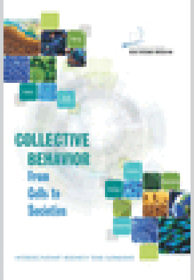

Collective Behavior: From Cells to Societies: Interdisciplinary Research Team Summaries

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The National Academies Keck Futures Initiative

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KECK FUTURES INITIATIVE

COLLECTIVE BEHAVIOR
From Cells to Societies

INTERDISCIPLINARY RESEARCH TEAM SUMMARIES

Conference
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Irvine, California
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The National Academies Keck *Futures Initiative* (NAKFI) was launched in 2003 with generous support from the W. M. Keck Foundation. It is a 15-year experiment to catalyze interdisciplinary research across fields of science, engineering, and medicine. NAKFI creates opportunities to cross both disciplinary and professional boundaries, which is of paramount importance in making scientific progress today. Together, the Academies and the W. M. Keck Foundation believed that advancing this common goal included catalyzing successful communication among the "best and brightest" who otherwise live in different worlds and speak different languages; conducting meetings that surface the best questions; and providing seed grants to bridge the gap between new ideas and sustained funding.

The *Futures Initiative* is designed to enable scientists from different disciplines to focus on new questions, upon which they can base entirely new research, and to encourage and reward outstanding communication between scientists as well as between the scientific enterprise and the public. The *Futures Initiative* includes three main components:

Futures Conferences

NAKFI accomplishes its mission by harnessing the intellectual horsepower of the brightest minds from diverse backgrounds who attend an annual "think-tank"-style conference to contemplate the real-world challenges of our day, having been prepared for deep conversations though preconference tutorials. NAKFI conferences are intentionally crafted to allow multiple ways for attendees to interact. Some of the conference components are familiar, such as poster sessions and plenary sessions, but the expected gives way to the unconventional at a NAKFI conference. The format of *Futures* conferences evolved from a traditional program of lectures and panel discussions to a meeting focused on providing a variety of venues for conversation. The foundation of this approach is the appointment of conference participants to Interdisciplinary Research (IDR) Teams charged with finding solutions to real-world problems. In addition to working in these concurrent groups—each of which reports on its work midway through the conference—participants have many opportunities for informal conversations and collaboration during "free" times and meals.

NAKFI has inspired its diverse network to "think big" at the frontiers of science, engineering, and medicine. And this is just the first step in its role as conversation shifter, idea incubator, career changer, and venture science funder.

***Futures* Grants**

Futures grants are awarded to conference participants to enable further pursuit of new ideas and inspirations generated at the conference, conceptualized as "venture science," similar to startup capital in the business world.

Futures grants serve as an incentive for attendees to collaborate after the conference and provide resources for startup research projects. Grants can also be awarded for meetings that explore a facet of *Futures* conferences in more depth or with a different audience. The grant application process is straightforward and reporting requirements are kept to a minimum. Principal investigators have already been vetted by the conference steering committee for attendance at the conference, and the grant selection committee looks for projects with the greatest potential to succeed. NAKFI encourages grantees to learn as they go and to make changes to their research plans as appropriate. Projects that experience unexpected delays or need more time can request a no-cost extension with a simple email explanation. Final reports cover a few key areas of interest to the program and encourage investigators to reflect on what worked, what didn't work, and why.

NAKFI Communications

The Communication Awards are designed to recognize, promote, and encourage effective communication of science, engineering, medicine, and/or interdisciplinary work within and beyond the scientific community. Each year the *Futures Initiative* awards $20,000 prizes to those who have advanced the public's understanding and appreciation of science, engineering, and/or medicine. The awards are given in four categories: books, film/radio/TV, magazine/newspaper, and online. The winners are honored during a ceremony in the fall in Washington, DC.

NAKFI cultivates science writers of the future by inviting graduate students from science writing programs across the country to attend the conference and develop IDR team discussion summaries and a conference overview for publication in this book. Students are nominated by the department director or designee and selected by program staff. They prepare for the conference by reviewing the preconference tutorials and suggested reading, and selecting an IDR team in which they would like to participate. Students then work with NAKFI's science writing consultant to finalize their reports following the conferences.

Facilitating Interdisciplinary Research Study

During the first 18 months of the Keck *Futures Initiative*, the Academies undertook a study on facilitating interdisciplinary research. The study examined the current scope of interdisciplinary efforts and provided recommendations as to how such research can be facilitated by funding organizations and academic institutions. *Facilitating Interdisciplinary Research* (2005) is available from the National Academies Press (www.nap.edu) in print and free PDF versions.

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Preface

At the National Academies Keck *Futures Initiative* Conference on Collective Behavior: From Cells to Societies, participants were divided into fourteen interdisciplinary research teams. The teams spent nine hours over two days exploring diverse challenges at the interface of science, engineering, and medicine. The composition of the teams was intentionally diverse, to encourage the generation of new approaches by combining a range of different types of contributions. The teams included researchers from science, engineering, and medicine, as well as representatives from private and public funding agencies, universities, businesses, journals, and the science media. Researchers represented a wide range of experience—from postdoc to those well established in their careers—from a variety of disciplines that included science and engineering, medicine, physics, biology, economics, and behavioral science.

The teams needed to address the challenge of communicating and working together from a diversity of expertise and perspectives as they attempted to solve a complicated, interdisciplinary problem in a relatively short time. Each team decided on its own structure and approach to tackle the problem. Some teams decided to refine or redefine their problems based on their experience.

Each team presented two brief reports to all participants: (1) an interim report on Friday to debrief on how things were going, along with any special requests, and (2) a final briefing on Saturday, when each team

Provided a concise statement of the problem;

Outlined a structure for its solution;

Identified the most important gaps in science and technology and recommended research areas needed to attack the problem; and

Indicated the benefits to society if the problem could be solved.

Each IDR team included a graduate student in a university science writing program. Based on the team interaction and the final briefings, the students wrote the following summaries, which were reviewed by the team members. These summaries describe the problem and outline the approach taken, including what research needs to be done to understand the fundamental science behind the challenge, the proposed plan for engineering the application, the reasoning that went into it, and the benefits to society of the problem solution. Due to the popularity of some topics, two or three teams were assigned to explore the subjects.

A series of tutorials was launched prior to the conference to help bridge the gaps in terminology used by the various disciplines. Participants were encouraged to view all of the tutorials prior to the November conference.

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To listen to the podcasts or view the conference presentations, please visit our website at www.keckfutures.org.

Conference Summary

Nadia Drake, Science Journalist

FROM ME TO WE: ADDING THE PARTS TOGETHER, PLUS SOME SECRET SAUCE

On this planet, most things of consequence are the result of collective behavior. A solitary cell cannot squeeze blood through a valve; a single honeybee cannot craft an elaborate hive. The skies are not blackened by the undulating waves of a solo starling or a lonely locust.

One person can neither ignite nor halt global warming.

Group behaviors are what press their fingerprints into our landscapes, from the Ice Bucket Challenge to wars, from eusocial insects supporting billion-dollar crops to the destruction wrought by fire ants and termites, from having a brain that cracks codes to developing a destructive tumor.

Those groups could be clusters of cells, a colony of insects, or humans interacting on a social network. They could even be swarms of robots programmed to achieve a larger goal.

The question is, how do those behaviors emerge? Can science explain how individual parts eventually add up to something with more functionality? Do the same principles describe how groups behave on scales spanning cells to cyborgs? How do communities maintain that fragile balance between cooperation and competition, individuality and conformity?

And what triggers the collapse of collective behavior?

Scientists trying to better understand and harness such powerful forces convened in Irvine, California, to discuss these and other questions at the 2014 National Academies Keck *Futures Initiative* Conference on Collective

Behavior. Emerging as a theme at the meeting was the issue of scale, and the desire to define principles that can leap from microbes to humans to robots.

"Even organisms that defy any definition of organismality can display social behavior," said keynote speaker Joan Strassmann, an evolutionary biologist at Washington University in St. Louis. Strassmann studies a social amoeba called *Dictyostelium discoideum*. Frequently referred to as a slime mold, these eukaryotes begin their lives as single-celled organisms, then merge into complex, multicellular groups. Within those groups, Strassmann sees evidence for familial altruism and cooperative interactions with bacteria—characteristics that are normally associated with primates or humans or things that have brains.

"Really everything is social, isn't it? If you broaden the definition enough," Strassmann said, then defined interactive behavior as "simply any time what you do is influenced by someone else."

During the conference, participants met in small groups to discuss nine different challenges determined in advance by the steering committee. Some of the groups were given discrete goals, while others were left to ponder seemingly unanswerable questions. For two days, teams wrestled with questions aimed toward understanding the fundamental underpinnings of collective behavior. It's not a directional arrow that science is normally comfortable drawing: Rather than breaking a thing apart and studying how all the pieces work, the conference challenged participants to write the rules that glue those myriad pieces into a functioning whole.

Adding a bit of unintentional irony to the proceedings was the fact that any time a large number of people get together, collective behaviors are going to emerge.

Some of these behaviors were puzzling, like the long, growing lines of people waiting to squeeze onto the same conference bus—even though a perfectly good, wait-free bus was just a few steps away. Some of the behaviors were predictable, like the often-awkward group dynamics that squelch or champion ideas. And then there was the friendly, intergroup competition. "We have the inevitable emergence of team rivalry," steering committee chair Gene Robinson observed wryly, after one team took a playful shot at their (slightly more organized) counterparts during the first set of group presentations.

Others were more amusing, like the growing popularity of Play-Doh sculptures, produced using tiny tubs of fluorescent clay left for each participant in their team rooms. At first, only a few groups included slides of their neon creations in their team updates; by the meeting's conclusion, those brightly colored 3-D doodles featured prominently in almost every report. Some even used the sculptures to represent behavioral strategies, such as avian brood parasitism.

In other words, the conference itself was, at times, so perfectly meta.

At the end of the meeting, some progress had been made in tackling the challenges. There is much still to be learned. But more importantly, interdisciplinary collaborations emerged among the participants, who included physicists, computer scientists, microbiologists, and primatologists. Maybe soon, we'll have more luck infiltrating colonies of antibiotic-resistant microbes, crafting smarter machines, or designing social networks that can positively influence human interactions.

Sometimes, It's Not As Simple As 1+1=2

The first step in studying group behavior is understanding what a "group" is—how it forms, functions, and comes apart. Tackling this problem from the bottom up meant asking Team 6 to identify the principles governing how the simplest group—a group of two—works.

Dyads are everywhere, the team noted, but they're also fluid, with identities morphing between "one," "two," and "many" with regularity.

Consider the difference between "one" and "two." It may sound obvious, but take, for example, a human. That one human grew from a dyad, the two gametes that merged during fertilization. One human may be singular, but it's a constellation of countless cells and microbes working together to form a discrete unit. Likewise, a pair of humans could be "one," just as many humans employed by the same company could also equal "one." So, on some levels, a single human is both more and less than one. But on another level, one human is simply "one."

The lines defining "one" and "two" are sufficiently blurry that Team 6 had trouble identifying characteristics of dyads applied to everything from protein dimers to merging corporations. They also wrestled with the question of whether a group of two displays truly collective behavior or is merely cooperative, and questioned whether a dyad really is the building block for larger groups.

In the end, the team settled on defining a dyad as something involving two interacting individuals, but noted that in some situations, such as organ transplants, dissolving the "two" and reverting to "one" is crucial. Understanding how dyads function, the team noted, should be possible with technology that can track how individual cells, fish, dancers, and others behave in different size groups.

FROM ME TO ME

John Donne wrote that no man is an island. Could the same be said of cells? None of the trillions of cells in a human exists in isolation. They all contain the same basic set of genetic instructions, and yet can be vastly different from one another. So how do cells form groups that evolution can act upon, and how do those groups then become organisms?

More simply, what governs the transition from cellular me to more complex me?

In tackling this question, Team 8A presented a hypothetical situation: Say you had a bag of cells. You grab one at random. Would you be able to figure out if that cell came from a multicellular organism? Does organismality write its signature into individual cells? It might, the team argued. Cells from a human may be slightly less hardy, and definitely more specialized than a unicellular organism's cells. The group then designed some experimental approaches to determine which elements of cells contribute to multicellularity.

Team 8B asked whether cells could be looked at as small, organic Turing machines, capable of storing information that can be read and modified by the environment. In keeping with that idea, the team turned to computer science, where tradeoffs between communication, space, and time dictate how costly it will be for a computer to accomplish a certain task. The same could be true for cells in search of energy, the team said, and plotted the positions of various organisms on a three-axis fitness landscape that evolution can act upon.

The last group considered this challenge through a more applied computer science lens, and looked how tradeoffs between speed and flexibility allow organisms to evolve. Team 8C compared multicellular assemblies, such as bacterial bioflims and tumors, to the hierarchy of hardware, software, and apps that make an iPad so flexibly functional. In the team's analogy, the cells in both biofilms and tumors are the equivalent of the system's hardware. Like hardware, they run quickly but are expensive to make. Operating systems, on the other hand, are cheaper but may not be exceptionally diverse. In a biofilm, bacterial cells are all running the same software that tells them how to communicate. That's why microbial colonies can adapt so easily to changing environments. Tumors, however, are made of cells that may not be running the same operating systems. This means they might be a bit slower to evolve, but are also much less easy to hack. Apps in this case are cheerful things like invasion and metastasis.

THE FOREST AND THE TREES

Sometimes we're so focused on details that we miss the forest and only see the trees. But the truth is, there would be no forest without those trees—just like there would be no groups without individuals. And except in rare cases, those individuals are not identical clones of one another. They operate according to different rules and response thresholds. So, to what extent do individual differences benefit a group behavior? When do those differences harm behaviors?

Both teams challenged to answer these questions crafted complex models that began to describe how individuals affect group activity. Team 4A considered how network characteristics such as group size, connectedness, and fluidity alter the impact of individual variation on group activity. The team hypothesized that, as each of these parameters increases, individuality matters less. Take, for example, cardiac muscle—or a biofilm in which cells are packed together tightly. In these situations, a malfunctioning cell might have a greater impact on total group activity than in a school of fish, where an errant individual swimming against the grain is unlikely to derail the rest of the fish.

Team 4B also considered schooling fish as an example, and laid out three hypotheses. The first is that schools where fish all follow a different set of rules can behave similarly to highly cohesive schools where there's no individual variation. But, Team 4B said, in a school of fish comprising dramatically different individuals, maintaining that similar outcome depends on high levels of interactions among the fish. Next, groups that are both highly interactive and include high levels of individual variation have a better chance of performing well on complex tasks in shifting environments. Finally, the team suggested that the interaction between variation and connectivity could be tested using a swarm of programmable robots.

COORDINATION, FROM CELLS TO CYBORGS

Cooperative behavior exists on every level, from single-celled organisms in microbial mats to empathetic, bipedal primates, to robots working an assembly line. But do the same principles describe how cooperation works, regardless of whether the components have brains or not?

Team 1 grappled with the challenge of defining principles that transcend this brainy divide, using cooperative systems in organisms with brains as a model.

Or rather, coordinated systems.

Choosing to make a distinction between coordination and cooperation, the team came down in favor of defining principles governing how individual actions create collective behavior rather than why that behavior ultimately exists. Cooperation, the team argued, carries implications—such as intent—that may not apply to mitochondrial–host cell interactions or the behaviors of bacteria in a biofilm.

Coordinated actions, however, sum to produce emergent behaviors, regardless of the intent behind that action. The term bridges the differences between cells and organisms, the team said, and can be extended to describe the behaviors of artificial life forms. Governed by a set of rules, coordinated behaviors can arise from commands coded into robots, from an organism's genetic instructions, and from the chemical gradients that direct signaling molecules to their targets.

A better understanding of how these rules allow organisms to interact with their environment should make it possible to translate organic behaviors into inorganic, brainless objects, the team said. Thus, it might be possible to transform a swarm of robots into something that acts very much like an ant or a honeybee colony, where the sums of coordinated behaviors produce spectacularly complex structures.

IGNITING COOPERATION

Cooperation is the fire over which emergent behaviors smolder, transform, and emerge. Without it, there would be no group achievement. But what is the kindling for that fire? And what lights it?

"Find the very spark that ignites cooperation," Frans de Waal, primate ethologist and conference steering committee member, challenged Team 3. First, the team defined cooperation as an interaction that, on average, benefits participants. "You might participate in cooperation and not always win," the team said. "On average, you will benefit from this. But any given time you don't have to."

Identifying the cooperative spark meant comparing a range of cooperative behaviors, from predator avoidance to pack hunting, and pulling out the must-have proximate conditions involved in each. Among those, the team listed environmental variability, plasticity in response to interactions, communication, and goal-directed activity.

But the group wasn't satisfied with merely creating a list. So, participants turned to evolutionary robotics and discussed an experimental framework to test how important each factor is for the development of cooperative behavior. Called the Artificial Test-bed for Experimentation into Cooperation and Helping, the experiment would involve manipulating these must-have conditions and then monitoring the fitness and performance of robot test subjects engaged in foraging or defense challenges. In particular, the team is interested in studying how the strength and type of emerging cooperative behavior varies with different signaling intensity or behavioral flexibility. Using the results of those experiments, the team would ultimately like to develop a model that can predict how organisms cooperate outside the lab.

A FRAGILE BALANCE

Eusociality, as seen in honeybee and termite colonies, is among the more successful behavior strategies, conference steering committee chair Gene Robinson said in a preconference interview. And yet, he noted, it's a remarkably rare system. In some cases, it even appears as though eusocial organisms have reverted to solitary or parasitic lifestyles. What tipped the balance out of favor?

Two teams were asked to evaluate the extent to which successful collective behaviors rely on both cooperation and competition. Is it enough to simply have an absence of conflict? Or is some level of conflict needed for optimal performance?

Conflict is essential, said Team 7A, which began by stating that some level of conflict is needed for efficient cooperation. In trying to determine the optimum balance between conflict and cooperation, the team decided to focus on The Point of No Return—a point where the balance is so out of whack that a group is destroyed. To do this, the team took a computational approach that involved plotting various groups (chimpanzees, humans, honeybees) on a triaxial grid of conflict, cooperation, and fitness, and then identifying where those tipping points might be.

Team 7B first noted that cooperation and conflict can occur simultaneously. To better understand how a shifting balance between the two contributes to group behavior, the team decided to study instances in which groups quickly form and dissolve—the schooling of fish, a murmuration of starlings, the rise and fall of nations. By looking at these edges of group existence, the team reasoned it could tease out the factors responsible for pushing groups in one way or another—and then begin to mine those data for factors spanning cells to societies.

NETWORKED NETWORKS OF NETWORKS

Most of the time, the human brain is the epitome of networked efficiency. It's a mega-network of networks, and Team 9 was asked to address the ways in which cooperation and competition help those networks generate things like perception, movement, and thoughts.

The group chose to use epilepsy as a model. Seizures are the outcome of network connectivity gone rogue, where the balance between cooperation and competition has tilted. Normally, neurons live in networks that, through intricate communication channels, regulate one another. But sometimes those channels get jammed; other times, they're too open.

Epileptic seizures occur when too many cells are talking to one another and the synaptic traffic lights are stuck on green. They're the whole-brain manifestation of a breakdown in network communication on a microscopic level. But, as Team 9 notes, approaches to studying and treating such disorders usually consider the problem at the whole-brain level, rather than looking at the smaller scales on which networks connect. Now, the group says, technologies exist that can help bridge that gap and determine how competition and cooperation regulate connectivity on a cellular level.

Among the mechanisms the team proposed studying are competition for metabolic resources, signaling through excitatory and inhibitory networks, and trauma repair. For each of these areas, the team designed experimental approaches to investigate their contribution to epilepsy at both the whole-brain and cellular levels. Together, the team said, the results should help construct a computational model linking signaling through neural circuits to the widespread malfunction present in epilepsy.

THE $100,000,000 QUESTION

There's a flip side to every coin. Many emergent behaviors result in positive outcomes, like accomplishing a task that no single individual could complete. But others, like the formation of terrorist networks and the spread of destructive ideologies, are decidedly negative. In a perfect world, we'd ditch the negative and promote the positive.

Let's say you were given $100 million, over the next five years, to study and harness the power of social networks for the public good. What would you do with that money? One might think devising a well-funded research program that could combat anti-vaxxers or mob mentalities would be a fun challenge—but neither team tackling the challenge seemed to find it particularly easy.

Team 2A began by considering various ethical angles involved the research, including privacy, data access, and whether "harnessing networks for the public good" is something that scientists are ethically able to do. The members of Team 2B struggled to conceptualize a question they deemed vast enough to merit $100 million, and began by taking a close look at different kinds of "social networks"—such as Facebook, microbial communities, or even responsive nanomaterials.

