reveal about the real world? *J Econ Perspect* 21:153–174.

Levy DJ, Glimcher PW (2012) The root of all value: A neural common currency for choice. *Curr Opin Neurobiol* 22(6):1027–1038.

Lewis LD, Weiner VS, Mukamel EA, Donoghue JA, Eskandar EN, Madsen JR, Anderson WS, Hochberg LR, Cash SS, Brown EN, Purdon PL (2012) Rapid fragmentation of neuronal networks at the onset of propofol-induced unconsciousness. *Proc Natl Acad Sci USA* 109(49):E3377–E3386.

Lewis PA, Rezaie R, Brown R, Roberts N, Dunbar RI (2011) Ventromedial prefrontal volume predicts understanding of others and social network size. *Neuroimage* 57(4):1624–1629.

Ley A, Vroomen J, Hausfeld L, Valente G, De Weerd P, Formisano E (2012) Learning of new sound categories shapes neural response patterns in human auditory cortex. *J Neurosci* 32(38):13273–13280.

Leyton M (2010) The neurobiology of desire: Dopamine and the regulation of mood and motivational states in humans. In *Pleasures of the Brain,* eds Kringelbach ML, Berridge KC (Oxford Univ Press, New York), pp 221–243.

Li Z (1994) *The Private Life of Chairman Mao* (Random House, New York).

Liang KC, Juler RG, McGaugh JL (1986) Modulating effects of posttraining epinephrine on memory: Involvement of the amygdala noradrenergic system. *Brain Res* 368(1):125–133.

Libet B, Gleason CA, Wright EW, Pearl DK (1983) Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): The unconscious initiation of a freely voluntary act. *Brain* 106(Pt 3):623–642.

Lieberman MD, Cunningham WA (2009) Type I and type II error concerns in fMRI research: Re-balancing the scale. *Soc Cogn Affect Neurosci* 4(4):423–428.

Light KR, Kolata S, Wass C, Denman-Brice A, Zagalsky R, Matzel LD (2010) Working memory training promotes general cognitive abilities in genetically heterogeneous mice. *Curr Biol* 20(8):777–782.

Lilienfeld SO (2007) Psychological treatments that cause harm. *Perspect Psychol Sci* 2(1):53–70.

Lilienfeld SO, Ammirati R, Landfield K (2009) Giving debiasing away: Can psychological research on correcting cognitive errors promote human welfare? *Perspect Psychol Sci* 4(4):390–398.

Lilla M (2003) *The Reckless Mind: Intellectuals in Politics* (New York Review of Books, New York).

Linardi S, McConnell MA (2008) Volunteering and Image Concerns. Social Science Working Paper 1282 (California Institute of Technology, Pasadena).

Lindal PJ, Hartig T (2013) Architectural variation, building height, and the restorative quality of urban residential streetscapes. *J Environ Psychol* 33(1):26–36.

Liotti M, Brannan S, Egan G, Shade R, Madden L, Abplanalp B, Robillard R, Lancaster J, Zamarripa FE, Fox PT, Denton D (2001) Brain responses associated with consciousness of breathlessness (air hunger). *Proc Natl Acad Sci USA* 98(4):2035–2040.

List JA, Berrens RP, Bohara AK, Kerkvliet J (2004) Examining the role of social isolation on stated preferences. *Am Econ Rev* 94(3):741–752.

Liu DLJ, Graham S, Zorawski M (2008) Enhanced selective memory consolidation following post-learning pleasant and aversive arousal. *Neurobiol Learn Mem* 89(1):36–46.

Liu X, Hairston J, Schrier M, Fan J (2011) Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neurosci Biobehav Rev* 35(5):1219–1236.

Liu X, Somel M, Tang L, Yan Z, Jiang X, Guo S, Yuan Y, He L, Oleksiak A, Zhang Y, Li N, Hu Y, Chen W, Qiu Z, Pääbo S, Khaitovich P (2012) Extension of cortical synaptic development distinguishes humans from chimpanzees and macaques. *Genome Res* 22(4):611–622.

Llinás R (2001) *I of the Vortex: From Neurons to Self* (MIT Press, Cambridge, MA).

Llinás R, Ribary U (1993) Coherent 40-Hz oscillation characterizes dream state in humans. *Proc Natl Acad Sci USA* 90(5):2078–2081.

LoBue V, Nishida T, Chiong C, DeLoache JS, Haidt J (2009) When getting something good is bad: Even three-year-olds react to inequality. *Soc Dev* 20(1):154–170.

Locher P, Krupinski EA, Mello-Thoms C, Nodine CF (2007) Visual interest in pictorial art during an aesthetic experience. *Spat Vis* 21(1–2):55–77.

Locke J, Campbell MA, Kavanagh DJ (2012) Can a parent do too much for their child? An examination by parenting professionals of the concept of overparenting. *Aust J Guid Couns* 22(2):249–265.

Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Anim Cogn* 9(1):36–46.

Lonsdorf EV, Bonnie KE (2010) Opportunities and constraints when studying social learning: Developmental approaches and social factors. *Learn Behav* 38(3):195–205.

Loui P, Alsop D, Schlaug G (2009a) Tone deafness: A new disconnection syndrome? *J Neurosci* 29(33):10215–10220.

Loui P, Wu EH, Wessel DL, Knight RT (2009b) A generalized mechanism for perception of pitch patterns. *J Neurosci* 29(2):454–459.

Low P (2012) *The Cambridge Declaration on Consciousness,* eds Panksepp J, Reiss D, Edelman D, Van Swinderen B, Low P, Koch C. Presentation at the Francis Crick Memorial Conference, Cambridge, UK. Available at http://fcmconference.org/img/CambridgeDeclarationOnConsciousness.pdf. Accessed April 26, 2013.

Lu H, Zou Q, Gu H, Raichle ME, Stein EA, Yang Y (2012) Rat brains also have a default mode network. *Proc Natl Acad Sci USA* 109(10):3979–3984.

Luca M (2011) Reviews, Reputation, and Revenue: The Case of Yelp.com. Working Paper 12-016 (Harvard Business School, Boston, MA). Available at http://hbswk.hbs.edu/item/6833.html. Accessed April 20, 2013.

Luck SJ, Chelazzi L, Hillyard SA, Desimone R (1997) Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J Neurophysiol* 77(1):24–42.

Lundholm H (1921) The affective tone of lines: Experimental researches. *Psychol Rev* 28(1): 43–60.

Luria AR (1968) *The Mind of a Mnemonist; A Little Book About a Vast Memory* (Harvard Univ Press, Cambridge, MA).

Lydic R, Baghdoyan HA (2005) Sleep, anesthesiology, and the neurobiology of arousal state control. *Anesthesiology* 103(6):1268–1295.

Lyell C (1863) *Geological Evidence of the Antiquity of Man* (Spottiswoode & Co., London).

Lyn H, Russell JL, Hopkins WD (2010) The impact of environment on the comprehension of declarative communication in apes. *Psychol Sci* 21(3):360–365.

MacDonald CJ, Lepage KQ, Eden UT, Eichenbaum H (2011) Hippocampal "time cells" bridge the gap in memory for discontiguous events. *Neuron* 71(4):737–749.

MacLean E, Hare B (2012) Bonobos and chimpanzees infer the target of another's attention. *Anim Behav* 83(2):345–353.

Maclean PD (1990) *The Triune Brain in Evolution: Role in Paleocerebral Functions* (Springer, New York).

Maess B, Koelsch S, Gunter TC, Friederici AD (2001) Musical syntax is processed in Broca's area: An MEG study. *Nat Neurosci* 4(5):540–545.

Maestripieri D (2007) *Macachiavellian Intelligence* (Univ of Chicago Press, Chicago).

Maheu FS, Joober R, Beaulieu S, Lupien SJ (2004) Differential effects of adrenergic and corticosteroid hormonal systems on human short- and long-term declarative memory for emotionally arousing material. *Behav Neurosci* 118(2):420–428.

Malin EL, McGaugh JL (2006) Differential involvement of the hippocampus, anterior cingulate cortex, and basolateral amygdala in memory for context and footshock. *Proc Natl Acad Sci USA* 103(6):1959–1963.

Malkova L, Mishkin M (2003) One-trial memory for object-place associations after separate lesions of hippocampus and posterior para hippocampal region in the monkey. *J Neurosci* 23(5):1956–1965.

Manapat ML, Rand DG (2012) Delayed and inconsistent information and the evolution of trust. *Dyn Games Appl* 2:401–410.

Manapat ML, Nowak MA, Rand DG (2013) Information, irrationality and the evolution of trust. *J Econ Behav Organ* 90(Suppl): S57–S75.

Mangan B (2001) Sensation's ghost: The non-sensory "fringe" of consciousness. *Psyche* 7(18). Available at www.theassc.org/files/assc/2509.pdf.

Mani A, Rahwan I, Pentland A (2013) Inducing peer pressure to promote cooperation. *Sci Rep* 3:1735.

Mankin EA, Sparks FT, Slayyeh B, Sutherland RJ, Leutgeb S, Leutgeb JK (2012) Neuronal code for extended time in the hippocampus. *Proc Natl Acad Sci USA* 109(47): 19462–19467.

Manns JR, Eichenbaum H (2006) Evolution of declarative memory. *Hippocampus* 16(9): 795–808.

Manns JR, Howard MW, Eichenbaum H (2007) Gradual changes in hippocampal activity support remembering the order of events. *Neuron* 56(3):530–540.

Mantini D, Vanduffel W (2013) Emerging roles of the brain's default network. *Neuroscientist* 19(1):76–87.

Margolis H (1993) *Paradigms and Barriers* (Univ of Chicago Press, Chicago).

Mark TA, Gallistel CR (1994) Kinetics of matching. *J Exp Psychol Anim Behav Process* 20(1): 79–95.

Marks I, Dar R (2000) Fear reduction by psychotherapies. Recent findings, future directions. *Br J Psychiatry* 176:507–511.

Marler P (1999) Origins of music and speech: Insights from animals. In *The Origins of Music*, eds Wallin NL, Merker B, Brown S (MIT Press, Cambridge, MA), pp 31–48.

Marr D, Poggio AT, Ullman S (2010) *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (MIT Press, Cambridge, MA).

Martin-Ordas G, Haun D, Colmenares F, Call J (2010) Keeping track of time: Evidence for episodic-like memory in great apes. *Anim Cogn* 13(2):331–340.

Mason MF, Norton MI, Van Horn JD, Wegner DM, Grafton ST, Macrae CN (2007) Wandering minds: The default network and stimulus-independent thought. *Science* 315(5810): 393–395.

Massen JJM, van den Berg LM, Spruijt BM, Sterck EHM (2010) Generous leaders and selfish underdogs: Pro-sociality in despotic macaques. *PLoS ONE* 5(3):e9734.

Massen JJM, van den Berg LM, Spruijt BM, Sterck EHM (2012) Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). *Am J Primatol* 74(2):145–156.

Masserman JH, Wechkin S, Terris W (1964) "Altruistic" behavior in rhesus monkeys. *Am J Psychiatry* 121:584–585.

Masuda N, Ohtsuki H (2007) Tag-based indirect reciprocity by incomplete social information. *Proc Biol Sci* 274(1610):689–695.

Matsumura N, Nishijo H, Tamura R, Eifuku S, Endo S, Ono T (1999) Spatial- and task-dependent neuronal responses during real and virtual translocation in the monkey hippocampal formation. *J Neurosci* 19(6):2381–2393.

Matzel LD, Han YR, Grossman H, Karnik MS, Patel D, Scott N, Specht SM, Gandhi CC (2003) Individual differences in the expression of a “general” learning ability in mice. *J Neurosci* 23(16):6423–6433.

Mauck B, Dehnhardt G (1997) Mental rotation in a California sea lion (*Zalophus californianus*). *J Exp Biol* 200(Pt 9):1309–1316.

McClelland JL, Goddard NH (1996) Considerations arising from a complementary learning systems perspective on hippocampus and neocortex. *Hippocampus* 6(6):654–665.

McClure SM, Berns GS, Montague PR (2003) Temporal prediction errors in a passive learning task activate human striatum. *Neuron* 38(2):339–346.

McDermott J, Hauser M (2004) Are consonant intervals music to their ears? Spontaneous acoustic preferences in a nonhuman primate. *Cognition* 94(2):B11–B21.

McDermott J, Hauser MD (2007) Nonhuman primates prefer slow tempos but dislike music overall. *Cognition* 104(3):654–668.

McEwen BS (2007) Physiology and neurobiology of stress and adaptation: Central role of the brain. *Physiol Rev* 87(3):873–904.

McFarlin SC, Barks SK, Tocheri MW, Massey JS, Eriksen AB, Fawcett KA, Stoinski TS, Hof PR, Bromage TG, Mudakikwa A, Cranfield MR, Sherwood CC (2012) Early brain growth cessation in wild virunga mountain gorillas (*Gorilla beringei beringei*). *Am J Primatol* 75(5):450–463.

McGaugh JL (1966) Time-dependent processes in memory storage. *Science* 153(3742):1351–1358.

McGaugh JL (1968) Drug facilitation of memory and learning. In *Psychopharmacology: A Review of Progress,* ed Efron DH. PHS Publ. No. 1836 (U.S. Government Printing Office, Washington, DC), pp 891–904.

McGaugh JL (1973) Drug facilitation of learning and memory. *Annu Rev Pharmacol* 13:229–241.

McGaugh JL (1983) Hormonal influences on memory. *Annu Rev Psychol* 34:297–323.

McGaugh JL (2000) Memory—a century of consolidation. *Science* 287(5451):248–251.

McGaugh JL (2002) Memory consolidation and the amygdala: A systems perspective. *Trends Neurosci* 25(9):456–461.