In the end, Team 2A focused on studying how social networks could increase resilience to negative influences, such as rumors or misinformation, and suggested crafting a user-generated platform for sharing scientific knowledge. Group members were also interested in studying social networks on multiple scales—individual, group, societal—and wanted to better understand how multispecies networks function (such as pollinator communication or humans working with artificial intelligence). Team 2B decided to ask whether there were unifying principles that describe how information flows through dynamic networks, and then look at how those networks, and the individuals involved, respond to perturbations. Ultimately, the team suggests, understanding such complex systems might provide insight into human behavior.

WHEN THINGS FALL APART

Just as it's important to study how the whole exceeds the sum of its parts, it's crucial to understand how the wholes can fall apart.

What triggers the collapse of a beneficial collective? Team 5 addressed this issue by wrestling with a problem known as the Tragedy of the Commons—the dissolution of a functioning economy wrought by individuals prioritizing their needs over group interests. Or, as summarized by the group, "Everybody could be better off without hurting anybody. And yet we don't do that."

It's a problem that has confounded economists, environmental scientists, criminologists, and others for decades. And the team's challenge was immense: Solve it.

Not surprisingly, that didn't quite happen. But Team 5 did start identifying factors that are present in different Tragedies of the Commons, such as the overuse of antibiotics (and the subsequent rise of drug-resistant microbes) and the depletion of our fisheries and pastures. The team was particularly interested in identifying variables that transcend scales and disciplines, and disciplines and might point the way toward a solution. Participants also noted that it's important to clarify the differences between tragedy, collapse, and resilience—tragedy being the first step toward collapse, and resilience being the first step toward a solution. "How do we move from the tragedy to the resilience of the commons? How do we start to solve this big problem?" the group asked.

Ultimately, the group said, they'd like to write a mathematical equation describing how all these variable interact; though that didn't happen at this conference, the team mentioned plans to submit a paper on the topic soon.

IDR Team Summary 1

Using our understanding of cooperation in cognitive organisms to understand cooperation in organisms or entities without brains and vice versa.

CHALLENGE SUMMARY

Much of the way we understand social interactions comes from observable behaviors among organisms with brains. These organisms demonstrate actions that are interpretable in a human context. Many concepts have arisen from such observations, including but by no means limited to altruism, kin recognition, eavesdropping, status badges, cheating, and veils of ignorance. The most general theories for the evolution of social behavior apply to these observations, including kin selection, and mutualism. But is it necessary that the actors have any form of cognition?

The purpose of this challenge is not to get caught in the mire of deciding what is and is not cognitive, or when a brain actually functions in one way or another, but to go to organisms, parts of organisms, and artificial life, both robots and programs like Avida, where brains are not present at all and explore the power of brain-based social understanding. Four areas come to mind: (1) the major transitions of life, (2) within-genome interactions, (3) microbial interactions, and (4) robots and artificial life.

The major transitions are the progression in complexity of life formulated by Maynard Smith and Szathmary, including genes into chromosomes, mitochondria and host cells into eukaryotes, single cells to multicellularity, and solitary to eusocial insects. Cooperation and control of conflict characterize these transitions, with some being formed of related individuals (fraternal transitions) and some being formed of different individuals, typically of different species (egalitarian transitions), to use terms chosen by Queller.

Within genome interactions include genomic imprinting (the differential expression in an offspring of maternally and paternally derived genes), the parliament of the genes, and selfish genetic elements and their control.

The current view is that microbes are nearly always social, living in a mix of relatives, non-relatives, predators, prey, and mutualists. Exactly who does what to whom is challenging and important, for microbes inhabit every nook of our bodies and can either make us sick or well. Do the models for cooperation, conflict, and control work for them? Are we missing something because microbes are so different? What about viruses?

The interplay among robots or artificial life units is another area for exploration. Under artificial life systems like Avida, different units with complementary functions may fuse to work more effectively. Robots may behave differently collectively, with the sum of actions becoming something different than the local decisions they arise from.

For each, the challenge is to ask whether we have fully mined brain-based concepts for potential applicability, and conversely whether we have been blinded to possible insights by beginning with brain-based ideas. It is important to keep in mind that actions that cognitive organisms display may not necessarily be the result of cognition. Insight into which actions this is true for might be found by examining behavior of noncognitive organisms under similar circumstances.

The interplay among robots or artificial life units is another area for exploration. Generally speaking the word robot may refer to both physical robots and virtual software agents. Talking to the experts in this field, it appears that there is no universal agreement on which machines/devices represent the robots; however, one has the general appreciation that robots could perform tasks including moving around, operating a mechanical limb, sensing and manipulating their environment, and exhibiting intelligent behavior. Particularly, one likes to see behavior that resembles intelligent beings such as humans or other animals. There exists consensus that "robot" signifies an apparatus (machine/device) that can be programmed to perform a variety of physical tasks or actions.

It is perceived that the two distinct ways that robots are different from actual beings are in the arena of cognition and biological features. Regardless of its human-like or dislike appearance, robots need programming to function properly. The advent of modern feedback control systems along with advances in computational powers of miniaturized electronics has made modern robots a lot more artificially intelligent. This allows them to perform tasks based on their own sensing of their surroundings and potentially perceived outcomes. This may be performed either by an individual robot or by a group (or swarm) of robots. In the swarm scenario the concept of particle swarm optimization technique could be used to control the movements of the robots. In this manifest the robots rely on their own individual sensing experiences (self awareness) of the environment and also utilize the collective knowledge (swarm knowledge) of the environment among all of them to guide the robots to move to the desired direction and/or desired outcome, i.e., the dream land! The human-like issues such as jealousy, sympathy, becoming number one, etc., could also be programmed into robots if this would be necessary to perform the desired tasks more effectively. The field of artificial intelligent is a rapidly growing field and modern electronics and miniaturized mechanical actuators have allowed the robot designers to make their robots amazingly powerful and self-supporting!

Key Questions

What concepts from the social sciences have not had an impact yet on understanding cooperation in microbes, across major transitions, or within genomes? What might we learn from closer attention to social science theory?

How is conflict controlled in microbes, across major transitions, within genomes, or among units of artificial life?

What mechanisms substitute for cognition and brains in microbes, across major transitions, within genomes, or among robots or units of artificial life?

What characterizes social science concepts, like veil of ignorance, for example, that are clearly important in microbes, across major transitions, within genomes, or among robots or artificial life units?

Inclusive fitness theory and mutualism theory are clearly powerful in explaining cooperation in microbes, across major transitions, or within genomes, so what can we add to that from social science theory?

What are we missing from the gap between these two social disciplines that closer discussion might reveal?

Are robots going to become a complete human?

Are some robots more powerful than the human in some task that necessitates multitasking and fast computations?

Could robots perform tasks beyond what is programmed in them?

Suggested Reading

Cook KS, Cheshire C, Rice ER, and Nakagawa S. Social exchange theory. In Handbook of Social Psychology, pp 61-68. Springer: New York, 2013.

Crespi BJ. The evolution of social behavior in microorganisms. Trends in Ecology & Evolution 2001;16(4):178-183. [Abstract available.]

Fehr E and Fischbacher U. The nature of human altruism. Nature 2003;425:785-791.

Griffin AS and West SA. Kin selection: Fact and fiction. Trends in Ecology & Evolution 2002;17(1):15-21.

Haig D. Transfers and transitions: Parent-offspring conflict, genomic imprinting, and the evolution of human life history. Proceedings of the National Academy of Sciences of the United States of America 2009;107:1731-1735.

Queller D and Strassmann J. The veil of ignorance can favour biological cooperation. Biology Letters 2013;9(6):20130792.

Queller DC. Cooperators since life began. Book review of: The Major Transitions in Evolution, by Maynard Smith J and Szathmáry E. Quarterly Review of Biology 72:184-188.

Queller DC. Expanded social fitness and Hamilton's rule for kin, kith, and kind. Proceedings of the National Academy of Sciences of the United States of America 2011;108, Suppl. 2:10792-10799.

Werren JH. Selfish genetic elements, genetic conflict, and evolutionary innovation. Proceedings of the National Academy of Sciences of the United States of America 2011;108;10863-10870.

West SA, Diggle SP, Buckling A, Gardner A, and Griffins AS. The social lives of microbes. Annual Review of Ecology, Evolution, and Systematics 2007;38:53-77.

Wilson RK. The contribution of behavioral economics to political science. Annual Review of Political Science 2011;14:201-223.

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IDR TEAM SUMMARY— GROUP 1

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IDR Team 1 was asked to use our understanding of cooperation in cognitive organisms to understand cooperation in organisms or entities that have brains, and organisms that don't.

Our scientific conception of social interaction is largely based on studies of organisms with brains. Humans and animals engage in a range of complex collective behaviors, from altruism to cheating to competition. But brainless entities also exhibit intricate social interactions. Bacteria use chemical signals to coordinate unified actions; a selfish gene can promote its own transmission at the cost of other genes and its whole organism; and robots can be programmed to work together, completing tasks as a swarm. IDR Team 1 set out to identify underlying properties of interaction that transcend cognitive context, comparing and contrasting the mechanisms at play in diverse social systems. The team focused on how best to consider social engagements across fields, with the goal of facilitating interdisciplinary dialogue and applying biotic concepts of sociality to robotics.

Coordination, not Cooperation

IDR Team 1 determined that "coordination," and not "cooperation," should be used to discuss, analyze, and compare collective behavior across scales. The team defined coordination as local, nonrandom interactions involving an exchange of information and a response. Cooperation, however, implied a higher-level, perhaps evolutionarily defined engagement, which delivered some "greater good" to an entity or species. A key difference between the two terms, the IDR team said, was that coordination is a *proximate* process, concerned with "how" a behavior occurs, while cooperation represents an *ultimate* process, focused on "why" a behavior occurs.

The IDR team emphasized coordination over cooperation for several reasons. First, the team said, it can be challenging to determine whether cooperation actually exists in a group. Relationships that seem cooperative or mutualistic may just represent some co-evolved dependency; the team used the example of mitochondria, a power-generating component of animal cells. It was believed that these organelles were once independent cells, engulfed by larger cells to the benefit of both. But, recent research suggests that mitochondria may have actually once been parasites, and they simply evolved over time into an integral part of animal cells. It is also possible that, while it might appear that bacteria are cooperating while sharing a public good, this is not an "intentional" relationship. A bacterium may secrete some compound when its internal concentration grows too high, and other microorganisms can then use the substance. The release of the compound is programmed on an individual level; it simply happened to benefit others. Even in cases where an action benefits all agents involved, "cooperation" may overestimate the actions of each entity, the IDR team posited. The team considered the example of a species of toxic algae: each cell appears to cooperate as they band together, dominating marine environments. As more cells accumulate, they can kill larger and larger prey. But, the team argued, each cell is simply acting in its own best interest, trying to individually find higher concentrations of food. The sum of individual coordination creates an emergent group behavior.

The IDR team agreed that coordination might represent an intermediate between solitary and collective behaviors, a "stepping stone" to cooperation at larger scales. Because defining cooperation can be challenging, the team felt coordination was the most parsimonious way to study interactions. Whether or not cooperation exists on an ultimate scale, any engagement requires coordination, and interactions can be studied and described in this way.

The team discovered that describing cooperation, conversely, is a challenge, as it has different connotations in different fields. For example, in molecular biology, two enzymes are called cooperative when one's binding state encourages a conformational change in its neighbor. This, an individual response to an environmental change, was not cooperation by the team's definition but the technical term still applied. So "coordination," the team argued, also provides a stronger common language to compare social mechanisms across disciplines.

This language can extend beyond the realm of biology and into that of technology, providing a way to compare biotic systems with robotic systems. As in groups of social insects, the team said, each robot in a swarm executes one individual part of an emerging group behavior. Considering the coordinative behavior of robots allows a focus on the building blocks of any larger collective swarm action, the team agreed, which could provide the greatest insight when designing new social engagements.

Still, IDR Team 1 agreed that some social behavior can be analyzed at the level of cooperation. The team used a metaphor: if an animal's tissues and organs represent cooperation, its genes represent coordination. It isn't always necessary to consider genetic code while studying an animal. But to compare disparate interactions or explore unfamiliar systems, coordination is the most useful method of study.

Mechanisms and Constraints

After defining and selecting coordination as an ideal method of analysis, IDR Team 1 examined its common mechanisms. Any coordinated social activity, the team concluded, is governed by a set of rules, which vary depending upon the system in question. Robots must follow the precise direction of their programming. But ants also have a "programming" of sorts, operating under what can be called "rules of thumb." For example, if her nest members are slow to accept her collected food, a foraging ant will delay her return to the foraging path. Even nanoparticles follow a set of rules that tells them how to drift through different concentrations of chemicals.

In addition to these rules, the team described four classes of systems that make coordination of activities possible. These were "recipes," or set patterns of action; "templates," or external information that individuals use to adjust their behavior; "stigmergy," an indirect communication through modification of the environment; and "self-organization," in which complex patterns arise from individual actions. Different contributions of each class are possible in different coordinated systems. IDR Team 1 noted that these mechanisms shape how interactions shape a society. As one team member summarized: "To understand things socially means to understand how processes are coordinated. Beyond that, the mechanisms of coordination place constraints on how coordinated systems evolve." Constraints are essential, the team agreed, in understanding biological societies and designing robotic ones.

The team also emphasized the importance of environmental factors in shaping coordinated behavior. The IDR team expanded its discussion of stigmergy, a method of storing cues in the environment that indirectly and anonymously affects other agents. The activity of a termite building a tunnel, for example, is directed by the previous construction of other colony members. The team also discussed other environmental constraints on coordinated behavior, noting that epigenetic changes can affect how a genome is expressed, the age and lifespan of organisms affect their social interactions, and the physical terrain that a robot must navigate can affect its performance.

The team said that constraints could cause conflict in a biological system—and conversely, biological conflict could constrain certain systems (for example, the development of cells is determined by genetic conflict in chromosomes). The team agreed that conflict drives evolution and development. Genetic conflict can lead to coordination at a species level—for example, opposing maternal and paternal imprinting of growth hormone genes in lions will ultimately evolve into healthy cubs. The team felt that it would be important to incorporate a biological model of constraint and conflict when designing social robots. Selecting the ways robots interact might define the limitations of the technological system as a whole—so engineers should choose carefully.

Bridging the Gap: Biology and Technology

The team asked whether elements of biological systems can be used to design robotic swarms. Natural systems “make cool things happen” under extensive constraints; the team wondered if it is possible to “import that insight” from biology into robotics, which has constraints such as limited battery life. The team suggested that stigmergy could be programmed into robots, if the concept could be understood and inferred from social insects. The team also discussed whether robots should be programmed to cheat—for example, if a robot was rewarded for saving energy while performing a group task, it might slack at its job at the expense of its neighbors. Finally, the IDR team wondered if evolution, a powerful selective force on biological communities, could be implemented in robotic swarms—was it important, the team asked, to “understand evolution from an engineering standpoint?” It could be beneficial to program “natural selection” into robotic swarms. Manufacturing differences could produce heterogeneity in robotic swarms, and if certain “weak” robots could be “pruned out” or assigned a different task, it might benefit the group at large.

Conclusion

Whether comparing technology and biology or different biological systems, IDR Team 1 agreed that it is essential to shift focus from cooperation to coordination. The team believed this would allow more efficient, accurate, and broadly applicable analysis of social interactions, the mechanisms by which they develop and change, and the constraints that shape such processes. Ultimately, the IDR team concluded this would advance our understanding of collective behavior as a whole, as well as our ability to construct and optimize coordinated systems in the technology of the future.

IDR Team Summary 2

How would you spend $100 million over the next five years to understand and harness the power of social networks?

CHALLENGE SUMMARY

In the twentieth century, many social scientists were focused on individual behavior, and the models they used to describe it colored their view of the world. Statisticians modeled individuals under the assumption that the actions of multiple individuals were independent. Economists assumed that individuals were self-interested. But increasingly we have come to realize that these models are deficient. We are influenced by and care about others.

An old way of dealing with this dependence is to conceptualize abstract collections of individuals as "groups" and to assume that individuals behave the same within these groups. Categories of race, class, and nationality served as proxies for individual interests and behavior in some of the most popular social theories of the twentieth century. But these models were also deficient because they ignored within group variation and had little to say about how and why the group influenced individual behavior.

The new science of social networks looks at the world in a different way. Rather than focusing on individuals or groups, it focuses on the relationships between individuals. This third way of seeing the world maintains individuals at the center (the "nodes" of a network), but it recognizes their interdependence by including explicit information about their interactions with other individuals (the "connections" in a network). If "groups" exert influence on individual behavior, they do so via the direct relationships between individuals. In fact, groups are primarily abstract representations of the "communities" that can be identified as parts of the network that have many connections within a set of individuals and few connections between that set and the rest of the network.

Although the science of social networks can be applied at many scales and to many organisms, it is especially in individualized societies based on memory of past interactions that we see mutual interdependence and long-term partnerships, often based on reciprocity, such as in the primates, elephants, dolphins, and other large-brained mammals (de Waal & Tyack, 2003). Here we focus on how to use social network theory to understand and improve outcomes for humans, even while recognizing that some of the issues are not limited to our species. A wide variety of research is making it clear that behaviors spread in social networks. There are already many specific models in sociology, economics, social psychology, and related fields on social influence, some of which address the flow of influence in networks. There is also work in computer science and what is now being called computational social science on networks and influence. However, this work suffers from (at least) six important problems.

1. It remains unclear which methods are best for measuring social influence.

Network science is a fast-growing field, and it is clear that perfect methods, free of any limitations or assumptions, do not exist for every sort of question one might want to ask with observational (or even experimental) data. The classic problem of distinguishing selection and contextual effects from influence remains, though recent advances suggest that sensitivity and bounds analysis may hold promise. Additionally, basic issues in coping with missing data (missing nodes, ties, covariates, waves), sampling (design effects and incomplete network ascertainment), and computation of standard errors are still being addressed.

2. Only a limited number of long-term longitudinal social network data sets exist.

A plethora of studies are based on available data from the Framingham Heart Study and National Longitudinal Study of Adolescent Health, but it is not clear if these networks are representative. Are there systematic differences in the strength of network effects or the processes by which they occur when studying networks of different sizes and composition? Are there important problems when defining the boundaries of these networks that may interfere with valid inferences?

3. The literatures that address social networks are rooted in very different fields of biology, sociology, economics, statistics, epidemiology, and physics, and a common model and language has not yet emerged.

Scholars in various fields continue to look inward toward models and solutions proposed by their close colleagues rather than reaching out to join forces across disciplinary boundaries. A large-scale effort to systematically explain the differences and similarities of the most used social influence models in various fields has not been conducted. As a result, it is difficult to know which models are working best and to transmit advances across the sciences.

4. Most studies focus on documenting network effects rather than identifying and testing their mechanisms.

If we want to alter the dynamics we observe in social networks, we need to understand what drives them. Current work is moving in this direction, but not quickly enough. We need to encourage scholars to identify the key aspects of the social processes or mechanisms involved and how network phenomena play out in different applications (e.g., to the spread of ideas, attitudes, norms, behavioral change) and different settings (especially online versus real-world networks). A unifying theory that explains when to expect various mechanisms to matter would help in improving our capacity to analyze novel phenomena. And ideally, one would have randomized experiments or rigorously designed quasi-experiments to allow the strongest tests of causal direction and provide opportunities to test specific mechanisms.

5. We do not yet understand how the transmission of behaviors through a network itself alters the structure of that network.

It is well known that network structure influences many human outcomes, but much less is known about how human behavior alters network structure. For example, the social networks of smokers changed dramatically over the past 40 years as social pressure campaigns marginalized them and public policies forced them into smaller spaces where they were more likely to connect to other smokers. Understanding the effect of influence on structure may thus be a critical element in any effort to use networks to change behavior.

6. In spite of recent advances in understanding the processes underlying social influence, there has been very little work showing how to apply

this understanding in interventions to improve our health, our wealth, our global environment, and our democratic institutions.

There are, of course, some notable exceptions like real-world network interventions that target central actors to prevent smoking and online network interventions to spread voter participation. But these are the exception that proves the rule. We need more experiments designed to test theories derived from observational studies, and more large-scale tests of interventions based on successful observational and experimental studies.

Key Questions

What models do we currently have that identify the role of social networks in this process, and where do we go from here? Is there a way to unify the proposed models or adjudicate among them so that we can agree on a central methodology? It might be possible to take a "top-down" approach by facilitating interchange among theorists representing the different models in an attempt to forge agreement on shared concepts, definitions, and methods. Another way would be to ask such a group of theorists first to design on their own how they would study the spread of a given phenomenon and then ask them, in the context of creating a single design, to capture emergent concepts and methods.