McGaugh JL (2003) *Memory and Emotion: The Making of Lasting Memories* (Columbia Univ Press, New York).

McGaugh JL (2004) The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annu Rev Neurosci* 27:1–28.

McGaugh JL (2005) Emotional arousal and enhanced amygdala activity: New evidence for the old perseveration-consolidation hypothesis. *Learn Mem* 12(2):77–79.

McGaugh JL, Gold PE (1976) Modulation of memory by electrical stimulation of the brain. In *Neural Mechanisms of Learning and Memory,* eds Rosenzweig MR, Bennett EL (MIT Press, Cambridge, MA), pp 549–560.

McGaugh JL, Gold PE (1989) Hormonal modulation of memory. In *Psychoendocrinology,* eds Brush RB, Levine S (Academic Press, New York), pp 305–339.

McGaugh JL, Herz MJ (1972) *Memory Consolidation* (Albion, San Francisco).

McGaugh JL, Petrinovich LF (1965) Effects of drugs on learning and memory. *Int Rev Neurobiol* 8:139–196.

McGaugh JL, Roozendaal B (2009) Drug enhancement of memory consolidation: Historical perspective and neurobiological implications. *Psychopharmacology (Berl)* 202(1–3):3–14.

McGaugh JL, Introini-Collison IB, Nagahara AH (1988) Memory-enhancing effects of post-training naloxone: Involvement of β-noradrenergic influences in the amygdaloid complex. *Brain Res* 446(1):37–49.

McGrath M, Oakley B (2012) Codependency and pathological altruism. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 49–74.

McIntyre CK, Hatfield T, McGaugh JL (2002) Amygdala norepinephrine levels after training predict inhibitory avoidance retention performance in rats. *Eur J Neurosci* 16(7): 1223–1226.

McIntyre CK, Miyashita T, Setlow B, Marjon KD, Steward O, Guzowski JF, McGaugh JL (2005) Memory-influencing intra-basolateral amygdala drug infusions modulate expression of Arc protein in the hippocampus. *Proc Natl Acad Sci USA* 102(30):10718–10723.

McIntyre CK, McGaugh JL, Williams CL (2012) Interacting brain systems modulate memory consolidation. *Neurosci Biobehav Rev* 36(7):1750–1762.

McKee RD, Squire LR (1993) On the development of declarative memory. *J Exp Psychol Learn Mem Cogn* 19(2):397–404.

McNelis NL, Boatright-Horowitz SL (1998) Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Anim Cogn* 1(1):65–69.

Meck WH, Church RM, Olton DS (1984) Hippocampus, time, and memory. *Behav Neurosci* 98(1):3–22.

Meltzoff AN, Moore MK (1977) Imitation of facial and manual gestures by human neonates. *Science* 198(4312):75–78.

Mendes N, Rakoczy H, Call J (2008) Ape metaphysics: Object individuation without language. *Cognition* 106(2):730–749.

Menon V, Levitin DJ (2005) The rewards of music listening: Response and physiological connectivity of the mesolimbic system. *Neuroimage* 28(1):175–184.

Mercier H, Sperber D (2011) Why do humans reason? Arguments for an argumentative theory. *Behav Brain Sci* 34(2):57–74, discussion 74–111.

Merker B (2007) Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behav Brain Sci* 30(1):63–81.

Meyer-Lindenberg A, Domes G, Kirsch P, Heinrichs M (2011) Oxytocin and vasopressin in the human brain: Social neuropeptides for translational medicine. *Nat Rev Neurosci* 12(9):524–538.

Meyers-Levy J, Zhu R (2007) The influence of ceiling height: The effect of priming on the type of processing that people use. *J Consum Res* 34(2):174–186.

Micheau J, Destrade C, Soumireu-Mourat B (1984) Time-dependent effects of posttraining intrahippocampal injections of corticosterone on retention of appetitive learning tasks in mice. *Eur J Pharmacol* 106:39–46.

Milinski M (2013) Chimps play fair in the ultimatum game. *Proc Natl Acad Sci USA* 110(6): 1978–1979.

Milinski M, Semmann D, Bakker TCM, Krambeck HJ (2001) Cooperation through indirect reciprocity: Image scoring or standing strategy? *Proc Biol Sci* 268(1484):2495–2501.

Milinski M, Semmann D, Krambeck HJ (2002a) Donors to charity gain in both indirect reciprocity and political reputation. *Proc Biol Sci* 269(1494):881–883.

Milinski M, Semmann D, Krambeck HJ (2002b) Reputation helps solve the "tragedy of the commons." *Nature* 415(6870):424–426.

Miller CS, Remington RW (2004) Modeling information navigation: Implications for information architecture. *Hum Comput Interact* 19(3):225–271.

Miller DJ, Duka T, Stimpson CD, Schapiro SJ, Baze WB, McArthur MJ, Fobbs AJ, Sousa AM, Sestan N, Wildman DE, Lipovich L, Kuzawa CW, Hof PR, Sherwood CC (2012) Prolonged myelination in human neocortical evolution. *Proc Natl Acad Sci USA* 109(41): 16480–16485.

Miller GA (1956) The magical number seven plus or minus two: Some limits on our capacity for processing information. *Psychol Rev* 63(2):81–97.

Mills LG (2008) *Violent Partners* (Basic Books, New York).

Milner B (1962) *Physiologie de l'Hippocampe*, ed Passouant P (CNRS, Paris), pp 257–272 (French).

Milner B (1972) Disorders of learning and memory after temporal lobe lesions in man. *Clin Neurosurg* 19:421–446.

Milner D, Goodale M (1995) *The Visual Brain in Action* (Oxford Univ Press, Oxford).

Milstein DM, Dorris MC (2007) The influence of expected value on saccadic preparation. *J Neurosci* 27(18):4810–4818.

Milton K (1981) Food choice and digestive strategies of two sympatric primate species. *Am Nat* 137(4):496–505.

Min BK (2010) A thalamic reticular networking model of consciousness. *Theor Biol Med Model* 7:10.

Minosi A, Martinola A, Mankan S, Balzarini F, Kostadinov, A.N, Prevostini, A (2003) Intelligent, low-power and low-cost measurement system for energy consumption. In *IEEE International Symposium on Virtual Environments, Human-Computer Interfaces and Measurement Systems* (IEEE, Washington, DC), pp 125–130.

Minsky M, Papert S (1987) *Society of Mind* (Simon and Schuster, New York).

Mirpour K, Arcizet F, Ong WS, Bisley JW (2009) Been there, seen that: A neural mechanism for performing efficient visual search. *J Neurophysiol* 102(6):3481–3491.

Mirpour K, Ong WS, Bisley JW (2010) Microstimulation of posterior parietal cortex biases the selection of eye movement goals during search. *J Neurophysiol* 104(6):3021–3028.

Mishkin M (1978) Memory in monkeys severely impaired by combined but not by separate removal of amygdala and hippocampus. *Nature* 273(5660):297–298.

Mishkin M, Delacour J (1975) An analysis of short-term visual memory in the monkey. *J Exp Psychol Anim Behav Process* 1(4):326–334.

Mishkin M, Malamut B, Bachevalier J (1984) Memories and habits: Two neural systems. In *Neurobiology of Learning and Memory,* eds Lynch G, McGaugh JL, Weinberger NM (Guilford Press, New York), pp 65–77.

Mishkin M, Suzuki WA, Gadian DG, Vargha-Khadem F (1997) Hierarchical organization of cognitive memory. *Philos Trans R Soc Lond B Biol Sci* 352(1360):1461–1467.

Mitani J (2006) Reciprocal exchange in chimpanzees and other primates. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, eds Kappeler PM, van Schaik CP (Springer, Berlin), pp 107–119.

Mitani JC, Hunley KL, Murdoch ME (1999) Geographic variation in the calls of wild chimpanzees: A reassessment. *Am J Primatol* 47(2):133–151.

Mithen S (2005) *The Singing Neanderthals: The Origins of Music, Language, Mind and Body* (Weidenfeld & Nicolson, London).

Miyashita T, Williams CL (2006) Epinephrine administration increases neural impulses propagated along the vagus nerve: Role of peripheral beta-adrenergic receptors. *Neurobiol Learn Mem* 85(2):116–124.

Mobbs D, Yu R, Meyer M, Passamonti L, Seymour B, Calder AJ, Schweizer S, Frith CD, Dalgleish T (2009) A key role for similarity in vicarious reward. *Science* 324(5929):900.

Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J (2005) Opinion: The neural basis of human moral cognition. *Nat Rev Neurosci* 6(10):799–809.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souza R, Grafman J (2006) Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc Natl Acad Sci USA* 103(42):15623–15628.

Monchi O, Petrides M, Strafella AP, Worsley KJ, Doyon J (2006) Functional role of the basal ganglia in the planning and execution of actions. *Ann Neurol* 59(2):257–264.

Montague PR, Sejnowski TJ (1994) The predictive brain: Temporal coincidence and temporal order in synaptic learning mechanisms. *Learn Mem* 1(1):1–33.

Montague PR, Dayan P, Sejnowski TJ (1996) A framework for mesencephalic dopamine systems based on predictive Hebbian learning. *J Neurosci* 16(5):1936–1947.

Montefiore SS (2004) *Stalin* (Alfred A. Knopf, New York).

Montgomery JC (1991) “Seeing” with nonvisual senses: Mechano- and electro-sensory systems of fish. *Physiology (Bethesda)* 6:73–77.

Moore T, Armstrong KM, Fallah M (2003) Visuomotor origins of covert spatial attention. *Neuron* 40(4):671–683.

Morin A (2011) Self-recognition, theory-of-mind, and self-awareness: What side are you on? *Laterality* 16(3):367–383.

Mormann F (2000) Mean phase coherence as a measure for phase synchronization and its application to the EEG of epilepsy patients. *Physica D* 144:358–369.

Morris G, Arkadir D, Nevet A, Vaadia E, Bergman H (2004) Coincident but distinct messages of midbrain dopamine and striatal tonically active neurons. *Neuron* 43(1):133–143.

Morris RGM (2001) Episodic-like memory in animals: Psychological criteria, neural mechanisms and the value of episodic-like tasks to investigate animal models of neurodegenerative disease. *Philos Trans R Soc Lond B Biol Sci* 356(1413):1453–1465.

Moruzzi G, Magoun HW (1949) Brain stem reticular formation and activation of the EEG. *Electroencephalogr Clin Neurophysiol* 1(4):455–473.

Moser MB, Trommald M, Andersen P (1994) An increase in dendritic spine density on hippocampal CA1 pyramidal cells following spatial learning in adult rats suggests the formation of new synapses. *Proc Natl Acad Sci USA* 91(26):12673–12675.

Moyo D (2009) *Dead Aid* (Farrar, Straus and Giroux, New York).

Mueller GE, Pilzecker A (1900) Experimentelle Beitrage zur Lehre vom Gedächtniss. *Z Psychol* 1(1):1–288.

Mulcahy NJ, Call J (2006) Apes save tools for future use. *Science* 312(5776):1038–1040.

Müller M, Höfel L, Brattico E, Jacobsen T (2010) Aesthetic judgments of music in experts and laypersons—An ERP study. *Int J Psychophysiol* 76(1):40–51.

Mumby DG, Pinel JP (1994) Rhinal cortex lesions and object recognition in rats. *Behav Neurosci* 108(1):11–18.

Mumby DG, Pinel JP, Wood ER (1990) Nonrecurring-items delayed nonmatching-to-sample in rats: A new paradigm for testing non-spatial working memory. *Psychobiology* 18:321–326.

Munar E, Nadal M, Rosselló J, Flexas A, Moratti S, Maestú F, Marty G, Cela-Conde CJ (2012) Lateral orbitofrontal cortex involvement in initial negative aesthetic impression formation. *PLoS ONE* 7(6):e38152.

Murphy FC, Nimmo-Smith I, Lawrence AD (2003) Functional neuroanatomy of emotions: A meta-analysis. *Cogn Affect Behav Neurosci* 3(3):207–233.

Murrie DC, Boccaccini MT, Guarnera LA, Rufino K (2013) Are forensic experts biased by the side that retained them? *Psychol Sci* Oct 24(10):1889–1897.

Nadal M, Munar E, Capó MA, Rosselló J, Cela-Conde CJ (2008) Towards a framework for the study of the neural correlates of aesthetic preference. *Spat Vis* 21(3–5):379–396.

Najjar N, Davis LW, Beck-Coon K, Carney Doebbeling C (2009) Compassion fatigue: A review of the research to date and relevance to cancer-care providers. *J Health Psychol* 14(2):267–277.

Nakahara H, Hikosaka O (2012) Learning to represent reward structure: A key to adapting to complex environments. *Neurosci Res* 74(3-4):177–183.

Nakamura M, Masuda N (2011) Indirect reciprocity under incomplete observation. *PLOS Comput Biol* 7(7):e1002113.

Naqshbandi M, Roberts WA (2006) Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Tests of the Bischof-Kohler hypothesis. *J Comp Psychol* 120(4):345–357.

Nasar JL (1988) *Environmental Aesthetics: Theory, Research, and Applications* (Cambridge Univ Press, Cambridge, UK).

National Research Council (2009) *Strengthening Forensic Science in the United States* (National Academies Press, Washington, DC).

National Research Council and National Academy of Public Administration (2010) *Choosing the Nation's Fiscal Future* (National Academies Press, Washington, DC).

Naya Y, Suzuki WA (2011) Integrating what and when across the primate medial temporal lobe. *Science* 333(6043):773–776.

Neider MB, Zelinsky GJ (2006) Scene context guides eye movements during visual search. *Vision Res* 46(5):614–621.

Neisser U, Winograd E, Bergman ET, Schreiber CA, Palmer SE, Weldon MS (1996) Remembering the earthquake: Direct experience vs. hearing the news. *Memory* 4(4):337–357.

Neiworth JJ, Johnson ET, Whillock K, Greenberg J, Brown V (2009) Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *J Comp Psychol* 123(1):10–17.

Neumann ID, Torner L, Wigger A (2000) Brain oxytocin: Differential inhibition of neuroendocrine stress responses and anxiety-related behaviour in virgin, pregnant and lactating rats. *Neuroscience* 95(2):567–575.

Nieder A (2009) Prefrontal cortex and the evolution of symbolic reference. *Curr Opin Neurobiol* 19(1):99–108, www.sciencedirect.com/science/journal/09594388.

Nielson KA, Arentsen TJ (2012) Memory modulation in the classroom: Selective enhancement of college examination performance by arousal induced after lecture. *Neurobiol Learn Mem* 98(1):12–16.

Nielson KA, Lorber W (2009) Enhanced post-learning memory consolidation is influenced by arousal predisposition and emotion regulation but not by stimulus valence or arousal. *Neurobiol Learn Mem* 92(1):70–79.

Nielson KA, Powless M (2007) Positive and negative sources of emotional arousal enhance long-term word-list retention when induced as long as 30 min after learning. *Neurobiol Learn Mem* 88(1):40–47.

Nielson KA, Radtke RC, Jensen RA (1996) Arousal-induced modulation of memory storage processes in humans. *Neurobiol Learn Mem* 66(2):133–142.

Ninokura Y, Mushiake H, Tanji J (2003) Representation of the temporal order of visual objects in the primate lateral prefrontal cortex. *J Neurophysiol* 89(5):2868–2873.

Nishijo H, Ono T, Eifuku S, Tamura R (1997) The relationship between monkey hippocampus place-related neural activity and action in space. *Neurosci Lett* 226(1):57–60.

Niv Y, Joel D, Meilijson I, Ruppin E (2002) Evolution of reinforcement learning in uncertain environments: A simple explanation for complex foraging beaviors. *Adapt Behav* 10(1):5–24.

Noack RA (2012) Solving the "human problem": The frontal feedback model. *Conscious Cogn* 21(2):1043–1067.

Norscia I, Palagi E (2011) Yawn contagion and empathy in *Homo sapiens. PLoS One* 6(12): e28472.

Northcutt RG, Kaas JH (1995) The emergence and evolution of mammalian neo-cortex. *Trends Neurosci* 18(9):373–379.

Nowak MA (2006a) *Evolutionary Dynamics* (Belknap, Cambridge, MA).

Nowak MA (2006b) Five rules for the evolution of cooperation. *Science* 314(5805):1560–1563.

Nowak MA, Highfield R (2011) *SuperCooperators: Altruism, Evolution, and Why We Need Each Other to Succeed* (Free Press, New York).

Nowak MA, Sigmund K (1998a) Evolution of indirect reciprocity by image scoring. *Nature* 393(6685):573–577.

Nowak MA, Sigmund K (1998b) The dynamics of indirect reciprocity. *J Theor Biol* 194(4): 561–574.

Nowak MA, Sigmund K (2005) Evolution of indirect reciprocity. *Nature* 437(7063):1291–1298.

Nowak MA, Page KM, Sigmund K (2000) Fairness versus reason in the ultimatum game. *Science* 289(5485):1773–1775.

Nowak MA, Tarnita CE, Antal T (2010) Evolutionary dynamics in structured populations. *Philos Trans R Soc Lond B Biol Sci* 365(1537):19–30.

O'Connell LA, Hofmann HA (2011) The vertebrate mesolimbic reward system and social behavior network: A comparative synthesis. *J Comp Neurol* 519(18):3599–3639.

O'Doherty JP (2004) Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Curr Opin Neurobiol* 14(6):769–776.

O'Keefe J, Dostrovsky J (1971) The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res* 34(1):171–175.

O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map* (Clarendon Press, Oxford).

Oakley B, Knafo A, Madhavan G, Wilson DS, eds (2011) *Pathological Altruism* (Oxford Univ Press, Oxford).

Oakley B, Knafo A, Madhavan G, Wilson DS, eds (2012a) *Pathological Altruism* (Oxford University Press, New York).

Oakley B, Knafo A, McGrath M (2012b) Pathological altruism—an introduction. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 3–9.

Ogawa S, Lee TM, Kay AR, Tank DW (1990) Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proc Natl Acad Sci USA* 87(24):9868–9872.

Ohtsuki H, Iwasa Y (2004) How should we define goodness?—Reputation dynamics in indirect reciprocity. *J Theor Biol* 231(1):107–120.

Ohtsuki H, Iwasa Y (2006) The leading eight: Social norms that can maintain cooperation by indirect reciprocity. *J Theor Biol* 239(4):435–444.

Ohtsuki H, Iwasa Y (2007) Global analyses of evolutionary dynamics and exhaustive search for social norms that maintain cooperation by reputation. *J Theor Biol* 244(3):518–531.

Ohtsuki H, Iwasa Y, Nowak MA (2009) Indirect reciprocity provides only a narrow margin of efficiency for costly punishment. *Nature* 457(7225):79–82.

Okuda S, Roozendaal B, McGaugh JL (2004) Glucocorticoid effects on object recognition memory require training-associated emotional arousal. *Proc Natl Acad Sci USA* 101(3):853–858.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9(1):97–113.

Olds J, Milner P (1954) Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. *J Comp Physiol Psychol* 47(6):419–427.

Olds ME, Fobes JL (1981) The central basis of motivation: Intracranial self-stimulation studies. *Annu Rev Psychol* 32:523–574.

Oliva A, Torralba A (2006) Building the gist of a scene: The role of global image features in recognition. *Prog Brain Res* 155:23–36.

Olton DS, Becker JT, Handelmann GE (1979) Hippocampus, space, and memory. *Behav Brain Sci* 2:313–365.

Onishi KH, Baillargeon R (2005) Do 15-month-old infants understand false beliefs? *Science* 308(5719):255–258.

Opitz B, Rinne T, Mecklinger A, von Cramon DY, Schröger E (2002) Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *Neuroimage* 15(1):167–174.

Ostrom E (1990) *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge Univ Press, Cambridge, UK).

Osvath M (2009) Spontaneous planning for future stone throwing by a male chimpanzee. *Curr Biol* 19(5):R190–R191.

Osvath M, Karvonen E (2012) Spontaneous innovation for future deception in a male chimpanzee. *PLoS ONE* 7(5):e36782.

Osvath M, Osvath H (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Anim Cogn* 11(4):661–674.

Ott WR (1989) Human activity patterns: A review of the literature for estimating time spent indoors, outdoors, and in transit. In *Proceedings of the Research Planning Conference on Human Activity Patterns,* ed Starks TH. EPA/600/4-89/004 (Environmental Protection Agency, National Exposure Research Laboratory, Las Vegas, NV), pp 3-1–3-38.

Owen R (1859) *On the Classification and Geographical Distribution of the Mammalia* (Parker, London).

Ozdemir E, Norton A, Schlaug G (2006) Shared and distinct neural correlates of singing and speaking. *Neuroimage* 33(2):628–635.

Pacheco JM, Santos FC, Chalub FACC (2006) Stern-judging: A simple, successful norm which promotes cooperation under indirect reciprocity. *PLOS Comput Biol* 2(12):e178.

Packard MG, Goodman J (2012) Emotional arousal and multiple memory systems in the mammalian brain. *Front Behav Neurosci* 6(2012):14.

Packard MG, McGaugh JL (1996) Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiol Learn Mem* 65(1):65–72.

Packard MG, White NM (1991) Dissociation of hippocampus and caudate nucleus memory systems by posttraining intracerebral injection of dopamine agonists. *Behav Neurosci* 105(2):295–306.

Packard MG, Cahill L, McGaugh JL (1994) Amygdala modulation of hippocampal-dependent and caudate nucleus-dependent memory processes. *Proc Natl Acad Sci USA* 91(18): 8477–8481.

Padoa-Schioppa C, Assad JA (2006) Neurons in the orbitofrontal cortex encode economic value. *Nature* 441(7090):223–226.

Panchanathan K, Boyd R (2003) A tale of two defectors: The importance of standing for evolution of indirect reciprocity. *J Theor Biol* 224(1):115–126.

Panchanathan K, Boyd R (2004) Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* 432(7016):499–502.

Panksepp J (1995) The emotional source of "chills" induced by music. *Music Percept* 13: 171–207.

Panksepp J (1998) *Affective Neuroscience: The Foundations of Human and Animal Emotions* (Oxford Univ Press, New York).

Panksepp J (2011) Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *PLoS ONE* 6(9):e21236.

Paré **D, Collins DR, Pelletier JG (2002) Amygdala oscillations and the consolidation of emo**tional memories. *Trends Cogn Sci* 6(7):306–314.

Parfitt GM, Barbosa AK, Campos RC, Koth AP, Barros DM (2012) Moderate stress enhances memory persistence: Are adrenergic mechanisms involved? *Behav Neurosci* 126(5):729–734.

Parker ES, Cahill L, McGaugh JL (2006) A case of unusual autobiographical remembering. *Neurocase* 12(1):35–49.

Parkhurst DJ, Niebur E (2003) Scene content selected by active vision. *Spat Vis* 16(2):125–154.

Parkinson JK, Murray EA, Mishkin MA (1988) A selective mnemonic role for the hippocampus in monkeys: Memory for the location of objects. *J Neurosci* 8(11):4159–4167.

Pastalkova E, Itskov V, Amarasingham A, Buzsáki G (2008) Internally generated cell assembly sequences in the rat hippocampus. *Science* 321(5894):1322–1327.

Patel AD (2003) Language, music, syntax and the brain. *Nat Neurosci* 6(7):674–681.

Patel AD (2008) *Music, Language, and the Brain* (Oxford Univ Press, New York).

Patel AD, Iversen JR, Bregman MR, Schulz I (2009) Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Curr Biol* 19(10):827–830.

Patterson RD, Uppenkamp S, Johnsrude IS, Griffiths TD (2002) The processing of temporal pitch and melody information in auditory cortex. *Neuron* 36(4):767–776.

Paukner A, Suomi SJ, Visalberghi E, Ferrari PF (2009) Capuchin monkeys display affiliation toward humans who imitate them. *Science* 325(5942):880–883.

Paus T (2000) Functional anatomy of arousal and attention systems in the human brain. *Prog Brain Res* 126:65–77.

Paus T (2001) Primate anterior cingulate cortex: Where motor control, drive and cognition interface. *Nat Rev Neurosci* 2(6):417–424.

Pavlov I (1927) *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex,* 1927 trans Anrep GV (Oxford Univ Press, New York).

Pedersen CA, Ascher JA, Monroe YL, Prange AJ, Jr (1982) Oxytocin induces maternal behavior in virgin female rats. *Science* 216(4546):648–650.

Pelletier JG, Likhtik E, Filali M, Paré D (2005) Lasting increases in basolateral amygdala activity after emotional arousal: Implications for facilitated consolidation of emotional memories. *Learn Mem* 12(2):96–102.

Penagos H, Melcher JR, Oxenham AJ (2004) A neural representation of pitch salience in nonprimary human auditory cortex revealed with functional magnetic resonance imaging. *J Neurosci* 24(30):6810–6815.

Pereda E, Quiroga RQ, Bhattacharya J (2005) Nonlinear multivariate analysis of neurophysiological signals. *Prog Neurobiol* 77(1–2):1–37.

Peretz I, Coltheart M (2003) Modularity of music processing. *Nat Neurosci* 6(7):688–691.

Perkins DN, Farady M, Bushey B (1991) Everyday reasoning and the roots of intelligence. In *Informal Reasoning and Education,* eds Voss JF, Perkins DN, Segal JW (Lawrence Erlbaum, Hillsdale, NJ), pp 84–105.

Perrett DI, Rolls ET, Caan W (1982) Visual neurones responsive to faces in the monkey temporal cortex. *Exp Brain Res* 47(3):329–342.

Pessiglione M, Seymour B, Flandin G, Dolan RJ, Frith CD (2006) Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature* 442(7106): 1042–1045.

Petanjek Z, Judaš **M, Šimic G, Rasin MR, Uylings HB, Rakic P, Kostovic I (2011) Extraordinary** neoteny of synaptic spines in the human prefrontal cortex. *Proc Natl Acad Sci USA* 108(32):13281–13286.

Petkov CI, Kayser C, Augath M, Logothetis NK (2006) Functional imaging reveals numerous fields in the monkey auditory cortex. *PLoS Biol* 4(7):e215.

Petrides M (1995) Impairments on nonspatial self-ordered and externally ordered working memory tasks after lesions of the mid-dorsal part of the lateral frontal cortex in the monkey. *J Neurosci* 15(1 Pt 1):359–375.

Petrides M, Pandya DN (2004) The frontal cortex. In *The Human Nervous System*, 2nd Ed, eds Paxinos G, Mai JK (Elsevier, New York).

Petrosino A, Turpin-Petrosino C, Finckenauer JO (2000) Well-meaning programs can have harmful effects! Lessons from experiments of programs such as Scared Straight. *Crime Delinq* 46(3):354–379.

Petrosino A, Turpin-Petrosino C, Buehler J (2003) Scared Straight and other juvenile awareness programs for preventing juvenile delinquency. *Ann Am Acad Pol Soc Sci* 589(1): 41–62.

Pfaus JG, Damsma G, Wenkstern D, Fibiger HC (1995) Sexual activity increases dopamine transmission in the nucleus accumbens and striatum of female rats. *Brain Res* 693(1–2):21–30.

Pfeiffer T, Tran L, Krumme C, Rand DG (2012) The value of reputation. *J R Soc Interface* 9(76):2791–2797.