What mechanisms result in the spread of influence, when? We must move beyond a mere demonstration of spread to studies that explain how and why things spread and the conditions that hasten or slow transmission.

What are the differences between modes of transmission and outcomes with respect to behavior change in particular?

In light of the geometric growth of online communities (Facebook, LinkedIn, Patients Like Me, and so on), will the same principles determine spread in online networks that determine spread in face-to-face networks?

How early in life can network effects be seen? For example, we are finding effects of social hierarchies in kindergarteners—are these due to their networks?

How do we model reciprocal effects of networks and behavior change? In particular, how do behaviors themselves alter the shape of social networks?

Over time, people who engage in stigmatized or illicit behaviors become more tangential within larger networks, but do they form new networks, and what effect do these have on their behavior? For example, there may be enhanced communication among smokers huddled in smoking areas outside of large office buildings.

What role do individual characteristics play in network structure and transmission? For example, is transmission facilitated in networks with more homogenous members (same gender, ethnicity, age, social class)?

How can the principles and approaches of social network research be applied to understand social interactions and cooperation in nonhuman species and groups involving multiple species?

How does the spread of information change a social network?

Reading

Bond RM, Fariss CJ, Jones JJ, Kramer ADI, Marlow C, Settle JE, and Fowler JH. A 61-million-person experiment in social influence and political mobilization. Nature 2012;489:295-298.

Centola D. The spread of behavior in an online social network experiment. Science 2010; 329:1194-1197.

Christakis NA and Fowler JH. Social contagion theory: Examining dynamic social networks and human behavior. Statistics in Medicine 2012;32:566-577.

de Waal FBM and Tyack PL. Animal Social Complexity: Intelligence, Culture, and Individualized Societies. Harvard University Press, Cambridge, MA, 2003.

Dodds PS and Watts DJ. Universal behavior in a generalized model of contagion. Physical Review Letters 2004;92(21):218701.

Lazer D, Pentland A, Adamic L, Aral S, Barabási A-L, Brewer D, Christakis N, Contractor N, Fowler J, Gutmann M, Jebara T, King G, Macy M, Roy D, and Van Alstyne M. Computational social science. Science 2009;323:721-723.

Salathé M, Kazandjieva M, Lee JW, Levis P, Feldman MW, and Jones JH. A high-resolution human contact network for infectious disease transmission. Proceedings of the National Academy of Sciences of the United States of America 2010;107(51):22020-22025.

Valente TW. Network interventions. Science 2012;337:49-53.

Because of the popularity of this topic, two groups explored this subject. Please be sure to review the other write-up, which immediately follows this one.

IDR TEAM MEMBERS—GROUP A

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IDR TEAM SUMMARY—GROUP 2A

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IDR Team 2A was asked to answer the question "how would you spend $100 million over the next five years to understand and harness the power of social networks?" The overall theme of the conference was collective behavior. Social networks are built on collective behavior. There is a wide range of challenges facing the area of social network research. The team started the conversation by addressing some of those challenges. The team also discussed where the money would be coming from and picked three main areas of study where it could focus research: (1) understanding the fundamentals, patterns, and structure of social networks; (2) dealing with multiplicity of scales, networks, and species and their interactions; and (3) harnessing the power of social networks for the public good.

Why Are Social Networks Important?

Social networks exert a powerful influence on human thoughts and behavior. They consolidate memory, shape emotions, cue investigative thinking and biases in judgment, influence in-group/out-group distinctions, and may affect the fundamental contents of personal identity. Because of these influences social networks are important in a variety of societal contexts: for example, they have been observed to change the course of insurgencies, and frame negotiations; they have played a role in political radicalization, and influence the methods and goals of social movements.

By studying social networks in the animal and insect kingdoms, i.e., ants, prairie dogs, bees, and butterflies, one may be able to infer how human social networks function. Principles from animal and insect networks have been shown to be applicable to other species, including humans. In addition studying the collective behavior of these species can provide insight into how to understand patterns in their collective behavior.

Research Challenges

Some of the challenges discussed were privacy, data access and standardization, ethics, and defining the scientist's role in social network studies. The first question the team posed was about how to make sure research subjects remained anonymous in any kind of social media or Internet-based research. Along with this issue of privacy is the lack of knowledge of how the Institutional Review Boards (IRBs) work among researchers who do not normally use it in their field. The team decided these researchers would need to be educated about how IRBs function before researchers could conduct studies with social scientists. Not only is there an issue of privacy, but it is also difficult to get data from companies. Large for-profit companies, i.e., Facebook and Twitter, have significant amounts of social network data, but it is difficult for researchers outside these companies to access these. If researchers can get access to the privately held data, it is often at great expense. The question of the scientist's role in using data from social networks was raised during the discussion. Are scientists supposed to just observe social networks or should they also intervene in the networks' activity?

Who Has the $100 Million?

After the team talked about the challenges with social network research, the participants discussed where the hypothetical $100 million would come from. Who provides the funds is important because that would influence what direction the research and spending would take. They discussed how projects would differ if the funding came from the National Science Foundation versus the Defense Advanced Research Projects Agency, National Institutes of Health, or a private organization. However, despite these differences, the team understood that they could narrow down the scope of potential expenditure to maximize the ultimate impact; for that, they needed to focus on the fundamental of social networks.

Fundamentals, Patterns, and Structure of Social Networks

One of the main questions the team focused on when discussing the fundamentals, patterns, and structures of social networks was how social network research can be leveraged to increase resilience to negative outside influences, such as rumors and general misinformation.

Another question raised about resilience was whether resilience was a reflection of confidence in society and the government. In trying to answer this question, the team discussed people's tendency to act based on emotional response rather than on facts—i.e., believing propaganda instead of looking for facts. The team also considered the propagation of rumors and information that alters society in major ways, as well as how this information is generated and how it spreads through social networks. An example of this is the supposed identity of the Boston Marathon bomber being spread throughout Reddit, which had led to a false arrest. Adding to the team's original definition of resiliency, they decided that a network could be more resilient if it could distinguish between perception and reality, which could help the network be resilient to the spread of rumors. Exactly how this would be accomplished technologically remains an important matter for study. An example of resilience that the team came up with was how networks can help people survive; during the Iraq war, people relied on their established social networks, as well as newly created networks with people living outside Iraq, to help them determine when it was safe to leave their homes. These networks helped keep people alive.

In addition to discussing resilience in networks the team also explored how social networks learn by adapting to change as well as how networks change over time.

Dealing with Multiplicity of Scales, Networks, and Species and Their Interactions

The second topic the team examined was how to look at different kinds of social networks on multiple scales and how those networks interact with each other. The team acknowledged that there was not sufficient research to examine social networks through multiple scales. The team decided they would want to use a multiscale, multilayered study that would look at social networks on a range of scales: on the individual level, on the group level, the societal/ecosystems level, and on a global scale.

They did not just want to focus on human social networks, however. There are social networks among insects and members of the animal kingdom as well. Social network studies can be performed with any animal that has a communication system, including ants, prairie dogs, and bees. The team discussed the need for more research on species-to-species communication. An example of this would be how pollination patterns of bees and butterflies affect each other and how these patterns interact. If the team were to do a study about something like cross-species pollination they could look at whether these behaviors resulted in competition, collaboration, or a combination of both.

The team also thought it would be interesting to look at multilayered networks that are interconnected, such as humans interacting with robots and other systems of artificial intelligence. In order to carry out this kind of study they would want to design a machine, using computer algorithms that would work symbiotically with human networks to drive the reward system and increase the resilience of the group. By building a relationship with the computer, the individuals involved would indirectly build relationships with other people. This computer-mediated resilience could allow the group to fact-check itself, thus building resilience to rumors and misinformation as well as a way to adapt in times of change and conflict. The team then tied this back to earlier discussion about creating a research infrastructure by exploring the question of how ecosystems achieve resilience through networks between species and also within species. All of these issues relate to societal impacts and public good.

Harnessing the Power of Social Networks for the Public Good

When they first examined this topic, the IDR team discussed using social networks to improve communication during crises such as natural disasters, mitigating the spread of epidemics, and using the power of social networks for counterterrorism, conflict resolution, and education.

After more discussions, the team came up with the idea of creating a social network that people would feel committed to, encouraging them to remain a part of the network over a long period of time. Part of the incentive structure would be that people could observe the consequences of their actions. Participants in the network could see how the ideas they contributed to the network were advancing knowledge on a certain topic.

The team discussed how they could build a network where people would feel connected, and they decided that some kind of nonmonetary incentive structure could be useful. The network would be similar to Wikipedia in that it would allow people to exchange knowledge and ideas. The team looked at how networks like Galaxy Zoo, a place where people can name new galaxies, works. They also proposed platforms similar to those used for crowdsourcing and the idea of citizen science to answer important scientific questions, as in the recent progress on twin primes made by the larger mathematical community. Anyone could participate in the network and post their answer to the questions that the team posed. Through this kind of social network, participants' cognitive surplus could be used to advance knowledge. A network like this could also help generate ideas about how to encourage society to engage in sustainable behavior. For example the team could pose a question about how people would solve the tragedy of the commons.

Conclusion

The team decided that they would spend $100 million over the next five years to harness the power of social networks for public good, and in order to achieve that goal, there must be research on understanding multi-scale, temporal, complex networks that included humans and nonhumans (computers, other species).

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IDR TEAM SUMMARY—GROUP 2B

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> ". . . We must learn to treat comparative data with the same respect as we would treat experimental results. . . ."
> - J. Maynard Smith & R. Holliday, 1979

IDR Team 2B was asked to theoretically spend $100 million over the next five years to understand and harness the power of social networks.

The team collectively decided that the discussion should focus on the ideas behind the concept rather than the $100 million itself. Research, in general, should be funded on how bold or innovative ideas are, rather than simply funding something expensive.

A four-question model was developed by the IDR team to address the research question: (1) How should the boundaries of networks be defined? (2) How can data mining tools be applied to networks to elicit information? (3) Should dynamic and static networks be differentiated? (4) Should naturally occurring networks and intentionally built networks be differentiated for purposes of study?

The size of the networks was defined as small (10-12 members), intermediate (1000 or more members), and large (millions of members). Three types of network model systems were identified: human, nonhuman animals, and artificial or inanimate systems.

The team saw the need to craft a question broad enough to capture the imaginative investors or funders in the event that there are enough good ideas to justify spending $100 million on research on social networks. The question developed would be a counter question to the research challenge question and intentionally tackle the key words that drive the research. In this case, the key words are “harnessing” and “understanding” the power of social networks. The team came up with this counter question:

Can unifying principles be identified for how information flows through networks and how networks respond to perturbations?

The IDR team members additionally framed individual counter questions:

What is the difference between information-based and material-based networks? If any?

How do we optimize networks when disaster strikes?

Are the appropriate technologies available to approach research on this question? If they are, how will those technologies be developed and adapted in using $100 million to understand and harness the power of social networks?

What are the tipping points and criticality that control a network response?

How is the initial condition important to understand the system?

Identifying Social Network Complexities

Each member of the IDR team provided a specific example of a social network, applicable to the counter research question, to achieve a clear focus. Six examples—chosen from many—could potentially be included in a $100 million social network research project.

The first example of a social network for study was about parenting—the interplay between the structure of a network and how individual members behave. With this problem, it is important to understand how social networks reach critical mass, or tipping points, and at what point amplification occurs, causing a phase transition and affecting the system. The team highlighted two very different specific topics. The first was societal factors that influence whether parents choose to vaccinate their children. The second example focused on tipping points in terrorist organizations. Terrorist organizations operate on interplay between familial, ethnic, and socio-political conventions that lead to the mobilization of a violent organization.

The third example of the complexity of social networks was disaster response systems. The IDR team wanted to understand the permeation of information in these networks to further study the behavior of individuals who respond to disasters. Disaster response networks, for purposes of this discussion, refer to only weather or naturally occurring hazards, like hurricanes or tornadoes, and what would drive individuals to flee from town or seek shelter in a basement.

The fourth example was about understanding how nanomaterials combine and interact in a microenvironment and how their properties change as a consequence (e.g., how nanomaterials act in the process of building self-driving cars).

The fifth example focused on microbial communities and how they change in group-level behavior and interaction, causing feedback to individual members. This discourse will help delineate the differences between macro- and microsystems and how it helps to make the track universal principles of networks better.

The sixth example was to identify and understand the process that social networks must go through to achieve a favorable end. One IDR team member used the example of setting up a global virus network for scientists. Labs of this kind have previously been established with the intent of streamlining communication among labs. Though the technologically advanced labs are readily available, they have not been used to their full potential.

Thus, this member is interested in researching what is needed to get nodes to engage in a network from which they would benefit.

Project Analysis

At the end of the sessions, the IDR team came up with several goals to achieve success in a $100 million research project with six examples of relevant social networks.

The IDR team also found it necessary to define why artificial networks should be studied when measuring the power of social networks to produce data that are particularly relevant to humans. The team finds that human systems are unpredictable and the complexity and attributes of human behavior need to be measured precisely. Therefore, measuring artificial systems is needed to wield more control for the researcher. It is understood that artificial systems do not necessarily recapitulate human systems, but measuring artificial networks first is useful to produce the generality needed to narrow down what should be measured in human networks.

The team set forth the basic principle that the understanding and harnessing of the power of social networks is not unidirectional, but iterative, or mutually informative. The study networks at various scales and levels (human, nonhuman animals, artificial/inanimate) as an iterative process will capitalize on the advantages of each approach.

To achieve optimal results, it is important to build a community of researchers across disciplines who work as collaborative teams to truly understand the basic principles of a social network, and most important, identify commonalities across networks. To achieve this goal an additional workshop, outside of NAKFI, is needed to get all the project researchers in one room and strive to reach a common goal.

Conclusions

With robust conversation and a complex problem, IDR Team 2B left the NAKFI conference with loose ends on the research question. Rather than itemizing the $100 million dollars toward harnessing and understanding of social networks, the IDR team identified several examples of present challenges to social networks where the money could be beneficial in aiding research.

Outlook

The IDR team collectively decided to apply for a seed grant to fund a small, 10- to 15-person workshop which would delve further into harnessing and understanding social networks. The interdisciplinary workshop team would host researchers with work relevant to the power of social networking. The primary goal of the workshop would be to find commonalities among the different systems of social networks (human, nonhuman animals, and artificial/inanimate) to produce content analyses. Researchers in the workshop would hope to develop a possible research program. The workshop will be the first step in building an interdisciplinary community of researchers who can effectively propose research that aims to understand and harness the power of social networks.

IDR Team Summary 3

What proximate mechanisms underlie helping and cooperation?

CHALLENGE SUMMARY

What kind of social tendencies and cognitive evaluations urge an individual to help another or to cooperate on a joint task? In order to cooperate with others, individuals need to choose partners or join an ongoing effort. They may also be recruited by others, and will need to decide if the joint effort will be worth their participation. Sometimes they just assist others who are in trouble or cannot reach their goal alone. There are basically two situations:

(a) Anonymous cooperation: Species without individual recognition and remembered experiences cooperate with other conspecifics. Here partner choice is guided by cues that simply indicate that the other individual is a member of the same nest, colony, or population. Anonymous cooperation with members of the same group likely evolved under conditions in which all group members were closely related kin, and thus it was unnecessary (and perhaps too costly for large groups) to distinguish among them. Alternatively, if groups are fairly stable and interactions are repeated, cooperative behaviors may benefit all members of the group and thus be selected for, even if relatedness among individuals is low. Finally, social interactions (and the underlying neurophysiological and cognitive pathways that drive these interactions) that evolved among members of a closely related kin group may have easily expanded to include less related individuals. For example, phylogenetic studies have indicated that social behavior evolved under conditions in which groups were headed by singly mated females, and mating number increased subsequently. Thus, once social interactions among closely related individuals became firmly established, the group could take advantage of the benefits of increasing genetic diversity and thereby enhancing immunity, task specialization, and division of labor. Similarly, it is theorized that maternal care evolved into sib-care; in this case, the underlying sensory pathways simply expanded to include siblings as well as offspring. This is not unlike ideas about mammalian empathy (below), which is thought to be rooted in maternal care neural circuitry.

(b) Individualized cooperation: Species in which individuals recognize each other and build up a history of interaction known as "social relationships."

Here we are concerned with individualized societies (e.g., mammals, birds, other vertebrates; de Waal & Tyack, 2003; also some invertebrates with individual recognition, such as paper wasps). Recruitment by means of communication is well developed, such as by vocalizations, postures, or gestures aimed at specific partners to solicit their support. For example, many primates have specific behaviors to activate supporters to help them in a fight. The decisions to cooperate are guided by previous experiences with the other (e.g., reliability and effectiveness) and its social rank, with high-ranking individuals being superior supporters. On the other hand, a partner of similar low rank is preferred to jointly overthrow the existing hierarchy. Choices are often guided by kinship, but also by mutual benefit and reciprocity, such as when chimpanzees share food with those who have groomed them before, or when fish recruit fish of another species that complements their hunting strategy.

Many of these cooperative situations are mutualistic; i.e., parties gain benefits at the same time. For example, when animals hunt in groups and together bring down large prey they benefit simultaneously. This kind of cooperation requires coordination, communication, and sharing of payoffs, but no altruism or long-term memory except memory of specific individuals and their effectiveness as partners. It also includes monitoring against freeloading.

The second kind of cooperation spreads benefits out over time so that one individual may gain now and his or her partner gains next time, an exchange known as reciprocity (Trivers, 1971). Several proximate mechanisms may produce reciprocity, but our understanding of how it works, and especially how it works outside of the primates, is still very limited. It is unlikely that animal actors know about reciprocity in the sense that they perform helping acts with future return benefits in mind. There are indications that some large-brained species may do so, but the planning of future exchanges is beyond most animals' cognition. This means that helping must have its own autonomous motivation. In humans, the main motivator is assumed to be empathy, which makes one person gain a stake in the other's situation. Without necessarily implying the cognitively advanced forms found in human adults (e.g., theory of mind), the empathy explanation takes as its basis bodily connections, involuntary mimicry, and emotional contagion. These mechanisms have been proposed to underlie helping in other mammals as well, and there are indeed reports on empathy from mice to elephants, and also birds (de Waal, 2008).

Key Questions

Apart from kinship, what determines partner choice in a cooperative context? Is it (a) the effectiveness of the partner on the task at hand, (b) trust based on other experiences with the partner (e.g., affiliation and friendship), (c) the payoff division to be expected (i.e., tolerance, sharing), or (d) fear of retaliation (i.e., punishment for not cooperating)?

Apart from kinship, what determines the tendency to help others in distress or trouble? Empathy is generally thought to be promoted by similarity and familiarity between individuals.

What are the mechanisms underlying reciprocal exchange of favors? Is reciprocity organized along tit-for-tat lines, requiring memory and score-keeping, or are there simpler mechanisms at work, including the generalized reciprocity reported for a few species?

How similar are the proximate mechanisms mediating anonymous and individualized cooperation? Are the differences simply due to differences in the level of resolution of individual recognition?

Suggested Reading

de Waal FBM. Putting the altruism back into altruism: The evolution of empathy. Annual Review of Psychology 2008;59:279-300.

de Waal FBM and Tyack PL. Animal Social Complexity: Intelligence, Culture, and Individualized Societies. Harvard University Press, Cambridge, MA, 2003.

Linksvayer TA and Wade MJ. The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: Maternal effects, sib-social effects, and heterochrony. Quarterly Review of Biology 2005;80:317-336.

Trivers RL. The evolution of reciprocal altruism. Quarterly Review of Biology 1971;46:35-57.

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IDR TEAM SUMMARY—GROUP 3

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IDR Team 3 was asked to determine the proximate mechanisms that give rise to cooperation between individuals. Cooperation is a core component of social evolution, allowing groups to adapt to selective pressures, even though it comes at a cost to altruistic individuals. This phenomenon is evident in all levels of life, from quorum-sensing unicellular bacteria to group-living primates. In 1964, William Hamilton proposed the theory of inclusive fitness, which holds that genetically similar individuals who cooperate indirectly improve the fitness of their group and the likelihood of passing on their shared, identical genes, including those that encode cooperative traits. However, inherited traits are ultimately the *result* of cooperation, rather than the proximate cause.

Primate ethologist and NAKFI Steering Committee member Frans de Waal challenged IDR Team 3 to find the very spark that ignites cooperation. This challenge is not just an exercise in scholarship, but may also provide fresh insights for the fields of behavioral economics, education, and artificial intelligence. Comprised of thought leaders from cellular through evolutionary biology, psychology, and computer science, the members of IDR Team 3 have collectively studied the social behaviors of ants, birds, primates, and simulated populations. By drawing from their collective expertise, IDR Team 3 established the conditions that are required for cooperation and compel organisms to cooperate and determined the *proximate elements* of cooperation. To determine the relative importance of these proximate elements—the cooperative spark—IDR Team 3 next turned to the field of evolutionary robotics, and conceived the Artificial Test-bed for Experimentation into Cooperation and Helping (ATECH).