Phelps EA (2006) Emotion and cognition: Insights from studies of the human amygdala. *Annu Rev Psychol* 57:27–53.

Picciuto E, Carruthers P (2013) The origins of creativity. In *The Philosophy of Creativity,* eds Paul E, Kaufman S (Oxford Univ Press, Oxford).

Pillemer DB (1984) Flashbulb memories of the assassination attempt on President Reagan. *Cognition* 16(1):63–80.

Pinker S (2002) *The Blank Slate* (Viking, New York).

Pirolli P (2007) *Information Foraging Theory: Adaptive Interaction with Information* (Oxford Univ Press, Oxford).

Pitman RK (2006) Secondary pharmacological prevention of PTSD: Therapeutic implications of a translational model. In *PTSD: Brain Mechanisms and Clinical Implications,* eds Kato N, Kawata M, Pitman RK (Springer, Berlin), pp 281–296.

Pitman RK, Sanders KM, Zusman RM, Healy AR, Cheema F, Lasko NB, Cahill L, Orr SP (2002) Pilot study of secondary prevention of posttraumatic stress disorder with propranolol. *Biol Psychiatry* 51(2):189–192.

Platek SM, Critton SR, Myers TE, Gallup GG (2003) Contagious yawning: The role of self-awareness and mental state attribution. *Brain Res Cogn Brain Res* 17(2):223–227.

Platt ML, Glimcher PW (1999) Neural correlates of decision variables in parietal cortex. *Nature* 400(6741):233–238.

Plomin R (2001) *Behavioral Genetics*, 4th Ed (Worth, New York).

Plotnik JM, de Waal FB, Reiss D (2006) Self-recognition in an Asian elephant. *Proc Natl Acad Sci USA* 103(45):17053–17057.

Poffenberger AT, Barrows BE (1924) The feeling value of lines. *J Appl Psychol* 8(2):187–205.

Pollard KS, Salama SR, Lambert N, Lambot MA, Coppens S, Pedersen JS, Katzman S, King B, Onodera C, Siepel A, Kern AD, Dehay C, Igel H, Ares M, Jr, Vanderhaeghen P, Haussler D (2006) An RNA gene expressed during cortical development evolved rapidly in humans. *Nature* 443(7108):167–172.

Polman L (2010) *The Crisis Caravan,* trans Walters L (Metropolitan Books, New York).

Popescu AT, Popa D, Paré D (2009) Coherent gamma oscillations couple the amygdala and striatum during learning. *Nat Neurosci* 12(6):801–807.

Postle BR (2006) Working memory as an emergent property of the mind and brain. *Neuroscience* 139(1):23–38.

Postuma RB, Dagher A (2006) Basal ganglia functional connectivity based on a meta-analysis of 126 positron emission tomography and functional magnetic resonance imaging publications. *Cereb Cortex* 16(10):1508–1521.

Potter MC (1975) Meaning in visual search. *Science* 187(4180):965–966.

Powell KL, Roberts G, Nettle D (2012) Eye images increase charitable donations: Evidence from an opportunistic field experiment in a supermarket. *Ethology* 118(11):1096–1101.

Price SA, Brosnan SF (2012) To each according to his need? Variability in the responses to inequity in non-human primates. *Soc Justice Res* 25(2):140–169.

Prior H, Schwarz A, Güntürkün O (2008) Mirror-induced behavior in the magpie (*Picapica*): Evidence of self-recognition. *PLoS Biol* 6(8):e202.

Proctor D, Williamson RA, de Waal FBM, Brosnan SF (2013) Chimpanzees play the ultimatum game. *Proc Natl Acad Sci USA* 110(6):2070–2075.

Pronin E, Kugler MB (2007) Valuing thoughts, ignoring behavior: The introspection illusion as a source of the bias blind spot. *J Exp Soc Psychol* 43(4):565–578.

Pronin E, Lin DY, Ross L (2002) The bias blind spot. *Pers Soc Psychol Bull* 28(3):369–381.

Quinsey VL, Ketsetzis M, Earls C, Karamanoukian A (1996) Viewing time as a measure of sexual interest. *Ethol Sociobiol* 17(5):341–354.

Quirarte GL, Roozendaal B, McGaugh JL (1997) Glucocorticoid enhancement of memory storage involves noradrenergic activation in the basolateral amygdala. *Proc Natl Acad Sci USA* 94(25):14048–14053.

Quirarte GL, Galvez R, Roozendaal B, McGaugh JL (1998) Norepinephrine release in the amygdala in response to footshock and opioid peptidergic drugs. *Brain Res* 808(2): 134–140.

Quiroga RQ, Reddy L, Kreiman G, Koch C, Fried I (2005) Invariant visual representation by single neurons in the human brain. *Nature* 435(7045):1102–1107.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna).

Raby CR, Alexis DM, Dickinson A, Clayton NS (2007) Planning for the future by western scrub-jays. *Nature* 445(7130):919–921.

Radley JJ, Rocher AB, Miller M, Janssen WG, Liston C, Hof PR, McEwen BS, Morrison JH (2006) Repeated stress induces dendritic spine loss in the rat medial prefrontal cortex. *Cereb Cortex* 16(3):313–320.

Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001) A default mode of brain function. *Proc Natl Acad Sci USA* 98(2):676–682.

Raihani NJ, McAuliffe K (2012) Does inequity aversion motivate punishment? Cleaner fish as a model system. *Soc Justice Res* 25(2):213–231.

Raihani NJ, Grutter AS, Bshary R (2010) Punishers benefit from third-party punishment in fish. *Science* 327(5962):171.

Raihani NJ, McAuliffe K, Brosnan SF, Bshary R (2012) Are cleaner fish (*Labroides dimidiatus*) inequity averse? *Anim* Behav 84(3):665–674.

Rajala AZ, Reininger KR, Lancaster KM, Populin LC (2010) Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: Implications for the evolution of self-recognition. *PLoS ONE* 5(9):e12865.

Rajji T, Chapman D, Eichenbaum H, Greene R (2006) The role of CA3 hippocampal NMDA receptors in paired associate learning. *J Neurosci* 26(3):908–915.

Rakic P, Bourgeois JP, Eckenhoff MF, Zecevic N, Goldman-Rakic PS (1986) Concurrent overproduction of synapses in diverse regions of the primate cerebral cortex. *Science* 232(4747):232–235.

Ramón y Cajal S (1937) *Recollections of My Life* (MIT Press, Cambridge, MA).

Rand DG, Nowak MA (2009) Name and shame. *New Sci* 204(2734):28–29.

Rand DG, Dreber A, Ellingsen T, Fudenberg D, Nowak MA (2009) Positive interactions promote public cooperation. *Science* 325(5945):1272–1275.

Rand DG, Greene JD, Nowak MA (2012) Spontaneous giving and calculated greed. *Nature* 489(7416):427–430.

Rand DG, Peysakhovich A, Kraft-Todd GT, Newman GE, Wurzbacher O, Nowak MA, Greene JD (2013) Intuitive Cooperation and the Social Heuristics Hypothesis: Evidence from 15 Time Constraint Studies. Working Paper. Available at SSRN: http://ssrn.com/abstract=2222683.

Range F, Horn L, Viranyi Z, Huber L (2009) The absence of reward induces inequity aversion in dogs. *Proc Natl Acad Sci USA* 106(1):340–345.

Rattenborg NC, Martinez-Gonzalez D (2011) A bird-brain view of episodic memory. *Behav Brain Res* 222(1):236–245.

Rauschecker JP, Scott SK (2009) Maps and streams in the auditory cortex: Nonhuman primates illuminate human speech processing. *Nat Neurosci* 12(6):718–724.

Rayner K (1998) Eye movements in reading and information processing: 20 years of research. *Psychol Bull* 124(3):372–422.

Rayner K, Castelhano MS, Yang J (2009) Eye movements when looking at unusual/weird scenes: Are there cultural differences? *J Exp Psychol Learn Mem Cogn* 35(1):254–259.

Read DW (2008) Working memory: A cognitive limit to non-human primate recursive thinking prior to hominid evolution? *Evol Psychol* 6:676–714.

Rege M, Telle K (2004) The impact of social approval and framing on cooperation in public good situations. *J Public Econ* 88(7):1625–1644.

Reinagel P, Zador AM (1999) Natural scene statistics at the centre of gaze. *Network* 10(4): 341–350.

Reisberg D, Hertel P (2003) *Memory and Emotion* (Oxford Univ Press, New York).

Reiss D, Marino L (2001) Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proc Natl Acad Sci USA* 98(10):5937–5942.

Reniers RLEP, Corcoran R, Völlm BA, Mashru A, Howard R, Liddle PF (2012) Moral decision-making, ToM, empathy and the default mode network. *Biol Psychol* 90(3):202–210.

Resnick P, Zeckhauser R, Swanson J, Lockwood K (2006) The value of reputation on eBay: A controlled experiment. *Exp Econ* 9(2):79–101.

Revonsuo A (2006) *Inner Presence: Consciousness as a Biological Phenomenon* (MIT Press, Cambridge, MA).

Reynolds GS (1961) Behavioral contrast. *J Exp Anal Behav* 4:441–466.

Rhee SH, Friedman NP, Boeldt DL, Corley RP, Hewitt JK, Knafo A, Lahey BB, Robinson J, Van Hulle CA, Waldman ID, Young SE, Zahn-Waxler C (2013) Early concern and disregard for others as predictors of antisocial behavior. *J Child Psychol Psychiatry* 54(2):157–166.

Ribot R (1882) *Diseases of Memory* (Appleton, New York).

Rickard NS (2004) Intense emotional responses to music: A test of the physiological arousal hypothesis. *Psychol Music* 32(4):371–388.

Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C (2002) A neural basis for social cooperation. *Neuron* 35(2):395–405.

Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR (2007) A comparison of resting-state brain activity in humans and chimpanzees. *Proc Natl Acad Sci USA* 104(43):17146–17151.

Ringo JL (1993) Spared short-term memory in monkeys following medial temporal lobe lesions is not yet established: A reply to Alvarez-Royo, Zola-Morgan and Squire. *Behav Brain Res* 59(1–2):65–72.

Ritchey M, Dolcos F, Cabeza R (2008) Role of amygdala connectivity in the persistence of emotional memories over time: An event-related fMRI investigation. *Cereb Cortex* 18(11):2494–2504.

Ritchey M, LaBar KS, Cabeza R (2011) Level of processing modulates the neural correlates of emotional memory formation. *J Cogn Neurosci* 23(4):757–771.

Ritterfeld U, Cupchik GC (1996) Perceptions of interiors of spaces. *J Environ Psychol* 16(4): 349–360.

Rizzolatti G, Fabbri-Destro M (2008) The mirror system and its role in social cognition. *Curr Opin Neurobiol* 18(2):179–184.

Rizzolatti G, Fabbri-Destro M (2009) The mirror neuron system. In *Handbook of Neuroscience for the Behavioral Sciences*, Vol 1, eds Berntson GG, Cacioppo JT (Wiley, New York), pp 337–357.

Roberts WA (2002) Are animals stuck in time? *Psychol Bull* 128(3):473–489.

Robson SL, Wood B (2008) Hominin life history: Reconstruction and evolution. *J Anat* 212(4):394–425.

Rockenbach B, Milinski M (2006) The efficient interaction of indirect reciprocity and costly punishment. *Nature* 444(7120):718–723.

Rodríguez F, López JC, Vargas JP, Gómez Y, Broglio C, Salas C (2002) Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *J Neurosci* 22(7):2894–2903.

Roediger HL, 3rd, Butler AC (2011) The critical role of retrieval practice in long-term retention. *Trends Cogn Sci* 15(1):20–27.

Rolls ET (1999) The functions of the orbitofrontal cortex. *Neurocase* 5:301–312.

Rolls ET (2004) The functions of the orbitofrontal cortex. *Brain Cogn* 55(1):11–29.

Rolls ET, Treves A (2011) The neuronal encoding of information in the brain. *Prog Neurobiol* 95(3):448–490.

Roma PG, Silberberg A, Ruggiero AM, Suomi SJ (2006) Capuchin monkeys, inequity aversion, and the frustration effect. *J Comp Psychol* 120(1):67–73.

Roozendaal B (2000) 1999 Curt P. Richter award. Glucocorticoids and the regulation of memory consolidation. *Psychoneuroendocrinology* 25(3):213–238.

Roozendaal B, McGaugh JL (2011) Memory modulation. *Behav Neurosci* 125(6):797–824.

Roozendaal B, Quirarte GL, McGaugh JL (2002) Glucocorticoids interact with the basolateral amygdala β-adrenoceptor–cAMP/cAMP/PKA system in influencing memory consolidation. *Eur J Neurosci* 15(3):553–560.

Roozendaal B, Hui GK, Hui IR, Berlau DJ, McGaugh JL, Weinberger NM (2006a) Basolateral amygdala noradrenergic activity mediates corticosterone-induced enhancement of auditory fear conditioning. *Neurobiol Learn Mem* 86(3):249–255.

Roozendaal B, Okuda S, Van der Zee EA, McGaugh JL (2006b) Glucocorticoid enhancement of memory requires arousal-induced noradrenergic activation in the basolateral amygdala. *Proc Natl Acad Sci USA* 103(17):6741–6746.

Roozendaal B, Castello NA, Vedana G, Barsegyan A, McGaugh JL (2008) Noradrenergic activation of the basolateral amygdala modulates consolidation of object recognition memory. *Neurobiol Learn Mem* 90(3):576–579.

Rosazza C, Minati L (2011) Resting-state brain networks: Literature review and clinical applications. *Neurol Sci* 32(5):773–785.

Rose J, Colombo M (2005) Neural correlates of executive control in the avian brain. *PLoS Biol* 3(6):e190.

Ross RS, Brown TI, Stern CE (2009) The retrieval of learned sequences engages the hippocampus: Evidence from fMRI. *Hippocampus* 19(9):790–799.

Routtenberg A, Lindy J (1965) Effects of the availability of rewarding septal and hypothalamic stimulation on bar pressing for food under conditions of deprivation. *J Comp Physiol Psychol* 60:158–161.

Roy A, Platt ML (2009) Neuronal Mechanisms of Gaze Following: Insights from a Choice Task. Program No. 455.5/Z1 (Society for Neuroscience, Chicago, IL).

Roy A, Shepherd SV, Platt ML (2014) Reversible inactivation of pSTS suppresses social gaze following in the macaque (*Macaca mulatta*). *Soc Cogn Affect Neurosci* 9(2):209–217.

Rudebeck PH, Buckley MJ, Walton ME, Rushworth MF (2006) A role for the macaque anterior cingulate gyrus in social valuation. *Science* 313(5791):1310–1312.

Rushworth MFS, Behrens TEJ, Rudebeck PH, Walton ME (2008) Contrasting roles for cingulate and orbitofrontal cortex in decisions and social behavior. *Trends Cogn Sci* 11(4): 168–176.

Rushworth MF, Mars RB, Sallet J (2013) Are there specialized circuits for social cognition and are they unique to humans? *Curr Opin Neurobiol* 23(3):436-442.

Russell JA (2003) Core affect and the psychological construction of emotion. *Psychol Rev* 110(1):145–172.

Russell JL, Lyn H, Schaeffer JA, Hopkins WD (2011) The role of socio-communicative rearing environments in the development of social and physical cognition in apes. *Dev Sci* 14(6):1459–1470.

Rutherford HJV, Lindell AK (2011) Thriving and surviving: Approach and avoidance motivation and lateralization. *Emotion Review* 3(3):333–343.

Saalmann YB, Pinsk MA, Wang L, Li X, Kastner S (2012) The pulvinar regulates information transmission between cortical areas based on attention demands. *Science* 337(6095): 753–756.

Sacher GA, Staffeldt EF (1974) Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. *Am Nat* 108(963):593–615.

Saffran JR (2003) Mechanisms of musical memory in infancy. In *The Cognitive Neuroscience of Music,* eds Peretz I, Zatorre RJ (Oxford Univ Press, New York), pp 32–41.

Sagan C, Druyan A (1992) *Shadows of Forgotten Ancestors* (Ballantine, New York).

Sakai T, Mikami A, Tomonaga M, Matsui M, Suzuki J, Hamada Y, Tanaka M, Miyabe-Nishiwaki T, Makishima H, Nakatsukasa M, Matsuzawa T (2011) Differential prefrontal white matter development in chimpanzees and humans. *Curr Biol* 21(16):1397–1402.

Sakai T, Matsui M, Mikami A, Malkova L, Hamada Y, Tomonaga M, Suzuki J, Tanaka M, Miyabe-Nishiwaki T, Makishima H, Nakatsukasa M, Matsuzawa T (2013) Developmental patterns of chimpanzee cerebral tissues provide important clues for understanding the remarkable enlargement of the human brain. *Proc Biol Sci* 280(1753):20122398.

Salimpoor VN, Benovoy M, Longo G, Cooperstock JR, Zatorre RJ (2009) The rewarding aspects of music listening are related to degree of emotional arousal. *PLoS ONE* 4(10): e7487.

Salimpoor VN, Benovoy M, Larcher K, Dagher A, Zatorre RJ (2011) Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nat Neurosci* 14(2):257–262.

Salimpoor VN, van den Bosch I, Kovacevic N, McIntosh AR, Dagher A, Zatorre RJ (2013) Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science* 340(6129):216–219.

Sallet J, Mars RB, Noonan MP, Andersson JL, O'Reilly JX, Jbabdi S, Croxson PL, Jenkinson M, Miller KL, Rushworth MF (2011) Social network size affects neural circuits in macaques. *Science* 334(6056):697–700.

Sander R, Taylor S, Jr (2012) *Mismatch* (Basic Books, New York).

Sandi C, Rose SPR (1994) Corticosterone enhances long-term retention in one-day-old chicks trained in a weak passive avoidance learning paradigm. *Brain Res* 647(1):106–112.

Sanz C, Morgan D, Gulick S (2004) New insights into chimpanzees, tools, and termites from the Congo Basin. *Am Nat* 164(5):567–581.

Sapolsky R (2004) *Why Zebras Don't Get Ulcers* (Holt, New York).

Satel S (2000) *PC, M.D.* (Basic Books, New York).

Saxe R (2006) Uniquely human social cognition. *Curr Opin Neurobiol* 16(2):235–239.

Schachner A, Brady TF, Pepperberg IM, Hauser MD (2009) Spontaneous motor entrainment to music in multiple vocal mimicking species. *Curr Biol* 19(10):831–836.

Schacter DL, Addis DR (2007) The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philos Trans R Soc Lond B* 362:7737–7786.

Schacter DL, Addis DR, Buckner RL (2007) Remembering the past to imagine the future: The prospective brain. *Nat Rev Neurosci* 8(9):657–661.

Scheibel ME, Scheibel AB (1978) The method of Golgi. In *Neuroanatomical Research Techniques*, ed Robertson RT (Academic, New York), pp 89–114.

Schiff ND, Plum F (2000) The role of arousal and "gating" systems in the neurology of impaired consciousness. *J Clin Neurophysiol* 17(5):438–452.

Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988) Allogrooming as a tension-reduction mechanism: A behavioral approach. *Am J Primatol* 16(1):43–50.

Schmid MC, Singer W, Fries P (2012) Thalamic coordination of cortical communication. *Neuron* 75(4):551–552.

Schmolck H, Buffalo EA, Squire LR (2000) Memory distortions develop over time: Recollections of the O.J. Simpson trial verdict after 15 and 32 months. *Psychol Sci* 11(1):39–45.

Schön D, François C (2011) Musical expertise and statistical learning of musical and linguistic structures. *Front Psychol* 2:167.

Schönwiesner M, von Cramon DY, Rübsamen R (2002) Is it tonotopy after all? *Neuroimage* 17(3):1144–1161.

Schönwiesner M, Novitski N, Pakarinen S, Carlson S, Tervaniemi M, Näätänen R (2007) Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *J Neurophysiol* 97(3):2075–2082.

Schröter MS, Spoormaker VI, Schorer A, Wohlschläger A, Czisch M, Kochs EF, Zimmer C, Hemmer B, Schneider G, Jordan D, Ilg R (2012) Spatiotemporal reconfiguration of large-scale brain functional networks during propofol-induced loss of consciousness. *J Neurosci* 32(37):12832–12840.

Schultz W (1998) Predictive reward signal of dopamine neurons. *J Neurophysiol* 80(1):1–27.

Schultz W (2007) Behavioral dopamine signals. *Trends Neurosci* 30(5):203–210.

Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. *Science* 275(5306):1593–1599.

Schulz JF, Fischbacher U, Thöni C, Utikal V (In press) Affect and fairness: Dictator games under cognitive load. *J Econ Psychol*.

Schütz AC, Trommershäuser J, Gegenfurtner KR (2012) Dynamic integration of information about salience and value for saccadic eye movements. *Proc Natl Acad Sci USA* 109(19):7547–7552.

Schwarze U, Bingel U, Sommer T (2012) Event-related nociceptive arousal enhances memory consolidation for neutral scenes. *J Neurosci* 32(4):1481–1487.

Scott BH, Mishkin M, Yin P (2012) Monkeys have a limited form of short-term memory in audition. *Proc Natl Acad Sci USA* 109(30):12237–12241.

Scoville WB, Milner B (1957) Loss of recent memory after bilateral hippocampal lesions. *J Neurol Neurosurg Psychiat* 20(1):11-21.

Searle JR (1980) Minds, brain and programs. *Behav Brain Sci* 3(3):417–457.

Searle JR (1992) *The Rediscovery of the Mind* (MIT Press, Cambridge, MA).

Searle JR (1996) *Minds, Brains and Science* (Harvard Univ Press, Cambridge, MA).

Searle JR (2000) Consciousness. *Annu Rev Neurosci* 23:557–578.

Searle JR (2005) *Mind: A Brief Introduction* (Oxford Univ Press, Oxford).

Segal SK, Cahill L (2009) Endogenous noradrenergic activation and memory for emotional material in men and women. *Psychoneuroendocrinology* 34(9):1263–1271.

Segal SK, Stark SM, Kattan D, Stark CE, Yassa MA (2012) Norepinephrine-mediated emotional arousal facilitates subsequent pattern separation. *Neurobiol Learn Mem* 97(4):465–469.

Seger CA, Spiering BJ, Sares AG, Quraini SI, Alpeter C, David J, Thaut MH (2013) Corticostriatal contributions to musical expectancy perception. *J Cogn Neurosci* 25(7):1062–1077.

Seinen I, Schram A (2006) Social status and group norms: Indirect reciprocity in a repeated helping experiment. *Eur Econ Rev* 50(3):581–602.

Semendeferi K, Armstrong E, Schleicher A, Zilles K, Van Hoesen GW (2001) Prefrontal cortex in humans and apes: A comparative study of area 10. *Am J Phys Anthropol* 114(3):224–241.

Semendeferi K, Lu A, Schenker N, Damasio H (2002) Humans and great apes share a large frontal cortex. *Nat Neurosci* 5(3):272–276.

Semendeferi K, Teffer K, Buxhoeveden DP, Park MS, Bludau S, Amunts K, Travis K, Buckwalter J (2011) Spatial organization of neurons in the frontal pole sets humans apart from great apes. *Cereb Cortex* 21(7):1485–1497.

Semmann D, Krambeck H-J, Milinski M (2005) Reputation is valuable within and outside one's own social group. *Behav Ecol Sociobiol* 57(6):611–616.

Senju A, Maeda M, Kikuchi Y, Hasegawa T, Tojo Y, Osanai H (2007) Absence of contagious yawning in children with autism spectrum disorder. *Biol Lett* 3(6):706–708.

Seth AK, Baars BJ, Edelman DB (2005) Criteria for consciousness in humans and other mammals. *Conscious Cogn* 14(1):119–139.

Seyfarth RM, Cheney DL (2012) The evolutionary origins of friendship. *Annu Rev Psychol* 63:153–177.

Seyfarth RM, Silk JB, Cheney DL (2012) Variation in personality and fitness in wild female baboons. *Proc Natl Acad Sci USA* 109(42):16980–16985.

Shadmehr R (2010) Control of movements and temporal discounting of reward. *Curr Opin Neurobiol* 20(6):726–730.

Shadmehr R, Orban de Xivry JJ, Xu-Wilson M, Shih TY (2010) Temporal discounting of reward and the cost of time in motor control. *J Neurosci* 30(31):10507–10516.

Shamay-Tsoory SG, Fischer M, Dvash J, Harari H, Perach-Bloom N, Levkovitz Y (2009) Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biol Psychiatry* 66(9):864–870.

Shapiro ML (2011) Memory time. *Neuron* 71(4):571–573.

Sharot T, Martorella EA, Delgado MR, Phelps EA (2007) How personal experience modulates the neural circuitry of memories of September 11. *Proc Natl Acad Sci USA* 104(1):389–394.

Shaw P, Kabani NJ, Lerch JP, Eckstrand K, Lenroot R, Gogtay N, Greenstein D, Clasen L, Evans A, Rapoport JL, Giedd JN, Wise SP (2008) Neurodevelopmental trajectories of the human cerebral cortex. *J Neurosci* 28(14):3586–3594.

Shepard RN (1990) *Mind Sights* (W.H. Freeman & Co., New York).

Shepherd SV (2010) Following gaze: Gaze-following behavior as a window into social cognition. *Front Integr Neurosci* 4:5.

Shepherd SV, Klein JT, Deaner RO, Platt ML (2009) Mirroring of attention by neurons in macaque parietal cortex. *Proc Natl Acad Sci USA* 106(23):9489–9494.

Sherwood CC, Wahl E, Erwin JM, Hof PR, Hopkins WD (2007) Histological asymmetries of primary motor cortex predict handedness in chimpanzees (*Pan troglodytes*). *J Comp Neurol* 503(4):525–537.

Sherwood CC, Bauernfeind AL, Bianchi S, Raghanti MA, Hof PR (2012) Human brain evolution writ large and small. In *Progress in Brain Research*, eds Hofman MA, Falk D (Elsevier, Amsterdam), pp 237–254.

Shettleworth SJ (2007) Animal behaviour: Planning for breakfast. *Nature* 445(7130):825–826.

Shettleworth S (2010) *Cognition, Evolution, and Behavior*, 2nd Ed (Oxford Univ Press, Oxford)

Shiller RJ (2007) Understanding Recent Trends in House Prices and Home Ownership (Cowles Foundation for Research in Economics, Yale University, New Haven, CT).

Shimojo S, Simion C, Shimojo E, Scheier C (2003) Gaze bias both reflects and influences preference. *Nat Neurosci* 6(12):1317–1322.

Shizgal P (1997) Neural basis of utility estimation. *Curr Opin Neurobiol* 7(2):198–208.

Short P (2004) *Pol Pot* (John Murray, London).

Shu SY, Ju G, Fan LZ (1988) The glucose oxidase-DAB-nickel method in peroxidase histochemistry of the nervous system. *Neurosci Lett* 85(2):169–171.

Sigmund K (2010) *The Calculus of Selfishness* (Princeton Univ Press, Princeton, NJ).

Silberberg A, Crescimbene L, Addessi E, Anderson JR, Visalberghi E (2009) Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). *Anim Cogn* 12(3):505–509.