Evolutionary Robotics: A Very Unnatural Selection

The field of evolutionary robotics grew from a seed first planted by Alan Turing in the 1950s. In *Computing Machinery and Intelligence*, Turing presaged that machines capable of learning and adaptation could not be created by man, but would rather be borne from an evolutionary process subject to mutation and selective reproduction. In the decades to follow, systems biologists developed computational algorithms to model and test evolutionary phenomena as the fields of artificial intelligence and robotics continued to flourish. In the 1990s, international teams of roboticists launched the first experiments in evolutionary robotics.

In an evolutionary robotics arena, robotic genomes are subject to survival of the fittest. In one of the earliest demonstrations, Dario Floreano, a pioneer in evolutionary robotics, challenged contenders to navigate a maze with mutably coded genomes that defined the patterns and activity of their neural networks; these networks in turn dictated the robots' actions in response to sensory input during the challenge. Robots earned a fitness score (f), commensurate with their performance in the maze, so that robots that successfully navigated the maze with few crashes received high f scores, while those that crashed frequently or did not complete the maze received low f scores. Following the challenge, a computer would select the genomes of robots with the highest scores, and pair them for genetic crossover and mutation. The resultant genomes were then used to reprogram the robots as a new generation, in a process that would be reiterated hundreds of times.

Robots quickly evolved beyond maze navigation. In a chess-like battle, miniature predator and prey robots co-evolved hunting and evasion tactics, while robots capable of autonomous design and fabrication adapted brain and structural morphologies to adapt to varied mechanical tasks. In 2006, Floreano joined forces with evolutionary entomologist Laurent Keller to challenge multiple kindred of genetically similar robots to collectively forage and transport food tokens. These robots could boost their individual fitness by foraging and transporting small tokens by themselves, or opt to incur a fitness cost by foregoing this low-hanging fruit and cooperatively moving larger, otherwise immoveable tokens to earn a larger distributed fitness score. Remarkably, Keller and Floreano found that cooperative token movement evolved first and most strongly between the most genetically similar robots. Hamilton's theory of inclusive fitness thus applies to the field of evolutionary robotics, which may provide the ideal means to investigate the proximate mechanisms of cooperation.

Finding the Spark

Before ATECH could be formed, IDR Team 3 established the relevant testing parameters that would give rise to cooperation. IDR Team 3 defined *cooperation* as "interaction that, on average, benefits all participants," which will be manifest in individual robots' fitness scores. In cooperative interaction, continual iterations will produce a benefit greater than the participants could achieve individually, as is the case with collective carrying and food sharing among ants. In simulations and robotics, successful cooperation earns a collective fitness score that is distributed among the group. However, sometimes cheaters come along, draw from the fruits of cooperation, and do not expend any cost of their own, as is the case of a worker ant that forgoes food gathering to attempt mating and egg-laying to the detriment of the colony. Similarly, a "cheating" robot would accumulate group fitness points while leaving its kin to do all of the work; these groups are at risk of losing fitness to competing robot groups. IDR Team 3 hypothesized that the proximate elements below will provide a graded and interactive context for cooperation, whose relative strengths and effects can be directly tested.

Environmental variability. Within homogenous or genetically similar populations, environmental variability places selective pressure and drives specialization of individuals. Within a heterogeneous group in which specialization may already exist, environmental variability may exert demands that surpass the capacity of the individual participants.

Flexible response to cooperation. Faced with a challenge such as predation or limited resources, participants must be able to respond in such a manner as to serve their own interest or help other participants at a cost. Partners must be able to respond to each other's actions and vary their own actions so that the sum effort is not so costly that it precludes collective benefit. In the case of altruism, however, an individual may incur great cost and even death to benefit the group, as is the case of a stinging honeybee that will die shortly after defending its queen and nest.

Communication. In order for participants to cooperate, it is essential that they be able to sense an environmental cue and recognize the cooperative "effort" of the other participants. For example, ant societies, which have evolved the ability to divide labor and collectively solve problems, communicate using pheromones, sound, and touch.

Goal-directed activity. In order for participants to cooperate, they must share a common goal or interact in a manner that is beneficial to achieving each other's goals, even though this goal need not be conscious. Goal-directed behavior occurs when one expends energy or effort toward an end, after which effort ceases (i.e., a feedback loop). Pack hunting by gray wolves is a prime example of this proximate element of cooperation.

Moving forward, IDR Team 3 proposes to manipulate the proximate elements of cooperation as test parameters to determine their impact on simulated and robotic fitness in cooperative challenges including foraging and defense from variably sized and challenging intruders. As ATECH develops and evolves, IDR Team 3 intends to develop predictive models that can be tested on model organisms to predict cooperation in nature.

IDR Team Summary 4

Develop general principles to understand the interplay between individual variation and group function.

CHALLENGE SUMMARY

Individuals in social groups have their own experiences and preferences, but must work together cooperatively in order for the social group to remain cohesive and function optimally. Do these individual differences contribute positively or negatively to the social group? Can individual variation be positive under some circumstances but negative under others? Do individuals retain their preferences and tendencies after joining the group, or does the "group mentality" and social environment override these differences? To address these questions, we must be able to track individuals and their behavioral preferences before and after joining the group, understand the mechanisms that create individual variation, examine the effects of social environment on individual variation, and study the consequences of individual variation for the group. Understanding the role of individual variation in group function will not only provide insights into the proximate mechanisms regulating the function of groups of biological organisms, but can also be applied to develop better functioning computational programs and robotics.

There is considerable evidence that there are relatively stable differences among individuals in the types of behaviors they perform and when they perform these behaviors. Individuals can vary in their response thresholds to certain stimuli; thus, some individuals may respond rapidly to cues presented at low intensities, while other individuals may require prolonged exposure to high intensities of these cues before they respond. Response thresholds to different cues can co-vary, and thus individuals can be categorized into specific "behavioral syndromes" or "personality types," such as bold or shy. This individual variation in behavior can be maintained across environmental conditions or throughout the lifetime of the animal.

The mechanisms underpinning individual variation are not yet fully characterized. Genetic variation among individuals is clearly critical in establishing individual variation in behavior. The environment experienced during development, juvenile and adult stages also shape behavior. Physiological conditions, including the individual's reproductive and nutritional state, can alter behavioral response thresholds. Finally, the experience of the individual—particularly learning and the positive and negative reinforcement received when performing the behavior—can modulate response thresholds. However, the molecular and physiological mechanisms by which these different factors cause changes in behavior, and whether they operate on the same pathways at these different timescales, remains to be determined.

Individual variation appears to play a largely positive role in establishing and maintaining successful social groups. Based on their differing response thresholds, individuals will segregate themselves among different tasks, with certain individuals preferentially performing specific tasks. Partitioning individuals among different tasks (division of labor) can improve the efficiency of task performance and the overall productivity of the group. Several studies have demonstrated the positive impacts of diversity on group performance, in both social insect societies and human groups. However, the optimal amount of diversity in behavioral task preferences, the proportion of individuals performing a given type of behavior, and the type of diversity needed (the ability to perform specific tasks well or the ability to flexibly move between tasks) may vary depending on the type of group, the duration of the group, and the goals of the group.

In contrast, the role of individual variation in collective behaviors has been woefully understudied. In collective behaviors, multiple individuals, regardless of their current activities, spontaneously perform a coordinated behavior, such as migration in locusts or birds, schooling in fish, or applause in audiences. Thus, it appears that the signals to perform the collective behaviors elicit responses from the majority of individuals, though there can still be variation in response thresholds to join the behavior. Furthermore, these collective behaviors can be quite novel, and distinct from any behavior the individual normally exhibits. The collective behavior also appears to generally override individual variation in behavior, such that all individuals perform essentially the same identical behavior. However, response thresholds among individuals must still exist in order to allow the group to form, disperse, and, in some cases, function optimally. In the case of swarms of honeybee colonies seeking a new nest site, there is a distinct group of individuals (scouts) that have more information and coordinate the behaviors of the other individuals.

The challenge to the working group is to develop general principles to understand the interplay between individual variation and group function: is individual variation beneficial or harmful to the functioning of the group and under what circumstances, how much is individual variation subsumed by the social environment, and what are the underlying mechanisms?

The interplay among robots or artificial life units is another area for exploration. Generally speaking the word robot may refer to both physical robots and virtual software agents. Talking to the experts in this field it appears that there is no universal agreement on which machines/devices represent the robots; however, one has the general appreciation that robots could perform tasks including moving around, operating a mechanical limb, sensing and manipulating their environment, and exhibiting intelligent behavior. Particularly, one likes to see behavior that resembles intelligent beings such as humans or other animals. There exists consensus that "robot" signifies an apparatus (machine/device) that can be programmed to perform a variety of physical tasks or actions.

It is perceived that the two distinct ways that robots are different from actual beings are in the arena of cognition and biological features. Regardless of its human-like or dislike appearance robots need programming to function properly. The advent of modern feedback control systems along with advances in computational powers of miniaturized electronics has made modern robots a lot more artificially intelligent. This allows them to perform tasks based on their own sensing of their surroundings and potentially perceived outcomes. This may be performed either by an individual robot or a group (or swarm) of robots. In the swarm scenario, the concept of particle swarm optimization technique could be used to control the movements of the robots. In this manifest the robots rely on their own individual sensing experiences (self-awareness) of the environment and also utilize the collective knowledge (swarm knowledge) of the environment among all of them to guide the robots to move to the desired direction and/or desired outcome, i.e., the dream land! The human-like issues such as jealousy, sympathy, becoming number one, etc., could also be programmed into robots if it becomes necessary in performing the desired tasks more effectively. The field of artificial intelligent is a rapidly growing field and modern electronics and miniaturized mechanical actuators have allowed the robot designers to make their robots amazingly powerful and self-supporting.

Key Questions

How much flexibility does an individual have in varying its behavior? What is the basis of behavioral plasticity and switching strategies in the context of sociality and under what circumstances should this be deterministic or stochastic?

Different factors underpin individual variation (genetic diversity, pre-adult and adult environmental conditions, learning). Do any have a greater impact on behavior? Do these factors operate on similar genes, gene networks, and physiological pathways?

What are the relative roles of genetic diversity, imprinting, and epigenetic mechanisms on regulating long-term differences in behavior?

What is the optimal balance between variation and uniformity is establishing successful social groups? (leaders vs followers, introverts/weakly connected vs extroverts/highly connected, information gatherers vs receivers, generalists and specialists)? Does this balance vary depending on the size of the group, the duration that the group remains together, the goals of the group, and the environmental conditions? For example, is more variation better in unstable environments?

In collective, group-level behaviors (swarming, migration), do individuals have inherent biases to join the group or do the collective behavior and its associated signals simply override any individual behaviors? Once in the group, are there still individual differences? Are pre- and postcollective differences among individuals conserved?

At what point does individual variation prevent integration into the group and have negative fitness consequences? How common is this? Under what conditions does this arise?

Is behavior flexibility more important for long-term versus short-term groups?

How do we measure individual variation and its consequences on groups? How do we model this?

Are robots going to become a complete human?

Are some robots more powerful than the human in some tasks that necessitate multitasking and fast computations?

Could robots perform tasks beyond what is programmed in them?

Reading

Beshers SN and Fewell JH. Models of division of labor in social insects. Annual Review of Entomology 2001;46:413-440.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, and Sih A. Behavioural syndromes and social insects: Personality at multiple levels. Biological Reviews 2014;89(1):48-67.

Jeanson R and Weidenmuller A. Interindividual variability in social insects—proximate causes and ultimate consequences. Biological Reviews 2013;89(3):671-687, doi: 10.1111/brv.12074.

Sih A, Bell AM, Johnson JC, and Ziemba RE. Behavioral syndromes: An integrative overiew. Quarterly Review of Biology 2004;79:241-277.

Webster MM and Ward AJ. Personality and social context. Biological Reviews 2011;86:759-773.

Whitman DW, Agrawal AA. What is phenotypic plasticity and why is it important? In Whitman DW, Ananthakrishnan TN, editors. Phenotypic Plasticity in Insects: Mechanisms and Consequences, pp. 1-63. Science Publishers 2009.

Because of the popularity of this topic, two groups explored this subject. Please be sure to review the other write-up, which immediately follows this one.

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IDR TEAM SUMMARY—GROUP 4A

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Team 4A was asked to generalize the principles governing the interplay between individual variation and group function.

With predictable frequency, humans—a disparate collection of diverse individuals—act collectively, whether it is a round of applause at the end of a show or an undulating "wave" of sports fans cheering at a game. From ants to naked mole rats, assemblages of diverse individuals throughout nature often navigate social environments, producing behaviors best understood on the group level. Studying a single ant in isolation, for instance, yields little insight into an entire ant colony's maintenance regimen, but studying a teeming anthill in action does. Analyzing an individual cancerous cell may not fully reveal what happens on the level of the tumor.

These behaviors sit atop a stratum of diverse individuals that vary in their experiences, preferences, occupations, environments, personalities, and biology. How does individual variation impact group functions, including collective behavior, and vice versa?

Individual Variation and Labor Partitioning

Team 4A began by assessing how individuals vary from one another. Individuals' genes—and how those genes interact with the environment—play an important role in helping to form a person's predispositions. Throughout development, moreover, individuals' social and physical environments affect their life histories by changing sensitivities to various stimuli. And from "viral" content on Twitter to unremarkable singers' improbable ascensions to fame, random effects are also nontrivial, a principle the team pithily dubbed "the Justin Timberlake effect."

In an effort to discuss behavioral variation in groups, conversation centered on what is known about partitioning of labor among social insects. Instead of characterizing divisions of labor as hard and fast, team consensus pointed to a more fluid concept of "task allocation," in which sufficiently plastic individuals can change tasks in order to address a given group's needs. However, there are costs associated with switching tasks and with "doing the wrong thing," so in some groups, individual flexibility is sometimes disadvantageous to the group or organism.

Group Activity versus Group Function

In the pursuit of general principles, Team 4A engaged in spirited debate over what constitutes group "function," in light of the fact that some groups appear to have identifiable, task-oriented purposes, while others do not. In an ant colony, for instance, individuals may behave collectively to defend or maintain a colony, while a school of fishes' coordinated movements decrease individuals' risk of being harmed. While this "function"—the collective accomplishment of a certain task—is intuitive and accessible to human observers, it may not reflect the totality of meaningful group activity, because observers may be biased toward seeing group-wide behaviors as optimal.

There are many evolutionarily stable groups in nature, however, that are far from optimized. Sparrows in groups may display different foraging strategies: Some sparrows actively seek out new food sources, while others simply wait around until new food is found, at which point they make a beeline for it. One can imagine that these different behavioral types generate appreciable group activity, and they do. The group-wide ratio between go-getter and freeloading sparrows remains stable through evolutionary time. However, the sparrows' observed use of available resources vastly differs from the optimal resource use, making it hard to say that the group "functions" in any way other than "poorly." For the purposes of a reliable common language, then, Team 4A considered "group activity."

A Path Toward Generalizing: Individual, Network, and Environment

The team hypothesized that variations in group-level activity depend upon the interplay among three different entities: the individual, the social network, and the external environment in which the individuals and networks reside. To understand schools of fish, then, one must understand how individual fish can act, how a school of fish is structured through time, and how both are situated within a body of water full of resources and threats.

Individuals' response thresholds for various stimuli—from both the social network and the nonsocial environment—depend upon the interplay between an individual's genetic predispositions and how they interact with the individual's world. Factors like epigenetic modification and learning allow this interplay to be embodied by the individual through development, leading to an individual having various response thresholds for various stimuli at a given time.

Not only is the individual's experience cumulative, but past experiences and the changes they imbue can also influence present behavior. Neglect of a child, for example, not only may affect a child's physical and psychological health in the short term, but its lasting effect may also influence the child's future behaviors and decisions. On the other hand, some children seem to be remarkably resilient. The explanation for this is open to more research.

As the preceding example suggests, differing interactions within social networks also introduce an important source of individual variation. An example from the microbial world is also illustrative. In a system in which individuals are largely identical at time zero—a clonal population of bacteria with managed microenvironments, for instance—the distribution of those microbes within networks creates differences in access to information, exposing the microbes to varying kinds and strengths of stimuli.

Social networks' structural features, dependent on individuals' ways of sensing one another, also play an important role in how individuals impact one another. Ants primarily communicate by "smelling" one another's chemical secretions, which can persist in the environment for a considerable amount of time. A scout ant, for example, can lay down a chemical trail that leads to a food source it discovers, allowing other ants in the colony to visit the food source in the future. Schooling fish, on the other hand, rely on less persistent cues—vision and pressure waves in the water—to detect other fish in the school. These different ways of signaling among individuals likely contribute to fundamental differences in how schooling fish and ant colonies can organize themselves.

Network Features That Impact the Effect of Individual Variation

Within this conceptual framework, the team discussed how features of network structure may influence individual variation's effects on group activity. The team focused on three prominent, intuitive features of networks: group size, network connectivity, and fluidity. *Group size* is the number of individuals in the group in question. *Network connectivity* is the number and distribution of connections per node—in other words, the diversity of ways that an individual can exist and connect to other individuals within a network. *Fluidity* is how much and how rapidly an individual's place within a network can change through time.

Multicellular tissues and biofilms, for instance, exhibit complex dynamics—a result of individuals' varying response thresholds and diverse environmental stimuli—but these systems network structures are fairly static and grid-like. An individual heart cell, for instance, cannot appreciably change its place within a network composed of its fellow cells, locked into place next to its neighbors by packing and the extracellular matrix. The packing geometry, moreover, places limits on the possible number of neighbors a cell or bacterium can have: heart cells have anywhere from two to ten neighbors, simply based on how they can fit together. These systems display low fluidity and low network connectivity, as the team defined them.

Other systems studied by team members seemed to fit along the continuum of increasing network connectivity and increasing fluidity. At any given moment in time, a school of fish appears fairly grid-like, and packing geometry places limits on the number of neighbors a given fish can have in the network. However, in contrast to heart cells, schools of fish are highly fluid, with individual fish moving within the school with ease. Social insects like ants display even higher measures of fluidity within their networks while also displaying massive increases in network connectivity, introducing greater structural diversity—and greater randomness—within the network. Similarly, human online networks also display high connectivity and high fluidity. Wikipedia, for instance, enables individuals to create and modify a mind-bogglingly large number of articles, and the types of contributions an individual can make vary widely with respect to content. Within this context, the team then asked how much an individual's variation matters in affecting group activity, hypothesizing that individual variation matters less with increases in group size, network connectivity, and fluidity. A small group of cardiac cells, for instance, will be more affected by a given individual's response to a stimulus than a massive ant colony would be. The greater stochasticity inherent in larger, more interconnected, and more temporally fluid systems may introduce more noise to the system, rendering any one individual's response less important.

Conclusions and Future Directions

Developing general principles for how diverse individuals generate group activity affords greater insight into how complex systems function at all scales, whether they are tumors composed of individual cells or online communities abuzz with millions of people. Greater understanding of these systems not only empowers researchers to develop better medical treatments and social institutions, but new insights also could lead to vast improvements in the function of robots and other systems of artificial intelligence.

The team's discussions point toward a unifying conceptual framework for assessing changes in group activity, recognizing the importance of how individuals vary, how these individuals are situated within networks, and how the external environment affects both individuals and networks. New experimental approaches could employ changes to any of these three components—alterations in individuals' response thresholds by genetic manipulation, for example—in order to observe changes of group activity. The team also considers this framework ripe for new computational modeling of group dynamics.

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IDR TEAM SUMMARY—GROUP 4B

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Develop general principles to understand the interplay between individual variation and group function.

In collective behavior, the combined actions of the members of a group yield outcomes that differ from the sum of those same individuals acting alone—sometimes in desirable or dramatic ways. Seething populations of bacteria in biofilms jointly produce chemicals that allow them to survive in challenging environments. Colonies of bees, ants, or other social insects gather and store valuable food stores through coordinated foraging efforts. Understanding the hidden mechanics of collective behavior that enable these and other groups to function could suggest solutions to current societal challenges: What is the best way to assemble and manage a committee or a team? Could many small robotic devices be designed to work together, in a "swarm," to perform complicated tasks in disaster sites or dangerous environments?

One intriguing aspect of the examples of successful groups given above is how much they differ in their composition. Some groups, including communities of bacteria or body tissues comprising somatic cells, are made up of nearly identical individuals. The members of other groups, such as colonies of bees or ants, packs of wolves, or primate societies, may vary greatly in their physical traits, personality, genetic background, motivations, or other characteristics. If both groups with low variation and groups with high variation can successfully function, does this variation matter? What are its costs and benefits to collective behaviors, and do these change depending on the environment, or the task being performed?