Silk JB, House BR (2011) Evolutionary foundations of human prosocial sentiments. *Proc Natl Acad Sci USA* 108(Suppl 2):10910–10917.

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302(5648):1231–1234.

Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaro J, Schapiro SJ (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437(7063):1357–1359.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proc Biol Sci* 276(1670):3099–3104.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* 20(15):1359–1361.

Silk J, Alberts S, Altmann J, Cheney D, Seyfarth R (2012) Stability of partner choice among female baboons. *Anim Behav* 83(6):1511–1518.

Silvia PJ, Barona CM (2009) Do people prefer curved objects? Angularity, expertise, and aesthetic preference. *Empir Stud Arts* 27(1):25–42.

Sin WC, Haas K, Ruthazer ES, Cline HT (2002) Dendrite growth increased by visual activity requires NMDA receptor and Rho GTPases. *Nature* 419(6906):475–480.

Singer RA, Zentall TR (2007) Pigeons learn to answer the question "where did you just peck?" and can report peck location when unexpectedly asked. *Learn Behav* 35(3):184–189.

Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303(5661):1157–1162.

Singer W (1993) Synchronization of cortical activity and its putative role in information processing and learning. *Annu Rev Physiol* 55:349–374.

Sirolli E (1999) *Ripples from the Zambezi* (New Society, Gabriola Island, BC).

Sirviö J, Riekkinen P, Jr, Jäkälä P, Riekkinen PJ (1994) Experimental studies on the role of serotonin in cognition. *Prog Neurobiol* 43(4–5):363–379.

Skinner BF (1992) *Verbal Behavior* (Copley, Acton, MA).

Skitka LJ (2012) Cross-disciplinary conversations: A social psychological perspective on justice research with non-human animals. *Soc Justice Res* 25(3):327–335.

Skov M, Vartanian O (2009) *Neuroaesthetics* (Baywood, Amityville, NY).

Small DM, Jones-Gotman M, Dagher A (2003) Feeding-induced dopamine release in dorsal striatum correlates with meal pleasantness ratings in healthy human volunteers. *Neuroimage* 19(4):1709–1715.

Smeets T, Otgaar H, Candel I, Wolf OT (2008) True or false? Memory is differentially affected by stress-induced cortisol elevations and sympathetic activity at consolidation and retrieval. *Psychoneuroendocrinology* 33(10):1378–1386.

Smith AD, Gilchrist ID, Hood BM (2005) Children's search behaviour in large-scale space: Developmental components of exploration. *Perception* 34(10):1221–1229.

Smith DV, Hayden BY, Truong TK, Song AW, Platt ML, Huettel SA (2010) Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *J Neurosci* 30(7): 2490–2495.

Smith P, Silberberg A (2010) Rational maximizing by humans (*Homo sapiens*) in an ultimatum game. *Anim Cogn* 13(4):671–677.

Smith VL (1987) Experimental methods in economics. In *The New Palgrave: A Dictionary of Economics,* eds Eatwell J, Milgate M, Newman P (Macmillan, London), pp 241–248.

Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (1987) *Primate Societies* (Univ of Chicago Press, Chicago).

Snider J (2011) Optimal random search for a single hidden target. *Phys Rev E Stat Nonlin Soft Matter Phys* 83(1 Pt 1):011105.

Snigdha S, Milgram NW, Willis SL, Albert M, Weintraub S, Fortin NJ, Cotman CW (2013) A preclinical cognitive test battery to parallel the National Institute of Health Toolbox in humans: Bridging the translational gap. *Neurobiol Aging* 34(7):1891–1901.

Snowdon CT, Pieper BA, Boe CY, Cronin KA, Kurian AV, Ziegler TE (2010) Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Horm Behav* 58(4):614–618.

Snyder LH, Batista AP, Andersen RA (2000) Intention-related activity in the posterior parietal cortex: A review. *Vision Res* 40(10–12):1433–1441.

Sober E, Wilson DS (1998) *Unto Others* (Harvard Univ Press, Cambridge, MA).

Sobolewski M, Brown J, Mitani J (2012) Territoriality, tolerance and testosterone in wild chimpanzees. *Anim Behav* 84(6):1469–1474.

Soetens E, D’Hooge R, Hueting JE (1993) Amphetamine enhances human-memory consolidation. *Neurosci Lett* 161(1):9–12.

Sommerfeld RD, Krambeck H-J, Semmann D, Milinski M (2007) Gossip as an alternative for direct observation in games of indirect reciprocity. *Proc Natl Acad Sci USA* 104(44):17435–17440.

Sommers CH (1995) *Who Stole Feminism?* (Simon & Schuster, New York).

Sommers CH (2001) *The War Against Boys* (Simon & Schuster, New York).

Sowell T (2012) *Intellectuals and Society,* Rev Ed (Basic Books, New York).

Spitzer M, Fischbacher U, Herrnberger B, Grön G, Fehr E (2007) The neural signature of social norm compliance. *Neuron* 56(1):185–196.

Spocter MA, Hopkins WD, Barks SK, Bianchi S, Hehmeyer AE, Anderson SM, Stimpson CD, Fobbs AJ, Hof PR, Sherwood CC (2012) Neuropil distribution in the cerebral cortex differs between humans and chimpanzees. *J Comp Neurol* 520(13):2917–2929.

Sporns O (2011) *Networks of the Brain* (MIT Press, Cambridge, MA).

Spreng RN, Mar RA, Kim AS (2009) The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *J Cogn Neurosci* 21(3):489–510.

Spruston N (2008) Pyramidal neurons: Dendritic structure and synaptic integration. *Nat Rev Neurosci* 9(3):206–221.

Squire LR (1992) Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychol Rev* 99(2):195–231.

Squire LR (2004) Memory systems of the brain: A brief history and current perspective. *Neurobiol Learn Mem* 82(3):171–177.

Squire LR (2009) The legacy of patient H.M. for neuroscience. *Neuron* 61(1):6–9.

Squire LR, Zola-Morgan S (1991) The medial temporal lobe memory system. *Science* 253(5026):1380–1386.

Squire LR, Zola-Morgan S, Chen KS (1988) Human amnesia and animal models of amnesia: Performance of amnesic patients on tests designed for the monkey. *Behav Neurosci* 102(2):210–221.

Squire LR, Stark CEL, Clark RE (2004) The medial temporal lobe. *Annu Rev Neurosci* 27: 279–306.

Squire LR, Wixted JT, Clark RE (2007) Recognition memory and the medial temporal lobe: A new perspective. *Nat Rev Neurosci* 8(11):872–883.

Stam CJ, van Straaten EC (2012a) Go with the flow: Use of a directed phase lag index (dPLI) to characterize patterns of phase relations in a large-scale model of brain dynamics. *Neuroimage* 62(3):1415–1428.

Stam CJ, van Straaten EC (2012b) The organization of physiological brain networks. *Clin Neurophysiol* 123(6):1067–1087.

Stamps AE (1999) Physical determinants of preferences for residential façades. *Environ Behav* 31(6):723–751.

Stanovich K (2009) *What Intelligence Tests Miss* (Yale Univ Press, New Haven, CT).

Stefanik MT, Moussawi K, Kupchik YM, Smith KC, Miller RL, Huff ML, Deisseroth K, Kalivas PW, LaLumiere RT (2013) Optogenetic inhibition of cocaine seeking in rats. *Addict Biol* 18(1):50–53.

Steidl S, Razik F, Anderson AK (2011) Emotion enhanced retention of cognitive skill learning. *Emotion* 11(1):12–19.

Steinvorth S, Corkin S, Halgren E (2006) Ecphory of autobiographical memories: An fMRI study of recent and remote memory retrieval. *Neuroimage* 30(1):285–298.

Stephens DW, Krebs JR (1986) *Foraging Theory* (Princeton Univ Press, Princeton, NJ).

Stephenson-Jones M, Ericsson J, Robertson B, Grillner S (2012) Evolution of the basal ganglia: Dual-output pathways conserved throughout vertebrate phylogeny. *J Comp Neurol* 520(13):2957–2973.

Sternberg EM, Wilson MA (2006) Neuroscience and architecture: Seeking common ground. *Cell* 127(2):239–242.

Stewart L, von Kriegstein K, Warren JD, Griffiths TD (2006) Music and the brain: Disorders of musical listening. *Brain* 129(Pt 10):2533–2553.

Stoet G, Geary DC (2012) Can stereotype threat explain the gender gap in mathematics performance and achievement? *Rev Gen Psychol* 16(1):93–102.

Stoet G, Geary DC (2013) Mixed blessings. *The Times Higher Education,* March 7, p 36 (lett).

Strange BA, Dolan RJ (2004) β-adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. *Proc Natl Acad Sci USA* 101(31):11454–11458.

Strassmann JE, Queller DC, Avise JC, Ayala FJ, eds (2011) *In the Light of Evolution, Volume V: Cooperation and Conflict* (National Academies Press, Washington, DC).

Stratton GM (1919) Retroactive hyperamnesia and other emotional effects on memory. *Psychol Rev* 26(6):474–486.

Straus MA (2007) Processes explaining the concealment and distortion of evidence on gender symmetry in partner violence. *Eur J Crim Policy Res* 13:227–232.

Straus MA (2008) Bucking the tide in family violence research. *Trauma Violence Abuse* 9(4): 191–213.

Straus MA (2009) Current controversies and prevalence concerning female offenders of intimate partner violence. *J Aggress Maltreat Trauma* 18(6):552–571.

Striedter G (2005) *Principles of Brain Evolution* (Sinauer Associates, Sunderland, MA).

Striedter GF, Avise JC, Ayala FJ, eds (2013) *In the Light of Evolution. Volume VI: Brain and Behavior* (National Academies Press, Washington, DC).

Stritzke M, Trommershäuser J (2007) Eye movements during rapid pointing under risk. *Vision Res* 47(15):2000–2009.

Stuss DT, Knight RT (2002) *Principles of Frontal Lobe Function* (Oxford Univ Press, New York).

Subiaul F, Vonk J, Okamoto-Barth S, Barth J (2008) Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Anim Cogn* 11(4):611–623.

Suddendorf T, Corballis MC (2007) The evolution of foresight: What is mental time travel, and is it unique to humans? *Behav Brain Sci* 30(3):299–313, discussion 313–351.

Sunstein CR (2005) Moral heuristics. *Behav Brain Sci* 28(4):531–542, discussion 542–573.

Sunstein CR (2009) *Going to Extremes* (Oxford Univ Press, New York).

Suomi SJ (2006) Risk, resilience, and gene × environment interactions in rhesus monkeys. *Ann N Y Acad Sci* 1094(1):52–62.

Sutton RS (1988) Learning to predict by the method of temporal differences. *Mach Learn* 3(1):9–44.

Sutton RS, Barto AG (1998) *Reinforcement Learning: An Introduction* (MIT Press, Cambridge, MA).

Suzuki S, Akiyama E (2007a) Evolution of indirect reciprocity in groups of various sizes and comparison with direct reciprocity. *J Theor Biol* 245(3):539–552.

Suzuki S, Akiyama E (2007b) Three-person game facilitates indirect reciprocity under image scoring. *J Theor Biol* 249(1):93–100.

Suzuki WA, Amaral DG (2004) Functional neuroanatomy of the medial temporal lobe memory system. *Cortex* 40(1):220–222.

Szathmáry E, Maynard Smith J (1997) From replicators to reproducers: The first major transitions leading to life. *J Theor Biol* 187(4):555–571.

Székely AD (1999) The avian hippocampal formation: Subdivisions and connectivity. *Behav Brain Res* 98(2):219–225.

Szpunar KK, Watson JM, McDermott KB (2007) Neural substrates of envisioning the future. *Proc Natl Acad Sci USA* 104(2):642–647.

Tadelis S (2007) The power of shame and the rationality of trust. Available at http://papers.ssrn.com/sol3/papers.cfm?abstract_id=1006169. Accessed April 20, 2013.

Takimoto A, Fujita K (2011) I acknowledge your help: Capuchin monkeys' sensitivity to others' labor. *Anim Cogn* 14(5):715–725.

Takimoto A, Kuroshima H, Fujita K (2010) Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: An experimental analysis of food-choice for conspecifics. *Anim Cogn* 13(2):249–261.

Talbot CF, Freeman HD, Williams LE, Brosnan SF (2011) Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. *Biol Lett* 7(5):680–682.

Tang YP, Shimizu E, Dube GR, Rampon C, Kerchner GA, Zhuo M, Liu G, Tsien JZ (1999) Genetic enhancement of learning and memory in mice. *Nature* 401(6748):63–69.

Tatler BW, Vincent BT (2009) The prominence of behavioural biases in eye guidance. *Vis Cogn* 17(6–7):1029–1054.

Tatler BW, Baddeley RJ, Vincent BT (2006) The long and the short of it: Spatial statistics at fixation vary with saccade amplitude and task. *Vision Res* 46(12):1857–1862.

Tavris C, Aronson E (2007) *Mistakes Were Made (But Not by Me)* (Houghton Mifflin Harcourt, New York).

Taylor AH, Elliffe D, Hunt GR, Gray RD (2010) Complex cognition and behavioural innovation in New Caledonian crows. *Proc Biol Sci* 277(1694):2637–2643.

Taylor KS, Seminowicz DA, Davis KD (2009) Two systems of resting state connectivity between the insula and cingulate cortex. *Hum Brain Mapp* 30(9):2731–2745.

Templer VL, Hampton RR (2013) Cognitive mechanisms of memory for order in rhesus monkeys (*Macaca mulatta*). *Hippocampus* 23(3):193–201.

Teng E, Stefanacci L, Squire LR, Zola SM (2000) Contrasting effects on discrimination learning after hippocampal lesions and conjoint hippocampal-caudate lesions in monkeys. *J Neurosci* 20(10):3853–3863.

Tervaniemi M, Rytkönen M, Schröger E, Ilmoniemi RJ, Näätänen R (2001) Superior formation of cortical memory traces for melodic patterns in musicians. *Learn Mem* 8(5):295–300.

Thompson C (2007) Clive Thompson thinks: Desktop orb could reform energy hogs. *Wired Magazine* 15(8).

Thorndike EL (1911) *Animal Intelligence* (Macmillan, New York).

Tillmann B, Janata P, Bharucha JJ (2003) Activation of the inferior frontal cortex in musical priming. *Brain Res Cogn Brain Res* 16(2):145–161.

Tillmann B, Koelsch S, Escoffier N, Bigand E, Lalitte P, Friederici AD, von Cramon DY (2006) Cognitive priming in sung and instrumental music: Activation of inferior frontal cortex. *Neuroimage* 31(4):1771–1782.

Tomasello M, Carpenter M, Call J, BehneT, Moll H (2005) Understanding and sharing intentions: The origins of cultural cognition. *Behav Brain Sci* 28(5):675–691.

Tononi G (2004) An information integration theory of consciousness. *BMC Neurosci* 5(1):42.

Tononi G (2012) Integrated information theory of consciousness: An updated account. *Arch Ital Biol* 150(2–3):56–90.

Tononi G, Edelman GM (1998) Consciousness and complexity. *Science* 282(5395):1846–1851.

Tononi G, Koch C (2008) The neural correlates of consciousness: An update. *Ann N Y Acad Sci* 1124:239–261.

Torgersen S, Lygren S, Oien PA, Skre I, Onstad S, Edvardsen J, Tambs K, Kringlen E (2000) A twin study of personality disorders. *Compr Psychiatry* 41(6):416–425.

Torralba A, Oliva A, Castelhano MS, Henderson JM (2006) Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychol Rev* 113(4):766–786.

Trainor LJ, McDonald KL, Alain C (2002) Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *J Cogn Neurosci* 14(3):430–442.

Traphagan JW (2012) Altruism, pathology, and culture. In *Pathological Altruism,* eds Oakley B, Knafo A, Madhavan G, Wilson DS (Oxford Univ Press, New York), pp 272–287.

Travis K, Ford K, Jacobs B (2005) Regional dendritic variation in neonatal human cortex: A quantitative Golgi study. *Dev Neurosci* 27(5):277–287.

Trevena J, Miller J (2010) Brain preparation before a voluntary action: Evidence against unconscious movement initiation. *Conscious Cogn* 19(1):447–456.

Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46(1):35–57.

Trivers R (2011) *Folly of Fools* (Basic Books, New York).

Tsao DY, Freiwald WA, Knutsen TA, Mandeville JB, Tootell RB (2003) Faces and objects in macaque cerebral cortex. *Nat Neurosci* 6(9):989–995.

Tsao DY, Freiwald WA, Tootell RB, Livingstone MS (2006) A cortical region consisting entirely of face-selective cells. *Science* 311(5761):670–674.

Tsukiura T, Cabeza R (2011) Shared brain activity for aesthetic and moral judgments: Implications for the Beauty-Is-Good stereotype. *Soc Cogn Affect Neurosci* 6(1):138–148.

Tulving E (1972) Episodic and semantic memory. In *Organization of Memory,* eds Tulving E, Donaldson W (Academic Press, New York), pp 381–402.

Tulving E (2002) Episodic memory: From mind to brain. *Annu Rev Psychol* 53:1–25.

Tulving E, Markowitsch HJ (1998) Episodic and declarative memory: Role of the hippocampus. *Hippocampus* 8(3):198–204.

Tung J, Barreiro LB, Johnson ZP, Hansen KD, Michopoulos V, Toufexis D, Michelini K, Wilson ME, Gilad Y (2012) Social environment is associated with gene regulatory variation in the rhesus macaque immune system. *Proc Natl Acad Sci USA* 109(17):6490–6495.

Twenge JM, Konrath S, Foster JD, Campbell WK, Bushman BJ (2008) Egos inflating over time: A cross-temporal meta-analysis of the Narcissistic Personality Inventory. *J Pers* 76(4):875–902; discussion 903–928.

Twenge JM, Campbell WK, Gentile B (2012) Generational increases in agentic self-evaluations among American college students, 1966–2009. *Self Ident* 11(4):409–427.

Uchida S, Sigmund K (2010) The competition of assessment rules for indirect reciprocity. *J Theor Biol* 263(1):13–19.

Ule A, Schram A, Riedl A, Cason TN (2009) Indirect punishment and generosity toward strangers. *Science* 326(5960):1701–1704.

Uller C, Lewis J (2009) Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Anim Cogn* 12(5):733–738.

Unsworth N, Engle RW (2007) The nature of individual differences in working memory capacity: Active maintenance in primary memory and controlled search from secondary memory. *Psychol Rev* 114(1):104–132.

U.S. Committee on Technology (2011) *A Policy Framework for the 21st Century Grid: Enabling Our Secure Energy Future* (Executive Office of the President, National Science and Technology Council, Washington, DC).

Uylings HBM, Groenewegen HJ, Kolb B (2003) Do rats have a prefrontal cortex? *Behav Brain Res* 146(1-2):3–17.

Vaiva G, Ducrocq F, Jezequel K, Averland B, Lestavel P, Brunet A, Marmar CR (2003) Immediate treatment with propranolol decreases posttraumatic stress disorder two months after trauma. *Biol Psychiatry* 54(9):947–949.

Van Baaren R, Holland R, Kawakami K, van Knippenberg A (2004) Mimicry and pro-social behavior. *Psychol Sci* 15(1):71–74.

van den Heuvel MP, Hulshoff Pol HE (2010) Exploring the brain network: A review on resting-state fMRI functional connectivity. *Eur Neuropsychopharmacol* 20(8):519–534.

Van der Gucht E, Vandesande F, Arckens L (2001) Neurofilament protein: A selective marker for the architectonic parcellation of the visual cortex in adult cat brain. *J Comp Neurol* 441(4):345–368.

Van der Werf YD, Witter MP, Groenewegen HJ (2002) The intralaminar and midline nuclei of the thalamus. Anatomical and functional evidence for participation in processes of arousal and awareness. *Brain Res Brain Res Rev* 39(2–3):107–140.

Van Hoesen GW, Morecraft RJ, Vogt BA (1993) Connections of the monkey cingulate cortex. In *The Neurobiology of the Cingulate Cortex and Limbic Thalamus: A Comprehensive Handbook,* eds Vogt BA, Gabriel M (Birkhäuser, Boston, MA), pp 249–284.

van Leeuwen E, Zimmermann E, Davila-Ross M (2011) Responding to inequities: Gorillas try to maintain their competitive advantage during play fights. *Biol Lett* 7(1):39–42.

van Praag H, Kempermann G, Gage FH (2000) Neural consequences of environmental enrichment. *Nat Rev Neurosci* 1(3):191–198.

van Stegeren AH, Goekoop R, Everaerd W, Scheltens P, Barkhof F, Kuijer JP, Rombouts SA (2005) Noradrenaline mediates amygdala activation in men and women during encoding of emotional material. *Neuroimage* 24(3):898–909.

van Stegeren A, Rohleder N, Everaerd W, Wolf OT (2006) Salivary alpha amylase as marker for adrenergic activity during stress: Effect of betablockade. *Psychoneuroendocrinology* 31(1):137–141.

van Stegeren AH, Wolf OT, Everaerd W, Scheltens P, Barkhof F, Rombouts SA (2007) Endogenous cortisol level interacts with noradrenergic activation in the human amygdala. *Neurobiol Learn Mem* 87(1):57–66.

van Stegeren AH, Roozendaal B, Kindt M, Wolf OT, Joëls M (2010) Interacting noradrenergic and corticosteroid systems shift human brain activation patterns during encoding. *Neurobiol Learn Mem* 93(1):56–65.

van Strien NM, Cappaert NLM, Witter MP (2009) The anatomy of memory: An interactive overview of the parahippocampal-hippocampal network. *Nat Rev Neurosci* 10(4): 272–282.

van Wolkenten M, Brosnan SF, de Waal FBM (2007) Inequity responses of monkeys modified by effort. *Proc Natl Acad Sci USA* 104(47):18854–18859.

Varela F, Lachaux J-P, Rodriguez E, Martinerie J (2001) The brainweb: Phase synchronization and large-scale integration. *Nat Rev Neurosci* 2(4):229–239.

Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, Van Paesschen W, Mishkin M (1997) Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277(5324):376–380.

Vartanian O, Goel V (2004) Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport* 15(5):893–897.

Vartanian O, Kaufman JC (2013) Psychological and neural responses to art embody viewer and artwork histories. *Behav Brain Sci* 36(2):161–162.

Vauclair J, Fagot J, Hopkins W (1993) Rotation of mental images in baboons when the visual input is directed to the left hemisphere. *Psych Sci* 4(2):99–103.

Verwer RWH, Meijer RJ, Van Uum HFM, Witter MP (1997) Collateral projections from the rat hippocampal formation to the lateral and medial prefrontal cortex. *Hippocampus* 7(4):397–402.

Vessel EA, Starr GG, Rubin N (2012) The brain on art: Intense aesthetic experience activates the default mode network. *Front Hum Neurosci* 6:66.

Vincent JL, Patel GH, Fox MD, Snyder AZ, Baker JT, Van Essen DC, Zempel JM, Snyder LH, Corbetta M, Raichle ME (2007) Intrinsic functional architecture in the anaesthetized monkey brain. *Nature* 447(7140):83–86.

Viswanathan GM, Buldyrev SV, Havlin S, da Luz MG, Raposo EP, Stanley HE (1999) Optimizing the success of random searches. *Nature* 401(6756):911–914.

Võ ML, Henderson JM (2010) The time course of initial scene processing for eye movement guidance in natural scene search. *J Vis* 10(3):11–13.

von der Malsburg C, Schneider W (1986) A neural cocktail-party processor. *Biol Cybern* 54(1):29–40.

Waite RGL (1977) *The Psychopathic God: Adolf Hitler* (Basic Books, New York).

Waites AB, Stanislavsky A, Abbott DF, Jackson GD (2005) Effect of prior cognitive state on resting state networks measured with functional connectivity. *Hum Brain Mapp* 24(1):59–68.

Walker B, Barrett S, Polasky S, Galaz V, Folke C, Engström G, Ackerman F, Arrow K, Carpenter S, Chopra K, Daily G, Ehrlich P, Hughes T, Kautsky N, Levin S, Mäler KG, Shogren J, Vincent J, Xepapadeas T, de Zeeuw A (2009) Environment. Looming global-scale failures and missing institutions. *Science* 325(5946):1345–1346.

Wallin N, Merker B, Brown S (2000) *The Origins of Music* (MIT Press, Cambridge, MA).

Wang X, Huang Y, Ma Q, Li N (2012) Event-related potential P2 correlates of implicit aesthetic experience. *Neuroreport* 23(14):862–866.

Ward LM (2011) The thalamic dynamic core theory of conscious experience. *Conscious Cogn* 20(2):464–486.

Warneken F, Tomasello M (2009) Varieties of altruism in children and chimpanzees. *Trends Cogn Sci* 13(9):397–402.

Warren WC, Hillier LW, Marshall Graves JA, Birney E, Ponting CP, Grützner F, Belov K, Miller W, Clarke L, Chinwalla AT, Yang SP, Heger A, Locke DP, Miethke P, Waters PD, Veyrunes F, Fulton L, Fulton B, Graves T, Wallis J, Puente XS, López-Otín C, Ordóñez GR, Eichler EE, Chen L, Cheng Z, Deakin JE, Alsop A, Thompson K, Kirby P, Papenfuss AT, Wakefield MJ, Olender T, Lancet D, Huttley GA, Smit AF, Pask A, Temple-Smith P, Batzer MA, Walker JA, Konkel MK, Harris RS, Whittington CM, Wong ES, Gemmell NJ, Buschiazzo E, Vargas Jentzsch IM, Merkel A, Schmitz J, Zemann A, Churakov G, Kriegs JO, Brosius J, Murchison EP, Sachidanandam R, Smith C, Hannon GJ, Tsend-Ayush E, McMillan D, Attenborough R, Rens W, Ferguson-Smith M, Lefèvre CM, Sharp JA, Nicholas KR, Ray DA, Kube M, Reinhardt R, Pringle TH, Taylor J, Jones RC, Nixon B, Dacheux JL, Niwa H, Sekita Y, Huang X, Stark A, Kheradpour P, Kellis M, Flicek P, Chen Y, Webber C, Hardison R, Nelson J, Hallsworth-Pepin K, Delehaunty K, Markovic C, Minx P, Feng Y, Kremitzki C, Mitreva M, Glasscock J, Wylie T, Wohldmann P, Thiru P, Nhan MN, Pohl CS, Smith SM, Hou S, Nefedov M, de Jong PJ, Renfree MB, Mardis ER, Wilson RK (2008) Genome analysis of the platypus reveals unique signatures of evolution. *Nature* 453(7192):175–183.

Wascher CAF, Bugnyar T (2013) Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS ONE* 8(2):e56885.

Watanabe K (2001) A review of 50 years of research on the Japanese monkeys of Koshima: Status and dominance. In *Primate Origins of Human Cognition and Behavior,* ed Matsuzawa T (Springer, Tokyo), pp 405–417.

Watson JB (1925) *Behaviorism* (Norton, New York); quoted in Baars BJ (2003) The double life of B. F. Skinner. *J Conscious Stud* 10(1):5–25.

Watson KK, Platt ML (2012) Social signals in primate orbitofrontal cortex. *Curr Biol* 22(23): 2268–2273.