A clearer understanding how individual variation among a group's members affects the collective behavior of that group could lead to better management and conservation of group-living species, and the better design of teams, whether of humans or machines. IDR Team 4B's goal was to hypothesize general principles for how individual variation affects group function.

Generalizable Terms for Addressing the Challenge

IDR Team 4B considered a broad range of examples of collective behavior, including both groups of living organisms and groups of robots. To come up with principles of group function that were generalizable across all cases, the team focused on the most basic elements of collective behavior:

Individual variation is the degree to which individual members of a group vary in their performance of a behavior. For example, in some species of ants, individuals within a colony vary greatly in size; size, in turn, affects an ant's ability to carry food or fight predators.

Level of interactions within a group describes how much influence the behavior each member of a group has on the behavior of other members. Interactions might occur through intentional communication, such as meerkats responding to a neighbor's alarm call, or, like birds in a flock following those in front of them, through passive signaling.

Group function is a collective behavior of a group with some measurable outcome. That outcome is expected to depend on the two terms defined above: individual variation among group members, and the level of interactions between those members.

In other words, individuals have preferences or rules for how they will behave in isolation; individuals forming a group have the opportunity to interact and influence the behaviors of other members. The combination of individual preferences and interactions between individuals will determine how the group behaves.

Considering the Simplest Case

To form hypotheses for the effect of individual variation on group function, IDR Team 4B considered a simplified case, in which the group behavior could be quantified by averaging the behavior of the group's members. In this simple case, many factors, including the effect of the environment on group members, the ability of group members to change the environment, and past experiences of individuals, are all ignored. One hypothetical example is the movement of a school of fish within an otherwise empty pool of water. The movement of the school could be measured by averaging together the movement of all the fish.

Based on the framework suggested by IDR Team 4B, changes in individual variation (differences in velocity of the individual fish), level of interactions (how much the fish influence each other's velocity), or both of these factors are expected to influence group function (how the school moves). The team proposed two hypotheses. First, *a group with no individual variation and no interactions may produce an output that is indistinguishable from a group with high individual variation and a high level of interactions.*

Consider a school of clone fish, in which each individual behaves according to the same set of rules. The fish will all go in the same direction and maintain a cohesive school. In a second school, each fish in isolation would have a unique set of rules for generating its movement, but interactions ensure that when in the school, the fish maintain a certain distance from each other. This group of "well-connected" fish will maintain a cohesive school indistinguishable from the first group of identical fish, even though the mechanisms that produced this result are very different.

Considering the dynamics of the well-connected school suggested a second hypothesis: *Increased individual variation requires an increased level of interactions to maintain group cohesion.* Without some type of interaction to coordinate behavior, the fish in the "well-connected" school would scatter as each followed its individual swimming preferences, and the school would dissolve. Individual variation can disrupt the stability of the group, while interactions can preserve stability.

These hypotheses, if tested, could produce useful guidelines for improving the way that groups of humans, animals, or machines work together. Hypothesis 1, for example, suggests that an engineer who is programming robots that must work together to perform a task could choose between two design options: simple, identical machines that cannot interact, or more complicated machines with a variety of abilities that coordinate their behaviors with each other. In most cases, though, there is not a simple relationship between the behavior of each individual within the group and the resulting collective behavior.

Introducing Complexity of Group Function

In real examples of collective behavior, many complex factors affect the behavior of group members and influence group function. The environment in which the group acts may be temporally dynamic or unpredictable, and may be altered by the behavior of group members. Size, organization or other properties of the group may change over time. The result of collective behavior might also be very complex; building a termite mound, for example, is not easy to break down into the behavior of many individual group members.

The team considered the impacts of these sources of complexity on the relationship between individual variation in behavior and group function, and proposed a third hypothesis: *In group functions with greater complexity, increased individual variation can increase the likelihood that at least one member of the group possesses behavioral rules needed to perform that function.* Combining this new hypothesis with hypothesis 2 predicts that in complex situations, just as in the simplified example, an increased level of interactions must accompany increased individual variation to maintain group cohesion. For example, if one honeybee in a colony is able to find a new flower patch, the bee cannot bring all of the nectar in that patch back to the hive by itself. However, interactions with other bees allow the information to be shared with and used by many other bees in the colony.

Pareto optimality theory, a concept from economics, has been used to describe a situation in which not all aspects of a behavior or a task can be optimized simultaneously. Pareto optimality was proposed by the team as a way to formalize predictions about specific systems in which groups engage in complex functions under various environments. In this framework, sources of complexity are modeled as constraints that limit what the group can do. The group must divide up its resources or abilities to satisfy these constraints.

In some cases, the trade-off between multiple constraints is weak—it is easy to partially satisfy multiple constraints simultaneously. In this situation, a generalist strategy, being a "jack of all trades," is most efficient. A group that consisted of identical generalists could do well in highly variable environments or in situations with a relatively low level of interaction. If a generalist encounters a task, it may complete it without much coordination from members of its group.

When the trade-off between constraints is strong—satisfying one constraint creates a big loss in the ability to satisfy another constraint—a generalist strategy is less efficient than a specialist strategy. The best strategy then is to invest only in maximizing the ability to satisfy one constraint. In this situation, a group with high individual variation and a high level of interaction to ensure that the group acts together could have the advantages of a generalist strategy (as it is able to satisfy multiple constraints through the individual strengths of its members), while escaping some of the costs (each individual within the group is still a specialist).

Conclusions

The hypotheses and framework proposed by IDR Team 4B can be used in the future to create predictions about the role of individual variation and interactions in specific examples of collective behavior. They provide a starting point for organizing ideas or data related to group function.

Understanding and predicting the impact of individual variation on group function is important for research efforts in both natural and human-designed systems. Ecologists and conservationists could use these theoretical tools to engineer environments that promote variation in populations of threatened species, helping those populations to survive and grow. Robots that will perform complex group functions could be designed in a more systematic way. This framework could even enable the construction of a more robust and peaceful human society, one in which better communication is used to reduce conflict and misunderstanding, and to allow us to take advantage of our great diversity of strengths and ideas.

IDR Team Summary 5

How do we solve the tragedy of the commons?

Challenge Summary

The challenge to this group is to develop a model of the tragedy of the commons that applies to a broad range of dwindling resources in different cultural and environment contexts and suggest a range of social or institutional solutions to the problem specifying the conditions under which they are likely to be effective. What do we know about potential solutions from various disciplines and what are their limitations? What problems have yet to be solved and how would we go about understanding them (i.e., what additional research needs to be done)?

A variety of factors have been identified as important to understand in the context of common pool dilemmas, including the nature of the resource, the effectiveness of incentives in altering behavior (either rewards for constraint or punishment for exploitation), strategic behavior, size of the community affected, networks and norms, the culture of the group, etc. Thorough consideration of the conditions under which these factors matter, when and how they might be linked, and which ones are the most critical when considering solutions to common resource problems should provide new insights and policy prescriptions. Given the range of domains in which these problems arise some comparative assessment would also be useful. How do solutions under consideration for renewable and nonrenewable resources differ? When do specific solutions to common pool problems generalize across types of resource? Examples include clean air, fish, coal, oil, water, etc. What are the limits to our knowledge in these domains about what works and what does not work? What do we know about social behavior in these contexts and how it can be modified to contribute to solutions?

Despite over three decades of work on this general topic there are still many unanswered questions about common pool resource dilemmas. Ostrom and her colleagues (e.g., 1990) and others have documented various institutional solutions to the problems involved but no general conclusions have yet been reached about the specific conditions under which various solutions emerge or how they are sustained over time. These solutions range from self-organizing efforts to coordinate activities that provide constraints on resource use to more institutionalized efforts in which those involved give over some autonomy to an authority or policing agent who manages the resource pool and monitors behavior to promote the collective good. In these situations individual self-interest conflicts with the good of the collective in restraining use of the resource that might lead to overuse and depletion of the resource over time.

Why not solved yet? There are general game theoretic models of the underlying collective action problem and empirical research in particular domains of what solutions have emerged in specific cultures to address the problem of the provision of a common good (or common pool resource). However, it does not appear that anyone has attempted to bring this work together across domains to see what we know about general solutions to these problems under specific conditions. An effort to synthesize this work across disciplines is timely and may have important implications for work on climate change and other environmental issues. One reason this has not yet been done seems to be that the work is located in disparate places and disciplines.

Key Questions

What is the current state of the theoretical work on the tragedy of the commons?

What do we know from empirical research about what solutions work in which domains where (which cultures)?

What specific conditions lead to resolution of the problem when? How are they sustained over time?

Reading

Axelrod R and Dawkins R. The Evolution of Cooperation. Basic Books: New York, 1984.

Hardin G. The tragedy of the commons. Science 1968;162(3859):1243-1248.

Hardin G and Baden J, eds. Managing the Commons. WH Freeman, San Francisco, 1977.

Ostrom E. How types of goods and property rights jointly affect collective action. Journal of Theoretical Politics 2003;15(3):239-270.

Ostrom E. Governing the Commons: The Evolution of Institutions for Collective Action. Cambridge University Press: Cambridge, U.K., 1990.

Thompson, Jr. BH. Tragically difficult: The obstacles to governing the commons. Environmental Law 2000;30:241-278.

Strassmann JE and Queller DC. Privatization and property in biology. Journal of Animal Behavior 2014.

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IDR TEAM SUMMARY—GROUP 5

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IDR Team 5 was asked to solve the question of the tragedy of the commons, which refers to the eventual exploitation of a common good because each individual is looking out for his or her own interest. This phenomenon has wide-reaching, often global, implications on resources such as fisheries, agriculture, and fresh water. The idea was popularized by Garett Hardin in 1968. Hardin noted that the tragedy of the commons is a problem with "no technical solution." Instead, he suggests that human morality must be collectively changed, so that maximizing individual rewards are not prioritized over the well-being of the group. Tragedy of the commons has been widely discussed since Hardin put forth the concept. Some institutional solutions have been proposed, notably by American political economist

Elinor Ostrom, but the sustainability and emergence of such solutions is poorly understood.

The example that Hardin used to illustrate the tragedy of the commons is livestock grazing on a shared pasture. To maximize profits, each farmer will graze as much livestock as possible, depleting the resource. The system "collapses" because the resource is exhausted to the point where nobody can benefit. Hardin's example became one of many used to describe tragedy of the commons. In fact, the phenomenon has primarily been described in terms of examples, often specific to a particular field. A unifying definition of the tragedy of the commons that is generally accepted across disciplines has not yet been developed. In keeping with the goal of the conference, which was to study collective behavior, the IDR team proposed that identifying the idiosyncrasies of different disciplines would be the first step toward understanding the conditions under which tragedy of the commons occurs and proposing methods for preventing collapse.

Defining Tragedy of the Commons

To first reach an initial understanding of tragedy of the commons, the IDR team came up with a "T-shirt slogan" that captures the issue in lay terms: "We can do better without hurting anybody, (and yet we don't)." Essentially, what this means is that tragedy of the commons may happen only if short-term individual goals are at odds with the ultimate goal of the collective or common good. While we could all collectively be better off by cooperating, we choose not to cooperate because we, as individuals, would not receive the maximum payoff that is possible through acting selfishly. Unbridled self-interest may benefit individuals in the short term, but it will lead to unfavorable results in the end. In addition, some economies, especially capitalism, incentivize such self-interest.

The IDR team cited a number of examples to illustrate how tragedy of the commons is represented across a number of fields, one such example being antibiotic resistance. Motivated by their own self-interest, in this case health, individuals may take antibiotics prescribed by a doctor or farmers may use antibiotics in their livestock, which are eventually consumed by people. Over time, this increases the chance that bacteria that are resistant to the antibiotics survive and proliferate, creating a new generation of antibiotic-resistant bacteria. The antibiotic that was once useful in keeping the individual healthy is no longer useful to the population as a whole.

Tragedy occurs when nobody benefits from antibiotics any longer, and the population is faced with diseases it cannot treat.

The IDR team also considered the tragedy of the commons in the context of economic theories. The group explored the relationship of the tragedy of the commons to Pareto's optimum, in which no participant can maximize its interests without hurting someone else, and Nash Equilibrium, in which individuals do not benefit from changing their strategy. Attempting to reach Nash equilibrium with the current payoff matrix does not favor cooperation. To combat this, the IDR team said, a new system in which there is a collective agreement to cooperate must be in place.

Tragedy, Collapse, and Resilience

A distinction that the IDR team agreed is important to make is between tragedy of the commons, collapse of the commons, and resilience of the commons. Collapse of the commons, the IDR team determined, refers to the complete depletion or destruction of a resource, whereas tragedy of the commons, as described by Garrett Hardin, is the process that may ultimately lead to collapse. In contrast, resilience refers to the increasing value (including economic or psychological value) of the commons over time. Optimistically, the IDR team took the stance that "tragedy is not destiny," meaning that we can redirect a path from tragedy to resilience, as shown in Figure 1. The IDR team noted than understanding factors that influence this redirection could potentially allow us to understand how to prevent collapse and perhaps turn tragedy into resilience.

Determining the Variables that Affect Tragedy of the Commons

Because tragedy of the commons has largely been defined through examples, the IDR team turned their attention to identifying the variables that lead to tragedy of the commons and the influence of each variable on the outcome of sharing commons. Identifying these variables, the IDR team said, would contribute to better cross-disciplinary understanding of tragedy of the commons. The factors the IDR team came up with are seen at both the individual and collective levels. The IDR team described eight main categories (resource demand, resource supply, scale, time, uncertainty, heterogeneity, implementation, and interactions/institutions). Hypothetically, many of these variables could be summarized in a mathematical equation, but it would need to be determined how influential each of these factors is.

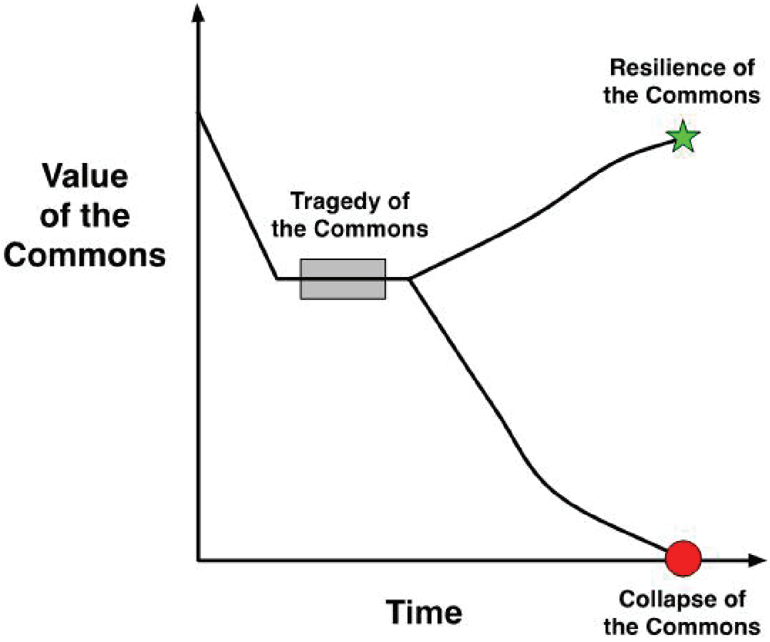

FIGURE 1 Tragedy of the commons can lead to either resilience of the commons or collapse of the commons depending on how the value of the commons changes over time.

Individual Variables

While tragedy of the commons cannot be solved at the individual level, the IDR team mentioned that the effects of tragedy of the commons can be seen in the individual and individuals can take steps toward a solution. The IDR team said that a shifting memory scale among generations may contribute to the tragedy. What this means is that though resources are being depleted, an individual grows up with this issue, becomes used to current conditions, and does not realize what was lost. While the resources become progressively depleted, individual attitudes do not change within a generation. In addition, the team mentioned that education or marketing of behaviors that promote commons resilience may influence individual actions. The IDR team referenced systems that allow people to see their water consumption throughout the day. Given this information consumers can determine what activities are using too much water and adjust their habits accordingly.

Collective Variables

The IDR team also recognized the importance of interactions among individuals in solving matters that create a tragedy of the commons. In particular, the group focused on trust in human systems (institutional trust, trust among relatives, etc.) and repeated interactions among individuals. The group believed that these two factors, which are not necessarily independent, play a vital role in motivating individuals to act in the interest of the collective rather than the individual. For example, a rancher may not want to overgraze a shared pasture if he or she knows and trusts the individuals sharing this pasture.

On a larger scale, the team noted that certain institutional changes might be effective in solving the tragedy. One such solution is the idea of using financial disincentives to prevent overconsumption. If the cost of depleting resources is prohibitive, to the point that the cost of using the resource outweighs the benefits, individuals will be less likely to deplete the resource to the point of collapse.

Understanding Tragedy of the Commons Across Disciplines

A central question present through IDR Team 5's discussion was how the concept of tragedy of the commons is represented across disciplines and how the variables that the IDR team came up with are assessed in the literature of those disciplines. The IDR team recognized that there are a number of these variables that will vary conceptually across fields. Perhaps a particular variable is irrelevant to a certain field. IDR Team 5 discussed the need to understand if these gaps are purposeful or if they show potential for further study. This would ultimately bring the scientific community a step further to understanding how variables within tragedy of the commons are weighted and if a unifying mathematical definition can be achieved.

The Next Step

IDR Team 5 conducted a preliminary literature search via Web of Science, looking at the distribution of the citation of the Hardin (1968) article, which the group considered the latest highly cited iteration of the concept, across fields. As would be expected, the search showed that some fields, such as environmental law, were citing this concept more frequently than others, such as criminology. This also illustrates the diversity of the conversation on tragedy of the commons and the need to bridge these gaps. The IDR team plans to publish a commentary to address these gaps and stimulate dialogue among the fields. The intention is that this commentary will bring interdisciplinary collaboration, as seen in NAKFI, to the rest of the scientific community to collectively address and solve tragedy of the commons.

IDR Team Summary 6

Are there fundamental principles underlying the transition from one to two individuals? Are these scalable to larger social groups?

CHALLENGE SUMMARY

The smallest group has just two members. These two members may be genetically the same, as would be the case if the group is made up of two attached yeast cells that failed to separate, or they may be genetically different as is the case of two parents collaborating to rear their young. Though a group of two is small, the behavior, physiology, and environment of the two social individuals can differ dramatically from the single, isolated individual. Furthermore, the group of two individuals can take advantage of new opportunities or experience different consequences. Two can be double the size of one, perhaps making them much less likely to be predated. Two can guard a resource 100% of the time. Two can specialize, perhaps one guarding more while the other forages more. Two can also compete over resources.

If we want to understand the fundamental principles and mechanisms underlying collective action, an excellent place to start is with groups of just two, for several reasons. (1) Such groups are likely to be simple, yet the effects of doubling the number of members will be great, much more than adding an individual to a group of 20, for example. (2) Groups of two are found across the tree of life, from microbes to insects to vertebrates, making it interesting to explore similarities and differences among different kinds of pairs. (3) Sexual reproduction combined with parental care creates a group of two parents, and the dynamics between these two individuals and their offspring can have great ramifications for fitness. (4) Groups of two are common at various stages of social bee and wasp colonies, presenting an ideal experimental framework to understand how interactions between two individuals can scale to a larger social groups. (5) Groups of two can be fraternal, made up of genetically related individuals, or egalitarian, made up of genetically unrelated individuals, allowing a comprehensive understanding of the possible factors facilitating social behavior. (6) Processes important in evolving groups of two are likely to be important in larger groups and much more apparent.

Key Questions

What are the costs and benefits of groups of two compared to singletons?

What are the pressures on groups of two making them drop to one, or increase to three or more?

Do groups necessarily grow from one to two, or can they grow from one to many, and what are the consequences?

How is conflict controlled in groups of two?

What is the impact of group stability and duration on the nature of the group?

How are groups of two distributed phylogenetically? What can we learn from these patterns?

How do fraternal and egalitarian groups of two differ in costs and benefits?

What can we learn from microbial groups of two of relevance to animal parents?

Reading

Brand N and Chapuisat M. Impact of helpers on colony productivity in a primitively eusocial bee. Behavioral Ecology and Sociobiology 2014;68:291-298.

Cockburn A. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B: Biological Sciences 2006;273:1375-1383.

Field J, Shreeves G, Sumner S, and Casiraghi M. Insurance-based advantage to helpers in a tropical hover wasp. Nature 2000;404:869-871.

Hogendoorn K and Velthuis HH. The sociality of *Xylocopa pubescens*: Does a helper really help? Behavioral Ecology and Sociobiology 1993;32:247-257.