Watson KK, Ghodasra JH, Platt ML (2009) Serotonin transporter genotype modulates social reward and punishment in rhesus macaques. *PLoS ONE* 4(1):e4156.

Waytz A, Zaki J, Mitchell JP (2012) Response of dorsomedial prefrontal cortex predicts altruistic behavior. *J Neurosci* 32(22):7646–7650.

Weber R (2012) Introduction to the special issue: Aesthetics and design!? *Empir Stud Arts* 30(1):3–6.

Wechkin S, Massserman J, Terris T (1964) Shock to a conspecific as an aversive stimulus. *Psychon Sci* 1(1):47–48.

Wedekind C, Braithwaite VA (2002) The long-term benefits of human generosity in indirect reciprocity. *Curr Biol* 12(12):1012–1015.

Wedekind C, Milinski M (2000) Cooperation through image scoring in humans. *Science* 288(5467):850–852.

Weinberger NM (2004) Specific long-term memory traces in primary auditory cortex. *Nat Rev Neurosci* 5(4):279–290.

Weinberger NM (2007) Associative representational plasticity in the auditory cortex: A synthesis of two disciplines. *Learn Mem* 14(1–2):1–16.

Weinstein B (1941) Matching-from-sample by rhesus monkeys and by children. *J Comp Psychol* 31:195–213.

Weintraub S, Dikmen SS, Heaton RK, Tulsky DS, Zelazo PD, Bauer PJ, Carlozzi NE, Slotkin J, Blitz D, Wallner-Allen K, Fox NA, Beaumont JL, Mungas D, Nowinski CJ, Richler J, Deocampo JA, Anderson JE, Manly JJ, Borosh B, Havlik R, Conway K, Edwards E, Freund L, King JW, Moy C, Witt E, Gershon RC (2013) Cognition assessment using the NIH Toolbox. *Neurology* 80(Suppl 3):S54–S64.

Weiss A, King JE, Figueredo AJ (2000) The heritability of personality factors in chimpanzees *(Pan troglodytes). Behav Genet* 30(3):213–221.

Wendland JR, Lesch KP, Newman TK, Timme A, Gachot-Neveu H, Thierry B, Suomi SJ (2006) Differential functional variability of serotonin transporter and monoamine oxidase A genes in macaque species displaying contrasting levels of aggression-related behavior. *Behav Genet* 36(2):163–172.

West CP, Huschka MM, Novotny PJ, Sloan JA, Kolars JC, Habermann TM, Shanafelt TD (2006) Association of perceived medical errors with resident distress and empathy: A prospective longitudinal study. *JAMA* 296(9):1071–1078.

Westbrook WH, McGaugh JL (1964) Drug facilitation of latent learning. *Psychopharmacology (Berl)* 5:440–446.

Wheatley T, Haidt J (2005) Hypnotic disgust makes moral judgments more severe. *Psychol Sci* 16(10):780–784.

White NM, McDonald RJ (2002) Multiple parallel memory systems in the brain of the rat. *Neurobiol Learn Mem* 77(2):125–184.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399(6737):682–685.

Wiesmann M, Ishai A (2011) Expertise reduces neural cost but does not modulate repetition suppression. *Cogn Neurosci* 2(1):57–65.

Wilder MH, Mozer MC, Wickens CD (2011) An integrative, experience-based theory of attentional control. *J Vis* 11(2), doi:10.1167/11.2.8.

Wilding J, Valentine E (1997) *Superior Memory* (Psychology Press, East Sussex, UK).

Wildman DE, Uddin M, Opazo JC, Liu G, Lefort V, Guindon S, Gascuel O, Grossman LI, Romero R, Goodman M (2007) Genomics, biogeography, and the diversification of placental mammals. *Proc Natl Acad Sci USA* 104(36):14395–14400.

Williamson DE, Coleman K, Bacanu SA, Devlin BJ, Rogers J, Ryan ND, Cameron JL (2003) Heritability of fearful-anxious endophenotypes in infant rhesus macaques: A preliminary report. *Biol Psychiatry* 53(4):284–291.

Wilson BJ (2012) Contra private fairness. *Am J Econ Sociol* 71(2):407–435.

Wilson DS (2003) *Darwin's Cathedral* (Univ of Chicago Press, Chicago).

Wilson EO (1975) *Sociobiology: The New Synthesis* (Belknap Press, Cambridge, MA).

Wilson MA, McNaughton BL (1993) Dynamics of the hippocampal ensemble code for space. *Science* 261(5124):1055–1058.

Wilson T (2011) *Redirect* (Little, Brown and Company, New York).

Wingfield JC, Hegner RE, Dufty AM, Jr, Ball GF (1990) The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am Nat* 136(6):829–846.

Winkielman P, Cacioppo JT (2001) Mind at ease puts a smile on the face: Psychophysiological evidence that processing facilitation elicits positive affect. *J Pers Soc Psychol* 81(6):989–1000.

Winslow JT, Hastings N, Carter CS, Harbaugh CR, Insel TR (1993) A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature* 365(6446):545–548.

Winston JS, O'Doherty J, Kilner JM, Perrett DI, Dolan RJ (2007) Brain systems for assessing facial attractiveness. *Neuropsychologia* 45(1):195–206.

Winters BD, Saksida LM, Bussey TJ (2008) Object recognition memory: Neurobiological mechanisms of encoding, consolidation and retrieval. *Neurosci Biobehav Rev* 32(5):1055–1070.

Wise RA (1978) Catecholamine theories of reward: A critical review. *Brain Res* 152(2):215–247.

Witter MP, Amaral DG (2004) Hippocampal formation. In *The Rat Nervous System*, 3rd Ed, ed Paxinos G (Academic, San Diego), pp 637–703.

Wittig R, Crockford C, Seyfarth R, Cheney D (2007a) Vocal alliances in chacma baboons, *Papio hamadryas ursinus. Behav Ecol Sociobiol* 61(6):899–909.

Wittig RM, Crockford C, Wikberg E, Seyfarth RM, Cheney DL (2007b) Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc Biol Sci* 274(1613): 1109–1115.

Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL (2008) Focused grooming networks and stress alleviation in wild female baboons. *Horm Behav* 54(1):170–177.

Wolfe JM, Võ ML, Evans KK, Greene MR (2011) Visual search in scenes involves selective and nonselective pathways. *Trends Cogn Sci* 15(2):77–84.

Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. *Nat Neurosci* 3(Suppl):1212–1217.

Wood ER, Dudchenko PA, Eichenbaum H (1999) The global record of memory in hippocampal neuronal activity. *Nature* 397(6720):613–616.

Wrangham R (2009) *Catching Fire: How Cooking Made Us Human* (Basic Books, Philadelphia).

Wright AA, Rivera JJ, Hulse SH, Shyan M, Neiworth JJ (2000) Music perception and octave generalization in rhesus monkeys. *J Exp Psychol Gen* 129(3):291–307.

Wright R, Cummings N, eds (2005) *Destructive Trends in Mental Health* (Brunner-Routledge, New York).

Xiao E, Houser D (2005) Emotion expression in human punishment behavior. *Proc Natl Acad Sci USA* 102(20):7398–7401.

Xie G, Deschamps A, Backman SB, Fiset P, Chartrand D, Dagher A, Plourde G (2011) Critical involvement of the thalamus and precuneus during restoration of consciousness with physostigmine in humans during propofol anaesthesia: A positron emission tomography study. *Br J Anaesth* 106(4):548–557.

Xu-Wilson M, Zee DS, Shadmehr R (2009) The intrinsic value of visual information affects saccade velocities. *Exp Brain Res* 196(4):475–481.

Xue S-W, Wang Y, Tang Y-Y (2013) Personal and impersonal stimuli differentially engage brain networks during moral reasoning. *Brain Cogn* 81(1):24–28.

Yadav A, Gao YZ, Rodriguez A, Dickstein DL, Wearne SL, Luebke JI, Hof PR, Weaver CM (2012) Morphologic evidence for spatially clustered spines in apical dendrites of monkey neocortical pyramidal cells. *J Comp Neurol* 520(13):2888–2902.

Yamagishi T, Horita Y, Takagishi H, Shinada M, Tanida S, Cook KS (2009) The private rejection of unfair offers and emotional commitment. *Proc Natl Acad Sci USA* 106(28): 11520–11523.

Yang G, Pan F, Gan WB (2009) Stably maintained dendritic spines are associated with lifelong memories. *Nature* 462(7275):920–924.

Yarbus AL (1967) *Eye Movements and Vision* (Plenum, New York).

Yartsev MM, Witter MP, Ulanovsky N (2011) Grid cells without theta oscillations in the entorhinal cortex of bats. *Nature* 479(7371):103–107.

Yassa MA, Stark CE (2011) Pattern separation in the hippocampus. *Trends Neurosci* 34(10): 515–525.

Yasuda M, Yamamoto S, Hikosaka O (2012) Robust representation of stable object values in the oculomotor basal ganglia. *J Neurosci* 32(47):16917–16932.

Yoshida M, Takayanagi Y, Inoue K, Kimura T, Young LJ, Onaka T, Nishimori K (2009) Evidence that oxytocin exerts anxiolytic effects via oxytocin receptor expressed in serotonergic neurons in mice. *J Neurosci* 29(7):2259–2271.

Young LJ (2002) The neurobiology of social recognition, approach, and avoidance. *Biol Psychiatry* 51(1):18–26.

Yu AJ, Cohen JD (2008) Sequential effects: Superstition or rational behavior? In *Advances in Neural Information Processing Systems*, Vol. 21, eds Koller D, Schuurmans D, Bengio Y, Bottou L (MIT Press, Cambridge, MA), pp 1873–1880.

Yu C, Zhou Y, Liu Y, Jiang T, Dong H, Zhang Y, Walter M (2011) Functional segregation of the human cingulate cortex is confirmed by functional connectivity based neuroanatomical parcellation. *Neuroimage* 54(4):2571–2581.

Yue X, Vessel EA, Biederman I (2007) The neural basis of scene preferences. *Neuroreport* 18(6):525–529.

Yuste R, Tank DW (1996) Dendritic integration in mammalian neurons, a century after Cajal. *Neuron* 16(4):701–716.

Zaidel DW, Nadal M (2011) Brain intersections of aesthetics and morals: Perspectives from biology, neuroscience, and evolution. *Perspect Biol Med* 54(3):367–380.

Zajonc RB (1980) Feeling and thinking. *Am Psychol* 35(2):151.

Zak PJ, Stanton AA, Ahmadi S (2007) Oxytocin increases generosity in humans. *PLoS ONE* 2(11):e1128.

Zaki J, Ochsner K (2012) The neuroscience of empathy: Progress, pitfalls and promise. *Nat Neurosci* 15(5):675–680.

Zatorre RJ (1985) Discrimination and recognition of tonal melodies after unilateral cerebral excisions. *Neuropsychologia* 23(1):31–41.

Zatorre RJ (1988) Pitch perception of complex tones and human temporal-lobe function. *J Acoust Soc Am* 84(2):566–572.

Zatorre RJ, Baum SR (2012) Musical melody and speech intonation: Singing a different tune. *PLoS Biol* 10(7):e1001372.

Zatorre RJ, Gandour JT (2008) Neural specializations for speech and pitch: Moving beyond the dichotomies. *Philos Trans R Soc Lond B Biol Sci* 363(1493):1087–1104.

Zatorre RJ, Halpern AR (2005) Mental concerts: Musical imagery and auditory cortex. *Neuron* 47(1):9–12.

Zatorre RJ, Schönwiesner M (2011) Cortical speech and music processes revealed by functional neuroimaging. In *The Auditory Cortex,* eds Winer JA, Schreiner CE (Springer, New York), pp 657–677.

Zatorre RJ, Evans AC, Meyer E (1994) Neural mechanisms underlying melodic perception and memory for pitch. *J Neurosci* 14(4):1908–1919.

Zatorre RJ, Belin P, Penhune VB (2002) Structure and function of auditory cortex: Music and speech. *Trends Cogn Sci* 6(1):37–46.

Zatorre RJ, Chen JL, Penhune VB (2007) When the brain plays music: Auditory-motor interactions in music perception and production. *Nat Rev Neurosci* 8(7):547–558.

Zhou J, Greicius MD, Gennatas ED, Growdon ME, Jang JY, Rabinovici GD, Kramer JH, Weiner M, Miller BL, Seeley WW (2010) Divergent network connectivity changes in behavioural variant frontotemporal dementia and Alzheimer's disease. *Brain* 133 (Pt 5):1352–1367.

Zinkivskay A, Nazir F, Smulders TV (2009) What-where-when memory in magpies (*Pica pica*). *Anim Cogn* 12(1):119–125.

Zola SM, Squire LR, Teng E, Stefanacci L, Buffalo EA, Clark RE (2000) Impaired recognition memory in monkeys after damage limited to the hippocampal region. *J Neurosci* 20(1):451–463.

Zola-Morgan S, Squire LR, Mishkin M (1982) The neuroanatomy of amnesia: Amygdala-hippocampus versus temporal stem. *Science* 218(4579):1337–1339.

Zola-Morgan S, Squire LR, Ramus SJ (1994) Severity of memory impairment in monkeys as a function of locus and extent of damage within the medial temporal lobe memory system. *Hippocampus* 4(4):483–495.

Zorawski M, Killcross S (2002) Posttraining glucocorticoid receptor agonist enhances memory in appetitive and aversive Pavlovian discrete-cue conditioning paradigms. *Neurobiol Learn Mem* 78(2):458–464.

Zysset S, Huber O, Ferstl E, von Cramon DY (2002) The anterior frontomedian cortex and evaluative judgment: An fMRI study. *Neuroimage* 15(4):983–991.

Index