McLanahan S, Tach L, and Schneider D. The causal effects of father absence. Annual Review of Sociology 2013;39:399-427.

Ratcliff WC, Denison RF, Borrello M, and Travisano M. Experimental evolution of multicellularity. Proceedings of the National Academy of Sciences of the United States of America 2012;109:1595-1600.

Stevens MI, Hogendoorn K, and Schwarz MP. Evolution of sociality by natural selection on variances in reproductive fitness: Evidence from a social bee. BMC Evolutionary Biology 2007;7:153.

Wong JW, Meunier J, and Koelliker M. 2013. The evolution of parental care in insects: The roles of ecology, life history and the social environment. Ecological Entomology 2013;38(2):123-137.

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IDR TEAM SUMMARY—GROUP 6

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IDR Team 6 was asked to probe the fundamental principles of the simplest group, that of two individuals.

The Challenge of Group Formation

Groups pass through phases of formation, growth, decline, and dissolution. They also change through the type and number of interactions among members. Rejuvenated or worn down by these alterations, the group can press on or drift into obscurity based on the health, number, and type of interactions that flow among group members.

One approach to understand group formation is to distill groups to their constituent components to draw out the basic principles of their interactions. This is an attractive approach given that the complexity of groups, in size and the nature of interactions, can strain resources to study them. Models of group behavior struggle to explain how groups form and change, or are too vague to have real-world applicability. Field observations lack the robust data measurements needed to capture the complete picture of group evolution. One reason for these difficulties is the lack of guiding principles of group formation, maintenance, and dissolution, especially the most fundamental steps that seed the group and root its purpose.

The simplest group consists of just two individuals, a dyad. Its formation is both fundamental and minimalist. There are only two members to form pairwise interactions and respond to the external environment. If common principles underlie the formation of the group of two, then the dyad forms the foundation of all group structures and could be a common framework to understand both group behavior and history.

With the importance of this undertaking in mind, IDR Team 6 confronted this challenge through two fundamental questions:

Are there fundamental principles in the formation, maintenance, and dissolution of a group of two?

What role does the group of two play in the formation, maintenance, or dissolution of larger groups?

One Plus One

The group of two permeates nature, from hydrogen gas to binary stars. The simplest definition of the group is two individuals joined or bonded by an interaction. But, in their deliberations, IDR Team 6 members quickly concluded that there is little else that universally links all groups of two. The examples from nature, history, sociology, and psychology are too varied in composition and interactions to draw more comprehensive conclusions or divine general principles for the formation of groups of two.

But, the examples the IDR team explored did illustrate how consideration of groups of two could be useful for understanding many different aspects of group formation, maintenance, growth, evolution, and dissolution. Team members believe their discussions will be most useful for future cross-disciplinary collaborations and investigations into group activity or collective behavior.

The Problem of Scale

The largest hurdle IDR Team 6 encountered in their deliberations centered on the fundamental principles of the group of two, or dyad. Armed with examples of dyads from across the natural world, from protein dimers to merging corporations, they readily identified qualities of different dyads and instances where some dyads shared characteristics, such as the chemical bond interactions between atoms or molecules, or social interactions among animals. But, no other commonality permeated all groups of two.

This difficulty centers on the issue of scale. Identity as a group or individual can vary depending on the observer's scale. Two genes can form pairwise interactions as a simple group. These genetic interactions can combine with other genes and environmental factors to form a more complex genetic network. This complex group, with a myriad of members and interactions, in turn defines a new level of individual, the living cell. Living cells can form new interactions and complex groups, forming a person. People interact to form societies, and so on. Each level is defined by a collection of individuals, each of whom is made of the complex group from the previous level. The only unifying principle for the dyads at each level is the involvement of two individuals, be they genes, cells, people, or societies.

Mergers

A group of two may revert to an individual identity rather than a cooperative dyad. Corporate mergers are an obvious example at a societal level. But, even the fragmentation of large corporations can eventually lead to the reformation of the original corporation. AT&T, for example, was recently reconstituted into a single corporate identity from the merger, acquisition, and absorption of smaller companies that had previously broken off from the telecoms giant. In Protestant Christianity, some denominations fragmented and later merged again in response to internal and external factors. Sexual reproduction is also a type of merger in which egg and sperm unite to form a single zygote, a new and novel individual.

Mergers are an important issue to understand in medicine. In organ transplantation, the donor tissue must be successfully integrated into the recipient's body without rejection. In autoimmune disease, the immune system no longer recognizes a specific cell type or tissue as a part of the whole body. An ideal treatment would merge the two parts into an individual identity.

The Dyad

In their discussions, IDR Team 6 members emphasized a distinction between collective behavior and cooperation when it applies to the group of two. The collective behavior of groups centers on the acquisition of a new function or role that is absent among the individuals. Cooperative activity, in contrast, is the sharing of tasks or roles among members of a group.

Biology is replete with dyads that demonstrate cooperative properties. Many aspects of parental behavior in animals involve cooperative behavior, where one parent might guard a nest while the other searches for food. But, cooperation can even exist on smaller scales, such as gene duplication. One homolog might assume a greater share of the ancestral gene function, while the other might take on a different function through mutation or regulatory changes.

IDR Team 6 members were less clear on whether the dyads always demonstrate cooperative behavior, and whether they take on any truly collective behaviors. Collective behaviors could include coordinated endeavors such as synchronization or a more generalized output such as mass hysteria. Either way, pairwise interactions can form the basis of later collective behaviors in larger groups, but it is unclear whether the dyad itself can exhibit these behaviors alone.

The dyad can also include unique evolutionary processes in which both members are changed irrevocably by selection pressures. In a "red queen" evolutionary arms race between a pathogen and a host, strong selection can ensure that both members of the group change dramatically through mutation accumulation as each tries to outmaneuver the offensive and defensive strategies of the other. In a whole-genome duplication event, evolutionary forces can act differentially on the homologous copies, yielding genetic and epigenetic divergence.

Dyads can also take on roles that are greater than the sum of interactions between the two individuals. These synergistic groupings include positive epistasis between two genes, drafting in migrating birds, and receptor-ligand binding in cell-cell interactions.

The Role of Two in Larger Group Formation

IDR Team 6 then took on the role that dyads play in the formation of larger groups and more complex networks. Many large groups, especially in cellular biology, are constructed from dyads. For example, the cytoskeleton, which plays indispensible roles in cell structure, transportation, and division, consists of polymers of protein dimers. Theoretical models of group formation indicate that the group of two can serve as a fundamental building block for constructing more complex and larger groups, but with a less structured network topology than trios.

Larger groups exhibit unique patterns that may reflect a common framework for formation and growth. For example, many large groups show a skewed distribution of sizes. Cities tend to be very large or small, with fewer mid-sized communities. Many other group phenomena, from chromosome sizes to journal citation patterns, also exhibit this "power-law" distribution pattern. Some theoretical models of group formation and game theories posit that pairwise interactions may underlie this skewed distribution of group size. But in general, data to support these models are lacking.

Technological and Experimental Gaps

IDR Team 6 members think there are now sufficient tools to track and manipulate group formation and response to ask whether the dyad is a common building block for larger complex groups. Tracking software can now measure position, speed, and coordination among group members, often on an automated basis. These tools have already been used to measure complex groups such as schools of fish and the myriad of interactions among dancers. Optogenetic techniques can manipulate nerve activity in model organisms such as fruit flies, allowing experimenters to isolate the neural and muscular responses necessary for collective behaviors. *In vitro* viral capsid and cytoskeletal assembly assays can measure assembly and disassembly of complex biochemical groups from their building blocks. Repeated and robust experiments with these new tools should reveal the fundamental building blocks of more complex groups at a variety of scales, potentially boosting the importance of the dyad in group formation and maintenance.

Implications for Group Formation

Groups of two are ubiquitous and enigmatic. They are also the gateway to understand the basic interactions among individuals in groups of all sizes, and potentially the building block of large and complex networks. The dyad in all of its iterations may aid in understanding how deleterious groups, from cancer to terrorist cells, form and thrive, adding urgency to this quest.

Recent advances in technological and experimental tools are the key to advancing group studies beyond abstract models and theories. The collective behavior field will soon be in a position to collect data that could address many of the IDR team's outstanding questions and concerns. The group of two is not as simple as 1+1=2, but its complexity is also not too far out of our reach.

IDR Team Summary 7

Evaluate the degree to which cooperation and conflict need to be balanced in order to facilitate the evolution, expansion, optimal performance, and maintenance of collective behaviors.

CHALLENGE SUMMARY

The major transitions in evolution (from molecules to cells, from prokaryotes to eukaryotes, from cells to organisms, from individuals to eusocial groups) as well as the formation of collective groups from independent units (human groups, migrating locusts, biofilms) required a reduction in conflict among formerly independent entities and an increase in cooperative interactions. Indeed, in many of the major transitions, the individual subunit loses its ability to function and survive outside of the cooperative body. However, it is clear that conflict remains, indicating that its suppression is not absolute. For example, there is evidence for conflict within cells (e.g., selfish genes, or between maternally and paternally inherited genes), among cells within an organism (e.g., cancerous cells), and among individuals in a group, even in eusocial groups (e.g., dominant reproductive and subordinate nonreproductive individuals).

Why does this conflict remain? Is it simply that the conflict is at low enough levels that it can import some selective advantage to the individual without negatively impacting the group? Does conflict arise only when "mistakes" are made, such as mutations in cancer cells that lead to unregulated growth? Or are there any scenarios in which conflict among individual subunits actually imparts some benefit to the group? Perhaps the ability to compete provides a certain degree of flexibility among individual subunits in the group, allowing individuals to assume different roles as needed and maximize the benefits of division of labor. Additionally, competition and conflict among group members may serve to ensure that cooperative behavior continues to provide a selective advantage. Competition is common with various species, including humans, and is even fostered within certain social organizations to promote productivity. Would scenarios in which conflict is advantageous only be possible at certain transitions, such as from individual to collective groups, but not among genes in a chromosome?

While most studies have focused on the factors that facilitate the evolution of social behavior from solitary behavior, the reverse is also possible and may be relatively frequent. Indeed, phylogenetic studies of eusocial evolution in bees have demonstrated that multiple lineages switched from eusocial to solitary behavior, or from eusocial to parasitic lifestyles. Thus, there appears be a great deal of flexibility, including reversibility, along the path from solitary to collective behaviors. What causes these reversals? It is simply an imbalance between conflict and cooperation within these lineages? If so, what causes these imbalances? In collective groups that form and dissipate more readily, are there dynamic changes in the levels of cooperation and conflict that mediate formation, maintenance, and breakdown of the group?

The challenge to the working group is to evaluate the degree to which cooperation and conflict need to be balanced in order to facilitate the evolution, expansion, optimal performance, and maintenance of collective behaviors. How does this balance vary depending on the nature of the units involved (e.g., cells, animals, and humans)?

Key Questions

Is it absolutely necessary for cooperation to be maximized and conflict minimized in order for collective behaviors to evolve? Or can high levels of cooperation support high levels of conflict?

Does the presence of conflict among individual subunits within a collective provide any selective advantage to the group, or is it always negative? Does it vary by species or units of analysis? How?

Is the same balance between cooperation and conflict required to facilitate the evolution, expansion, optimal performance, and maintenance of collective behaviors, or can/should this balance vary among these different stages?

Fraternal major transitions allow the cooperative benefits to flow to relatives while egalitarian ones necessarily must benefit directly. What are the ramifications of these differences? How does one inform the other?

What balance between cooperation and conflict is needed in order for collectives to reach the point of "no-return," where reversion of the individual subunits to independent life is impossible?

What conditions facilitate the evolution of solitary behavior from social behavior?

What factors increase the level of cooperation among individuals in a group? Kinship is thought to be a major driver of social evolution, but some of the major transitions (molecules to cells, prokaryotes to eukaryotes) were likely not facilitated by kinship.

Reading

Danforth BN, Cardinal S, Praz C, Almeida EA, and Michez D. The impact of molecular data on our understanding of bee phylogeny and evolution. Annual Review of Entomology 2013;58:57-78.

Hughes W, Oldroyd B, Beekman M, and Ratnieks F. Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science 2008;320(5880):1213-1216.

Maynard Smith J and Szathmary E. The Major Transitions in Evolution. Oxford University Press, New York, 1995.

Queller DC. Cooperators since life began. Review of: J. Maynard Smith and E. Szathmáry, The Major Transitions in Evolution. Quarterly Review of Biology 1997;72:184-188.

Queller DC and Strassmann JE. Beyond society: The evolution of organismality. Philosophical Transactions of the Royal Society B 2009;364:3143-3155.

Because of the popularity of this topic, two groups explored this subject. Please be sure to review the other write-up, which immediately follows this one.

IDR TEAM MEMBERS—GROUP A

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IDR TEAM SUMMARY—GROUP 7A

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IDR Team 7A's challenge was to focus on evaluating the degree to which cooperation and conflict need to be balanced to facilitate the evolution, expansion, optimal performance, and maintenance of collective behaviors. Collective behavior is defined as a spontaneous behavior that a large number of individuals within a group undertake that is different from the group's previous actions. The classic example of collective behavior is seen within a honeybee colony, in which evolution selected for individuals to work together in various castes, from the worker bees to the nurse bees to the queen bee, and form societies that are truly well-oiled machines. Of course, collective behavior can be seen in human societies or groups of cells and a variety of other societies, as well.

The team began with a thorough discussion about the definitions of cooperation and conflict, which shaped all of Team 7A's key questions and made up a significant portion of the topic. However, the team found that while cooperation is well defined, the definition of conflict is a bit murkier. It was agreed that cooperation is something that brings a net benefit to one or more players, while conflict occurs when fitness interests are not fully aligned among interacting entities.

While the fitness benefits of cooperation are often rather straightforward, the benefits of conflict may be less clear. Conflict arises when individuals, be they humans or honey bees, need to consume limited resources. Altough such conflicts may lead to tragedies of the commons and population extinctions, conflict may also play a productive role. To be productive, conflict does not have to be optimizing, it just has to be something that doesn't completely destroy the group. Moreover, conflict between certain groups often heightens cooperation among those in specific groups. For example, in competition between businesses, one business might come up with an innovative strategy to fix a problem. Not only will the individuals in this innovative business work harder to implement this strategy, but so will the business's competitors as they want to come up with their own strategy. Therefore, conflict can be beneficial at the group level.

The team decided to focus on a diagram by Washington University professors of biology Joan E. Strassmann and David C. Queller that represents conflict-cooperation space (Figure 1). It features two intersecting axes,

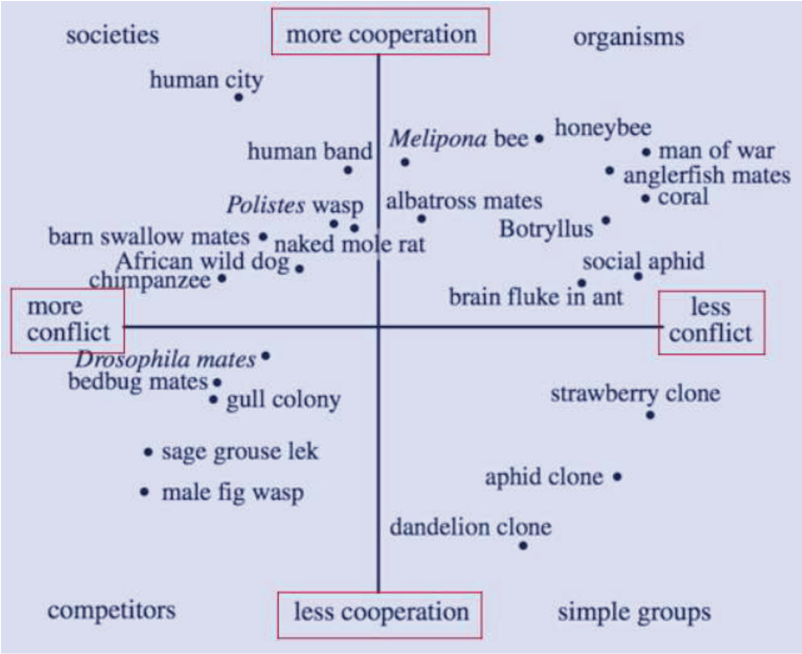

FIGURE 1

the x axis representing conflict and the y axis representing cooperation. In this plot, various groups like chimpanzees, coral, social aphids, and human cities are represented, and their interactions are qualitatively plotted, showing where the groups lie in terms of conflict and cooperation.

The team believed the “more conflict, more cooperation” quadrant seemed like the most interesting to delve into because it matches how we primarily characterize human-to-human interactions. The team also wanted to know what causes an individual or group to be unable to move back to a specific quadrant or place on the plot, or to be able to determine the point of no return. For example, honeybees, operating in eusocial societies, have evolved to a level with a lot of cooperation with very little conflict. However, if they cooperated even more or had even less conflict, would their eusocial societies fall apart?

There was a heavy focus on this point of no return. The team reasoned that the system may never be optimal, but a certain level of conflict and cooperation can help the system from breaking apart completely. A system breaking apart could look like the species or group dying out. After some discussion, the group also decided that although, in theory, having the greatest amount of cooperation with no conflict might seem desirable, maintaining certain levels of conflict is good; if there is an environmental change, some individuals or groups will be better able to weather the change if conflict exists. This is natural selection exemplified. However, the team reasoned that there is no life at all when there is no conflict or cooperation.

Strassmann and Queller's plot shows large clusters and gaps, and this spurred conversation as to whether these gaps are truly possible, which would suggest that certain combinations of conflict and cooperation make groups go extinct, or whether they are a function of the plot being made using only qualitative and no quantitative data.

After this lengthy discussion, Team 7A came up with its own statement of the problem:

> Identify the modalities of combining cooperation and conflict to
>
> 1. Be beneficial to an individual or society—what are the successful combinations?
> 2. Determine dynamic pathways that lead to stable/improved states.
> 3. Predict a point of no return.

As a solution, the team thought it would be a good idea to expand upon Strassmann and Queller's plot by adding a third dimension, or a z axis, that represents fitness (Figure 2). This z dimension would look like a fitness landscape, which is a 3-D plot that shows how well an organism or group does at reproducing. This z-axis various peaks and valleys would represent organisms, societies, groups, etc. and their relative levels of fitness. These peaks and valleys would be based upon the levels of conflict and cooperation inside an organism or group.

This new representation of Strassmann and Queller's plot would show where phylogenetic pathways continually reoccur, and the number of species in certain parts of the plot would show at what levels of interaction there is more likely to be extinction or survival of species.

However, the problem with this 3-D representation is that although we are interested in the point of no return, with a fitness landscape, it looks as if the groups can always go back to where they came from originally. This is because in a fitness landscape, any individual at the top of a peak can fall back down into a valley, and is generally free to move around the landscape. This point of no return is therefore not accurately represented using this model.

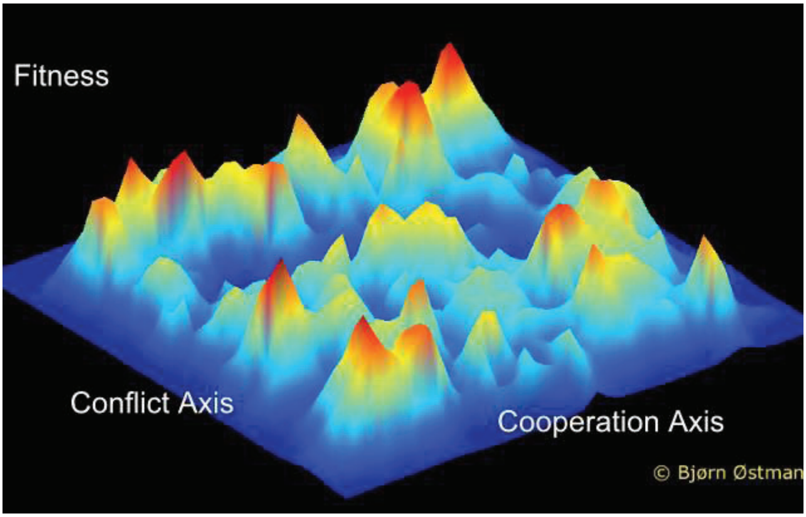

FIGURE 2

To solve this problem, the group decided to create another model that projected the fitness landscape back into two dimensions with a grid (Figure 3). The nodes where the grid lines intersect represent groups or individuals, as well as where they reside in terms of their conflict and cooperation levels. There can then be pathways going between the various nodes to show where these groups or individuals could or could not possibly go; this effectively illustrates the point of no return in regards to whatever constraints lie in the individual or group's particular environment.

With further experimentation, these particular models would be able to address whether there are areas on the plot where there are clusters or gaps among groups, as well as whether points of no return exist. The group also wanted to do further experiments to determine the role of scale in these models, the costs of moving from one place to another on the plot, or the costs of dealing with the interdependencies of entities as the social environment changes. As stated above, it is currently unknown whether humans are a true exception in that we have high levels of conflict and cooperation, and the group would want to do experiments to parse through that question.

To address the problem, the group recommended models like the NK model (fitness landscape), n-player game theory models, network models, and probabilistic models that would allow researchers to make predictions about various groups, including humans.

The group also suggested using comparative frameworks to identify

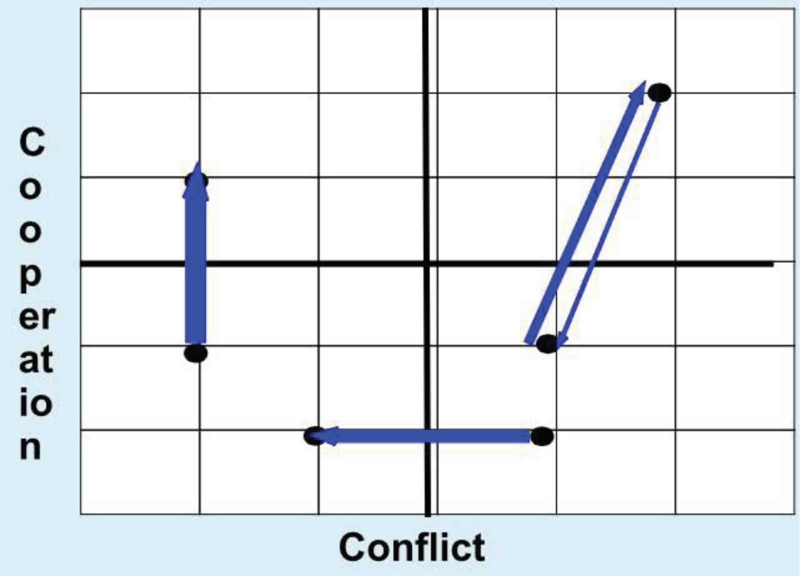

FIGURE 3

commonalities of the landscapes across scale. Scientists could also do experimental evolution using various organisms and microbes like green algae to increase the environmental complexity and modulate cooperation and conflict; this would allow them to determine whether there are points of no return or "dead zones" on the plot where species cannot exist.

From here, researchers could do simulations, and if enough quantitative information was derived, use big data strategies to solve the various facets of the problem statement above.

The team believes that the benefits to society these experiments will have can both promote the good and inhibit the bad. Our understanding of collective behavior and human cooperation can promote economic or other growth, be used to protect the environment, as well as support tenuous cooperation, like that of a ceasefire. We can also use points of no return to perturb cooperation in pests, pathogens, and disease, as well as prevent or stop war and restructure economic systems.

It will take a lot of cooperation—and some conflict—to better understand cooperation and conflict, but in the end, our society will be better for it.

IDR TEAM MEMBERS—GROUP B

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IDR TEAM SUMMARY—GROUP 7B

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IDR Team 7B was asked to evaluate the degree to which cooperation and conflict must be balanced in order to facilitate the evolution, expansion, optimal performance, and maintenance of collective behaviors.

Collective behaviors, or the coming together by members of a unit, can be immensely beneficial for the group. In humans, for example, the varied components of a cell—proteins, DNA, cell membrane—interact to form an efficient unit. Cells further work together in a complex individual, who in turn collaborates with other persons in various societal groups. These unified phenomena span different creatures and objects—from the collaborating parts of bacteria or humans, to atoms interacting to form intricate elements. But perhaps more intriguing, various individuals pool together to create complex groups—colonies of insects and bees, schools of fish, and, in humans, social groups, governments, and even armies. The units all work towards a common, if not always positive, purpose.

IDR Team 7B agreed that implicit in all collective behaviors is the need for cooperation, but conceded that conflict is also evident in most, if not all, interactions. The cancer cell goes rogue at the expense of the whole, competing queens fight for dominance in some species of social bees, dissenting parties are found in social media groups among humans, and murderers abound in virtually all human communities. The question for the team, then—to what extent cooperation and conflict affect the formation and stability of collective behaviors—seemed especially imperative.

Imperative, but complex. What was needed was to reduce the parts of the collective to the simplest units, while retaining enough complexity to make meaningful observations. As a first step, the team chose to limit its discussions to living organisms. It also considered the cells as the smallest unit of the collectives. To foster the interdisciplinary approach that the topic warranted, the team further allowed for, even actively solicited, the expertise of the physicists, computer scientists, psychologists, and policy analysts that complemented the biologists in the group. Equally important, the group appreciated the need for disagreements, simple or radical. With these ground rules, the team had become what it intended to study: its own interplay of cooperation and conflict in a collective unit.

The first challenge to answering an inquiry is to understand the question. The next, and perhaps most vital, step for the team became to eke out reasonable definitions of "cooperation" and "conflict." An exercise of anonymous brainstorming recorded on yellow and pink and orange post-it notes quickly underscored the importance of the exercise. Initial thoughts on the meaning of cooperation ranged from "interacting individuals with shared interests," through belief of what "increases happiness." Other takes included "individuals working together for a specific outcome" and "parts working together for positive benefits for all or to lower free energy."

After a spirited deliberation, the group settled on a working definition of cooperation as "interactions that increase utility function for the elements involved in the interactions." There was a caveat: utility is context-dependent. In other words, the utility may differ depending on the group involved. For some eusocial insects, the context may be to protect the egg-laying queen and larva; for a terrorist group it may be to cripple a true or imagined foe; and for the atoms in an element, the utility function may be to achieve a state of order or to lower free energy.

Turning to conflict, the group reached a definition relatively more quickly: "Interactions that decrease the utility function of a subset of the elements involved in the interactions." One caution was that conflict is not necessarily the opposite of cooperation. Conflicts must also not be viewed as "bad." Such care to withhold moral judgments is important to view the interplay between the phenomena—cooperation and conflict—from a strictly utilitarian or functional perspective. The team reached a yet other consensus: Cooperation and conflict can occur simultaneously.

In research, areas of major or rapid changes offer the best chances for capturing the reasons for what is happening. The team needed to harness this power. Of the possible outcomes of the evolution, expansion, optimal performance, and maintenance of collective behaviors, the power inherent in moments of change, or transitions, appears to center on when groups *form* and when they *dissolve*. The team opted to concentrate on these areas of transitions.

The ideal situation would be to study such periods of transition in evolution—when ants transitioned from being solitary individuals to being a formidable collective, or when some species of social bees revert back to solitary lives. But evolutionary phenomena rarely happen in human timescales. Hence, studying these transitions in nature would be less practical and entail huge cost, resources, and time—none of which the team had.

Fortunately, biology is replete with groups that form and stop rapidly, even cyclically: the murmur of starlings, tribes of bees, bacterial colonies, the cooperative breeding of some birds and animals, social collectives on the Internet, formation of nation states, and even phase transition in physics. Is there a utility function that can be generalized from these ephemeral groups, across scales, from cells to society? The team hypothesized that there likely is, but if that is not true, why? Further, what is the minimum number of phenomena that can describe the transitions—what are the simplest (but not too simple) utility functions at play? In the interplay between cooperation and conflict, what factors about temporal collective behaviors can researchers measure at the times they form and dissolve, factors that can be captured through an equation? The team conjectured that groups form when the utility function for the collective is maximized, and can only be achieved when cooperation exceeds conflict. When conflicts surpass cooperation, groups dissolve.

The next step in the inquiry would be to run the data gleaned from studying these varied examples in nature through a few or several models, to uncover what stands out. The results can then be plugged into more permanent collectively behaving groups in nature, to see what can be learned. Some promising models to start with could include

1. Cellular automata,
2. Agent-based models with adaptive/evolutionary dynamics, and
3. Formal population genetics model with probabilistic state transitions, which posits that states are phenotypes in cooperation × conflict space, and approaches like those from the neutral theory of biodiversity based on master equations.

Indeed, in the complex, interconnected world with an increasing constraint on resources, it has become of dire importance to better understand the interplay between cooperation and conflict in the formation, expansion, performance, and maintenance of collective behavior. Such understanding is a necessary first step if we must control collective behavior. Perhaps then science can have a positive effect on human conflicts, endangered species, epidemiology and diseases, and—some members of the team insisted on adding—the U.S. Congress.

IDR Team Summary 8

From single cells to tissue: What causes organismality to emerge from individual cells, achieving control of conflict at lower levels so the organism becomes the unit of adaptation?

CHALLENGE SUMMARY

No cell is an island, to paraphrase John Donne. We have somewhere between 10 and 70 trillion cells in our bodies all with the same genetic material we inherit from our parents. How then do we become who we are with all our organs and tissues integrated into the whole organism and how do these organs remember what they are throughout life? These questions are fundamental problems in biology—still. What causes organismality to emerge from individual cells, achieving control of conflict at lower levels so the organism becomes the unit of adaptation?

We have gained a tremendous understanding of the sequence, alphabet, and language of the genome, our knowledge of molecules and many of signaling pathways in normal and cancer cells has filled thousands and thousands of pages of journals, yet our fundamental understanding of how the organism in its collectivity becomes the unit of physiological function is at best quite rudimentary. Whereas "the role of individual variation in collective behaviors has been woefully understudied" in population studies, the reverse is true in biological sciences: We are losing the organism for the cells or to use a more common expression: We are losing the forest for the trees!

But the above have inescapable relevance to why we age and why we get cancer. So why do we still know so little about the fundamentals behind the how and the why? This may be because the majority of cell and molecular biologists have been intensely interested in single cells and molecules, developmental biologists have been involved intensely in genetic manipulations to discover single players in pathways in developing organs, and the physiologists have dealt essentially with the already formed complex organism or organs. The bioinformaticists—who these days are dealing with huge data sets to make sense of the whole—often have not studied biology, so the models become speculations at best. In each of these disciplines, we are poorly equipped to think about the other areas; what is worse, we are forced by the system of rewards and survival to go solo, look only under the light and inside the box, and stick with our own tool box.

Under these circumstances, simple logic often is not played: if we have all these cells that have the same genes shouldn't there be something else that brings specificity? Some of us have argued that this is the microenvironment and the context the cells and tissues find themselves.

A movement is afoot to get the physicists and engineers together with the biologists. This is good. But the problem is that these disciplines are far from each other and will take decades to truly train both sides to understand each other and there is much arrogance to go around! But why shouldn't physiologists and molecular biologists who are much closer in discipline collaborate to answer our fundamental problems, for example?

The challenge for the working group is to answer the following question:

What causes organismality to emerge from individual cells, achieving control of conflict at lower levels so the organism becomes the unit of adaptation? How do we define "microenvironment" vs the "genes," and whether it makes sense to ask: what is the hen and what is the egg?

Could we explore if there are similarities or differences between the ways we study single cells and groups of cells within a tissue in biology and those tools used and similar questions posed in social sciences for individuals versus groups? Can we learn from the behavior of other species in biology such as honeybees and microbes? Also, why have biologists been hampered in their understanding of how an organism comes to pass from its individual cells? This fundamental question needs to be better understood before we can also understand why and how we age and why cancer cells prefer not to cooperate with each other.

Key Questions

Do you believe that "no cell is an island"? Does this analogy work? If yes or no, why? Do you think the statement that we have 10-70 trillion cells in our bodies and that these essentially have the same genes, correct?

If yes, how would you go about explaining why your nose and elbow are different? How would you explain this point to your students if you were to write a textbook? Was there anything about this point in your last biology textbook you looked at? What is the definition of the microenvironment here and is it important?

Does it make sense to have such a broad umbrella for this NAKFI meeting? Can social sciences teach anything useful to biologists and vice versa?

Does IDR Team Challenge 1 "Using our understanding of cooperation in cognitive organisms to understand cooperation in organisms or entities without brains and vice versa" have relevance to this challenge?

Do single cells by themselves and individual cells within a tissue or organ differ functionally? If so, what is the evidence? What are the advantages if these were similar? What are the disadvantages? Are the movements from single cell to tissue reversible? When tissues are digested, do single cells retain their memory of the group or do they revert to the original, "uneducated" form?

How much "plasticity" is there? How much can be tolerated? Can cells perform tasks outside the body that do not usually exist in the body? How would they do it? What would it mean? Can we debate the following: "Don't ask what a cell can do, ask what it does do"?

Is epigenetics relevant to the above questions? Have you studied this area? What do you think it means? How broadly should we define this term? Is it important? How does the epigenome play a role in the first question above?

Do you, or should you, think about Descartes? Did he say anything that is useful? Are we too uncritical of Darwin, i.e., are we too Darwinian? Are there analogies between Darwin and Freud? If so, why and what are the lessons—good and bad?

Is there anything in biology that is linear? Should we continue to think of signaling pathways as linear? How did you learn signaling from a textbook? Did any of your professors argue that biology in general is or is not linear? Is anything in biology "flat"? If so, how would it work?

Is there anything in biology that is self-organizing? What does this mean to you?

The title of a volume of a journal is "From Single Cell to Biology." Does this make sense? Do you think there is something missing? Should it say from single cells to organs (or some such)? Why is this question being posed?

Reading

Bhat R and Bissell MJ. Of plasticity and specificity: Dialectics of the microenvironment and macroenvironment and the organ phenotype. Wire Developmental Biology 2013;3(2):147-163.

Bissell MJ and Hines WC. Why don't we get more cancer? Nature Medicine 2011;17:320-329.

Bissell MJ. Website: http://www.lbl.gov/lifesciences/BissellLab/main.html (This includes TED talk.)

Hayden EC. Human genome at ten: Life is complicated. Nature 2010;464:664-667.

Zhu L, Aonoa M, Kim S-J, and Haraa M. Amoeba-based computing for traveling salesman problem: Long-term correlations between spatially separated individual cells of *Physarum polycephalum*. BioSystems 2013;112(1):1-10.

Moiseffi A and Copeland J. Firefly synchrony: A behavioral strategy to minimize visual clutter. Science 2010;329(5988):181.

Queller DC and Strassmann JE. Beyond society: The evolution of organismality. Philosophical Transactions of the Royal Society B 2009;364(1533):3143-3155.

Queller D and Strassmann JE. The veil of ignorance can favor biological cooperation. Biology Letters 2013;9(6):20130365.

Furuta S, Jeng Y-M, Zhou L, Huang L, Kuhn I, Bissell MJ, and Lee W-H. IL-25 causes apoptosis of IL-25R–expressing breast cancer cells without toxicity to nonmalignant cells. Science Translational Medicine 2011;3(78):78ra31.

Sathie S, Khetan N, and Nanjundiah V. Interspecies and intraspecies interactions in social amoebae. Journal of Evolutionary Biology 2014;27(2):349-362.

These very famous words quoted from Meditation XVII, a prose work published in 1624, remind us of the relevance to the above:

> "No man is an island, entire of itself; every man is a piece of the continent, a part of the main; if a clod be washed away by the sea, Europe is the less, as well as if a promontory were, as well as if a Manor of thy friends or of thine own were; any man's death diminishes me, because I am involved in Mankind; and therefore never send to know for whom the bell tolls; it tolls for thee."
> -John Donne

Because of the popularity of this topic, three groups explored this subject. Please be sure to review the other write-ups, which immediately follow this one.

IDR TEAM MEMBERS—GROUP A

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IDR TEAM SUMMARY—GROUP 8A

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IDR Team 8A was assigned the task of investigating what causes organismality to emerge from individual cells, achieving control of conflict at lower levels so the organism becomes the unit of adaptation. Each of the three groups with this task approached it in a different way, and IDR Team 8A focused primarily on identifying the qualities most important to making multicellular organisms work—and fail.

Experimenters have seen normal cells changing type entirely or growing out of control when put in a petri dish. They have seen tumor cells reverting to normal activity when put back into the right environment. Scientists who study wound healing, breast development, and neuron growth see isolated cells reacting very differently from those embedded in a system. Researchers in regenerative medicine test different complex three-dimensional scaffolds to grow cells into functional tissues, and roboticists, synthetic biologists, and computational modelers try to build complicated systems with specialized units working synergistically. And yet, there's no way to carry practical knowledge of what works across different scales, levels of complexity, or types of organism.

Multicellular organisms make up so much of the world, and so much of ourselves, but we don't have generalizable knowledge of how they work or a framework for how to combine the knowledge and techniques of different fields to get there. IDR Team 8A sought to understand the properties, intercellular interactions, and cell-environment interactions that allow multicellular organisms to function as a single unit and exhibit collective behavior.

Fulfilling the Social Contract . . . or Going Rogue

If we had a bag of cells, could we pick out the ones that came from a multicellular organism? Team 8A noted that such cells might be less hardy than single-celled organisms and they might be more specialized—they have generally had to compromise acting on their own behalf for a particular, globally important function.

A key characteristic of cells in many multicellular systems, including our own bodies, is the tendency toward differentiation: the cells start out uniform, but will diverge into dramatically different types based on their environment and surrounding cells as they reproduce. The more they differentiate, the less flexible they are and the more focused role they play within the body. And cells that have differentiated to fill a specific function make the ultimate sacrifice: they have a limited number of divisions before they die, and they will undergo planned cell death to help overall development of the organism.

The cells that make up multicellular organisms are not robust on their own but gain adaptability as part of the group by sharing energetic tasks and differentiating or specializing to different levels to suit the organism's overall needs. But in some cases, such as when a cancer cell detaches from its original tissue and migrates to a different part of the body in the process of metastasis, a cell will entirely abandon its responsibilities and race elsewhere to grow. Scientists do not yet fully understand the characteristics of a cell that allow it to work within a multicellular unit and the stressors that can disrupt that or prompt a transition.

Hierarchy of Properties and Interactions

In order to run sensible experiments on the behavior of multicellular organisms, Team 8A discussed how researchers have to choose variables to restrict using a two-dimensional substrate or three-dimensional scaffold, limiting the interaction to only one or a few different types of cells, or narrowing down which aspects of the cells' microenvironment are incorporated into the system. The team also considered whether any particular stimulus is needed to form a multicellular organism and whether multiple or diverging cell types are necessary. They noted that changing the physical shape of a tissue changes its function, and observed that it is not yet possible to predict how that will happen.

The process right now cannot be standardized: nobody has quantified which elements are needed for cells to form a multicellular unit, or carry out particular functions, and which are just part of the environment. Knowing that would let researchers design targeted, efficient tests and build working multicellular systems without unnecessary complexity.

Toward Understanding

It can seem like a paradox: how do you start investigating before you know which elements of the cells and environment are important? But by simultaneously experimenting and modeling, researchers could reverse-engineer how multicellular systems work while narrowing down to the important variables.

Essentially, there would be two levels of complexity. Researchers would measure as many physical properties of component cells and their microenvironment as possible, looking at how they interact with one another on a small scale. They would then let the system grow and measure the characteristics and collective behavior of the tissues that emerge. At the same time, they would form a model of the cellular system with the measured parameters and then let that model develop, investigating the emergent patterns that form. By comparing the real and virtual tissues and changing the breadth of characteristics included in the virtual cells, the researchers will be able to tell which elements of the real cells are contributing to successful multicellular function. That way, when tissue engineers or cancer researchers set out to influence cellular systems and induce collective behaviors, they will know which aspects are most important to control.

Most of the technology needed for this kind of in-depth experimentation is already available: single-cell sequencing, identification and characterization of proteins, chemical analysis of the microenvironment, and microscopy; we also have tools to look at the physical changes the system goes through over time and how easily cells can move around. As technology moves forward, researchers will be able to measure properties less invasively and even change cell properties without interrupting the whole system. Tools that allowed scientists to characterize the three-dimensional microenvironment without interrupting an experiment and take time-dependent measurements with single-cell resolution would make this kind of analysis even easier and more productive.

Opening New Research Doors

Ultimately, filling in the framework would let researchers figure out what functional tissues and other multicellular structures have in common. They would find the smallest necessary set of properties, interactions, and environmental cues to generate tissue, and they would understand how the properties apply to multicellular organisms on different scales. They might even identify alternate, simpler ways to build those same structures. Researchers would also be able to clarify how multicellular systems respond to stress and understand what specifically can incite cells to break off independently, as in cancer metastasis.

As the team's final-day presenter put it: "We can identify those key knobs, and once we do that we can begin to play with them." And, through that play, researchers would get a handle on how organisms develop and build a bridge between basic biological principles and broader, macrocosmic interactions. Their discoveries would apply everywhere from biological threats like cancer to our own origins and the development of life.

IDR TEAM MEMBERS—GROUP B

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Michael D. Goodisman, Georgia Tech
Maria Pellegrini, W.M. Keck Foundation
Luis M. Rocha, Indiana University
Daniel Segre, Boston University
Blanka Sharma, University of Florida
Elizabeth Van Volkenburgh, University of Washington
Douglas White, Georgia Institute of Technology

IDR TEAM SUMMARY—GROUP 8B

Douglas White, NAKFI Science Writing Scholar
Georgia Tech and Emory University

Introduction: A Multidisciplinary Approach to Answering a Timeless Question—How Did Complex Life Evolve?

IDR Team 8B was asked to address the emergence of multicellular organisms from individual cellular units. This question had two distinct parts which were each important to consider. First, what are the properties that define multicellular organisms? Second, what factors in the environment cause evolution to act on groups of cells instead of just single cells? The synergism of these two ideas captures the massive scope of the question posed to IDR Team 8. Understanding the evolution of multicellularity would provide insights understanding tissue regeneration, cancer, and metabolic diseases (e.g., type 2 diabetes mellitus) which are open and important challenges in human health.

IDR Team 8B consisted of a mix of computer scientists, neurologists, plant biologists, physiologists, geneticists, and experts on social insects. Using their multidisciplinary approach, they drew upon concepts from metabolism, computer science, and evolutionary biology to try and explain how multicellular organisms evolved from single cells.

What Defines a Multicellular Organism?

The team started by tackling the first half of this question: what makes a multicellular organism different from just a group of cells? The idea of specialization—that each cell can take on a specific role—came up early in the conversation. The freedom of cells to specialize is a hallmark of a multicellular organism as specialization allows the organism to perform more complex tasks with greater ease. Each cell can now focus on becoming a master at a specific task instead of having to become a jack of all trades. Interestingly, the team also observed that while specialization may be necessary in some cases, there is also a cost associated with specializing, and the system as a whole becomes more vulnerable with specialization.

The team also discussed what other properties are necessary to define an organism. The idea of cells as Turing machines was used to explain cell behavior. A Turing machine is a theoretical concept which consists of two parts: a piece of memory which stores information, and a machine capable of storing information on that memory. This analogy provided many useful parallels when considering cells and how they evolve with respect to their environment and themselves. In the first iteration of this, the DNA was the information, while the cellular machinery responsible for reading and writing that DNA was considered the machine. However, several other types of information storage were considered including proteins, carbohydrates, voltage potentials, and RNA. One team member brought up an interesting concept that all of these types of information have a trade-off between the time it takes to read the information versus the stability of the information over time. While DNA stores information in an incredibly stable manner, it takes hours to respond to a signal. In contrast electrical potentials are transient phenomena but can open and close protein channels on the cell membrane on the order of seconds.

After hashing out the different mediums a cell can use to store information, an inevitable discussion of what has access to this cellular memory ensued. Can the environment influence cellular memory, or does only the cell have access to it? This was simply a surreptitiously packaged form of the age-old nature versus nurture debate which the group ultimately answered using the abstraction of the Turing machine. The cell as the machine can write to the memory, but that does not stop external forces, such as the environment, from also writing to the same memory. Thus, the group came to a consensus that, in the context of the evolution of multicellular organisms, both the environment and cellular genetic makeup are important.

A New Way to Understand Evolutionary Theory: A Computer Science Approach

The theory of evolution specifies that evolution is driven by some gain in fitness. The IDR team decided to subsequently explore what this means specifically with respect to the evolution of multicellular organisms. The requirements put in place via the environment certainly constrain how organisms evolve, and the team chose to think of these constraints as a fitness landscape. The team often chose to use an organism's access to energy as a proxy for fitness. Given the question of how an organism evolves to maximize its access to energy, the team drew on another analogy from computer science: the space, time, communication complexity axes. Briefly, the idea behind using these axes in computer science is that they provide a quantitative way to compute the cost associated with completing a given task.

For example, if a computer is asked to solve a very large problem there are several ways it can accomplish this task. If time is not an issue, one computer can run until it solves the problem. This method would have a high time cost, but does not require complex communication or more than one computer. In another solution multiple computers could run in parallel to solve the problem. This would have a high space cost because more than one computer is required to solve the problem, but the two in parallel would solve the problem faster than a single computer which corresponds to a lower time cost. In a final example two computers divide the task up, and each computer specializes on solving a different part. This would also minimize the time cost but the two computers are required to share information to complete the task; thus there is an increase in communication complexity. Thus, though multiple different solutions exist for a single problem, each of them has a different cost associated with the solution.

In the context of biological systems, the team decided to rename these axes as the communication cost, space cost, and time cost required to solve any given biological problem. The team again related this to energy, and in a thought experiment, asked how different single cells could solve a task. In this task a cell had to drill through a barrier to get to a food supply. The group proposed three main solutions, which were analogous to those described in the computer examples. In the first example, a single cell could attempt to drill through the wall, sense how close it was to the food, and then move to the food and consume it. This would have a long time cost, but would not pay a cost for space or communication. In the second example, multiple cells could try to chew through the wall all in tandem. They would breach the wall faster, reducing the time cost, but the space cost would increase as more cells are needed to accomplish the task. In the third example a group of cells divide the task into movement, chewing and sensing to ultimately reach the food. They would reach the food much faster than the previous two examples, thus a low time cost, but pay a cost both in terms of the communication between the various specialized units, and the increase in the number of cells necessary.

The group used these analogies to analyze how various different organisms would fall on the space, time, and complexity axes. Bacteria and other single-celled organisms can grow into large colonies if the food source is plentiful. However, the rate at which they can consume food is directly proportional to the number of bacteria, and thus this strategy only works if a lot of bacteria are present (high space cost), or they have a long time to consume the food (high time cost). If there was a way to consume the energy faster, this would provide a fitness advantage over this single-celled approach. In multicellular organisms cells take on specific roles related to sensing, moving, and harnessing energy resources. Due to this cooperative approach multicellular organisms can consume food much faster than their single-cell counter parts, but all of this specialization requires an increase in communication between these cell types (high communication cost). Interestingly, plants have addressed this problem by taking advantage of sunlight, which is a nearly infinite and plentiful resource but is chemically extremely difficult to harness. Thus considering biological evolution in the context of this three-axis energy landscape was extremely useful in helping to describe some of the underlying principals governing the evolution of multicellular systems.

Conclusions

IDR Team 8B took a unique and refreshing approach on tackling an age-old problem in biological theory. By combining ideas from evolutionary theory with modern abstractions from computer science, the group was able to come up with a framework for understanding the evolution of multicellular organisms. Though the concepts and equations governing this approach are still rough and undeveloped, it provides a starting point and a common language to enhance discussions about future study. Using this approach the team hopes to probe the fitness landscape to understand the conditions necessary for multicellular life to evolve. Understanding these principals could allow the creation of artificial multicellular organisms designed to complete specific tasks. Similarly, this approach could be harnessed to understand the evolution of cancer and metabolic diseases which would provide an avenue to developing more effective therapeutics and designs.

IDR TEAM MEMBERS—GROUP C

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IDR TEAM SUMMARY—GROUP 8C

Claire Maldarelli, NAKFI Science Writing Scholar
New York University

Team 8C was asked to answer a question seen universally in nature: What causes organismality to emerge from individual cells, achieving control of conflict at lower levels so the organism becomes the unit of adaptation?

Team 8C initially approached the problem by looking at specific examples in nature where individual cells interact with each other to become a greater functional unit, such as how a biofilm forms, how cancer cells grow into a tumor, or how an ant colony functions. Cells are not autonomous. Single cells within a multicellular organism do not work by themselves. The functionality of a multicellular organism does not come from every singular cell working on its own; it comes from the cells working together. This multicellular system and the systems around it create a microenvironment, which all multicellular organisms must rely on to function. By understanding the microenvironment of an organism, for example a type of cancer's microenvironment, a better understanding of that cancer's functionality can be inferred. We can then begin to understand what it is in the cellular environment that makes a cell become a cancer cell.

The team quickly realized that in order to succeed in life, most organisms follow a randomization strategy. In a human, most cells have almost the same genetic information, but slight differences allow cells to differentiate, to become different tissues and organs. By following a randomized strategy, slight differences develop and life thrives, allowing for adaptation to a changing environment. This system of randomization is seen universally throughout nature.

The team also noticed that within all functional units, a universal mechanism is at play. To establish a common model of functionality on an organismal level, the group likened its organizational hierarchy to Apple's iPad. This architecture, they believe, governs how any group of cells functions as its own organ or organism. By studying biological systems and other systems in nature in adherence with this architecture, generalizations can be drawn and predictions can be made. At the top of this layered architecture is the hardware. As in an iPad or any electronic device, hardware is fast, yet costly and not very diverse—for any given device, most hardware systems operate in the same way. The next level in this design is the operating system. This system is unique in that it is not very diverse—very few operating systems exist—yet from those few, an enormous amount of diversity arises. A very large number of apps can work on an iPad's operating system. And when writing an app, only the type of operating system that the app is going to use needs to be considered. So, in general, it is very easy and inexpensive to write an app.

The group was also able to see this layered architecture in every biological system they discussed. For example, in biofilms, the hardware is the cell. The operating system is the intercellular communication, the chemical gradients, and the mechanical forces that are at play. On top of that there are the functions, or apps, that are implemented on the layer of the biofilm. The biofilm's "apps" would be the cellular differentiation that develops as well as biofilm-level reproduction.

Using this design, they found, allows for life to grow, change, and adapt—and quickly. The reason bacteria can swap genes is that they are running exactly the same operating system. A gene comes in and it is simply a "plug and play"—they plug into the existing system that they are already familiar with and start working. However, the team noted that there is a major problem with this architecture. The universally shared operating system is hijackable. In bacteria, just as genes can be transferred, so can viruses. The way cancer develops is very similar to a biofilm. The hardware is the cells and the operating system is the intercellular communication and chemical and mechanical forces at play. The apps for a cancer cell are initiation, invasion, and eventually metastasis. Specifically, the operating system in a cancer cell is there to do tissue regeneration of wound healing. The cancer cell has essentially hijacked a normal cell in this process. So while it is normally beneficial to have this beautifully layered architecture, it allows for unwanted invaders, such as viruses or cancer, to take over.

The team concluded that with this architecture comes a balance of trade-offs. While the hardware is fast, it is inflexible, and while the operating system gives rise to a huge diversity of apps, it is hijackable. These patterns of trade-off with speed and flexibility are essential in understanding what drives organismality to emerge from individual cells and how biological noise allows organisms to grow, change, and find niche areas in which to thrive—whether we want them to or not.

IDR Team Summary 9

How do general principles of cooperation and competition influence our understanding of brain networks?

CHALLENGE SUMMARY

Traditional neurophysiology has gone a long way via the classic method for studying brain functions, where the responses of individual neurons to external stimuli are examined one at a time. In recent decades, new neurophysiological and neuroimaging techniques have been developed to study neural circuits and specific brain networks that support a specific function. Although these localized networks have advanced our knowledge about the details of how the cooperation and competition between neural processes take place, a crucial question in neuroscience still involves how the brain can support functions that transcend the functions of specialized networks.

Previous studies of functional interactions between large-scale brain networks have identified broad neural networks that operate in apparent competition and cooperation with one another. For example, some networks support internally oriented processing, and others mediate attention to external stimuli. Recently, it has been found that with challenging tasks, cooperation amongst internal networks increase, and the amount of increase co-varies with better performance in the specific task. Although this level of understanding is available, what is still missing is a mechanistic understanding of how cooperation and competition give rise to the emergent physiological functions in a self-organized sense.

The anatomical connectivity between different brain regions remains relatively stable, but the cooperative and competitive interactions between them are dynamic. With the emergence of the BRAIN initiative and efforts to develop high-density neural sensors, dense ensemble time-series recordings will give us a better glimpse of how cooperative and competitive interactions through the whole brain process achieve specific functions. Realistically, we should also remember that the study on cooperative and competitive interactions between brain networks is generally challenging in part because of the challenges in understanding the dynamics of highly nonlinear elements interacting in complex networks. As such, we should place as much emphasis on new acquisition tools in neuroscience as we should in advancing our theoretical models that make predictions about how local competitive and cooperative subunits give rise to predictive, emergent functions. In parallel with this, there is an unmet need of evolving time-invariant statistical methods toward scalable, dynamic methods that can quantify dynamic interactions in a large stochastic network of systems over physiologically relevant timescales. These new dynamic statistical methods will have the potential to be applied to ensemble time series reflecting neurophysiological data as well as those of social behaviors.

Ideally, the advancement of sensors, modeling, and statistical approaches will help us understand the dynamic aspects of cooperative and competitive mechanisms within the brain as well as across social species. These approaches, if carefully developed in unison, have the potential to not only shed light on contributions to individual differences in behavior, but also on how the flexibility of normal brain functions is disrupted in neurological disorders.

Key Questions

Can the brain generate complex functions that transcend those of specialized networks by virtue of the patterns of cooperation and competition of overlapping functional networks?

How can we develop a quantitative method to dynamically track the evolution of cooperative and competitive interactions of segregated brain regions?

What are the similarities and differences in the application of the concepts of cooperation and competition to brain networks compared to whole organisms?

Reading

Cocchi L, Zalesky A, Fornito A, and Mattingley JB. Dynamic cooperation and competition between brain systems during cognitive control. Trends in Cognitive Sciences 2013;17(10):493-501.

Fornito A, Harrisona BJ, Zaleskya A, and Simonsd JS. Competitive and cooperative dynamics of large-scale brain functional networks supporting recollection. Proceedings of the National Academy of Sciences of the United States of America 2012;109(31):12788-12793.

Kim S, Quinn CJ, Kiyavash N, and Coleman TP. Dynamic and succinct statistical analysis of neuroscience data. Proceedings of the IEEE 2014;102(5):683-898.

IDR TEAM MEMBERS

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IDR TEAM SUMMARY—GROUP 9

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IDR Team 9 was asked to explore how general principles of cooperation and competition can inform the scientific community's understanding of brain networks.

The team examined examples of cooperative and competitive interactions across multiple scales of brain activity—from competitive principles governing the wiring of neural circuits to cooperative interactions between functionally specialized brain regions that ultimately let an organism perceive the world and produce adaptive behavior.

The team identified a fundamental disconnect between new research demonstrating brain-wide changes in network connectivity in people with neurological disorders such as autism and epilepsy and more basic research into mechanistic explanations of these disorders at the level of neurons and synaptic connections.

The team chose to narrow the focus of their mission to develop a research strategy to bridge this gap in scientific approaches to neurological disease. They chose to focus on epileptic seizures as a relatively simple disordered network state around which to develop a broad strategy for examining the connection between specific competitive and cooperative brain mechanisms and the healthy and diseased network dynamics they produce.

The Problem: The Black Box

The human brain contains approximately 86 billion neurons. Each neuron contacts thousands to hundreds of thousands of its fellows in intricate and overlapping networks. Our consciousness is the flux of electrical activity through these webs of connectivity.

Modern psychiatry frequently treats brain diseases as whole-organ problems, the team noted. Many epilepsy drugs work by wholesale manipulation of the chemical signals used by diverse networks across the brain. Taking a different approach, neurosurgeons try to eliminate epilepsy by cutting out chunks of brain tissue suspected of sparking seizures.

However, in recent years, new technology has made possible a more fine-grained mapping of neural connections and the flow of activity between regional brain networks. Large-scale research efforts—such as the Human Connectome Project and the Obama Administration's Brain Initiative—have arisen to extend these technological developments.

The team determined that the time seemed ripe for a new approach that could connect diseased activity patterns at the whole-brain level to the small-scale mechanisms that cause them. In particular, they emphasized the need to determine how potential mechanisms affect competitive and cooperative interactions at the under-researched middle scale of brain networks.

Network Connectivity and Psychiatric Disease

Human neuroimaging experiments suggest that at a broad scale, the brain is organized into a so-called "small-world" architecture, in which tightly interconnected local networks are linked to one another by rarer long-distance connections. This network organization enables highly efficient information transfer and may also keep network activity in a stable, balanced state. Departures from "small-worldness" may be a key factor in the development of psychiatric and neurological disease.

The team focused in particular on epilepsy because seizures—excessive network activity linked to out-of-control positive feedback loops—are a relatively straightforward network phenomenon. Previous research has proposed a number of potential genetic and molecular mechanisms that may generate seizures in epileptic brains.

Neuroimaging experiments show that patients with epilepsy have many more long-distance connections than control subjects. This expanded connectivity in patients with epilepsy may contribute to producing seizures that can spread rapidly through the brain. Such changes in connectivity may be caused by synaptic plasticity—the ability of neurons to dynamically shift and reform their connections with one another. But the mechanisms that cause these changes are not yet understood.

The team set itself the goal of laying out a new strategy to bridge these scales: to investigate the mechanistic basis (at the microscale) for observations of altered functional connectivity in epilepsy (at the macroscale). The team proposed examining mid-scale network mechanisms of cooperation and conflict in the context of three potential classes of mechanism—resource competition, plasticity regulation, and circuit repair—which may form the basis for modulation of synaptic plasticity and maladaptive consequences for network activity.

The Strategy: Top Down

The team outlined a strategy of beginning with the ultimate emergent consequence of altered brain networks—in this case epileptic seizures—and drilling down in scale to identify the mechanisms behind them. Their logic was that establishing a clear large-scale network phenomenon in humans should allow subsequent experimental investigations of possible causes for that phenomenon to stay focused and directed.

For each potential constraint they identified, the team outlined a two-pronged experimental approach to examine connections between defects at the macrolevel (whole brain) and microlevel (neurons and synapses).

Competition for Metabolic Resources

The brain is the body's primary consumer of energy, by far. The brain accounts for 2% of the body's mass, but 20% of its energy consumption, over twice that of any other organ. Synapse production and maintenance requires energy as a resource. Finite resources require optimization, balancing gains and costs of synaptic density.

Understanding how energy metabolism affects the onset of seizures in brain networks might shed new light on why the ketogenic diet, which generally stabilizes the body's rate of energy use, is as effective as medication in preventing seizures in many people.

Macrolevel approaches: The team proposed measuring energy consumption in real time in patients under different levels of glycemic load. Specifically, they proposed using magnetic resonance spectroscopy and positron emission tomography to measure local dynamics of creatine and glucose levels respectively in the brain.

Microlevel approaches: The team proposed measuring the distribution and activity of mitochondria within neurons and around synapses, as well as local metabolite profiles measured under different dietary parameters.

Regulation of Excitation and Inhibition

Brain networks strive to maintain a balance between excitatory signaling using the neurotransmitter glutamate and inhibitory signaling using the neurotransmitter GABA. Inhibition is crucially important in neural networks—without it, a highly interconnected excitatory network is subject to positive feedback loops that produce runaway excitation, also known as a seizure. A reduced ratio of GABA synapses to glutamate synapses has been hypothesized to play a role in epilepsy. An open question is why this imbalance occurs in the first place.

Macrolevel approaches: The team proposed taking advantage of recent advances in ultra-high-field (7 Tesla) magnetic resonance spectroscopy to measure local levels of glutamate and GABA in the human brain in real time. The team proposed that drugs could be used to disrupt the balance of excitation and inhibition to directly test the consequences for brain-wide network activity.

Microlevel approaches: The team proposed probing the mechanisms behind the changes in excitatory/inhibitory balance seen in human neuroimaging using drugs, optogenetic control of neuronal activity, and measurement of synaptic density in mice.

Trauma Repair and Plasticity

Epilepsy is a relatively common consequence of brain injury, though seizures may not develop for years after the original brain damage. One reason is that the brain must balance the need for plasticity to repair damaged circuits with the danger that too much plasticity may disrupt previously stable network relationships.

One way the brain limits plasticity is to impose structural barriers on synaptic formation. In particular, extracellular matrix structures called perineuronal nets (PNNs) grow around neurons in later stages of brain development to restrict further alterations to neural circuits. Previous research has linked the formation of PNNs to the closure of critical periods for learning and stabilization of network function.

Following injury, resident microglia or blood-derived white cells may locally remove structural constraints on plasticity using soluble factors such as matrix-degrading enzyme matrix metalloprotease (MMP9). Neurons themselves may also secrete MMP9 following injury. Reinstating plasticity enables the brain to repair damage and networks to reestablish themselves. However, heightened plasticity also means that injured brain circuits become susceptible to excessive synaptic sprouting, an overcompensation that may impact network function and potentially lead to seizures.

Another potential consequence of injury is the formation of glial scars, an additional structural barrier that may regionally isolate neural circuits. By analogy to cardiac scars that form following heart injury, these barriers may disrupt local circuits by forcing them to reroute activity around the barriers, creating new stress points that may be related to seizure activity.

Macrolevel approaches: The team proposed developing models of network connectivity that include effects of structural barriers and rewiring. These models can be tested to explore the consequences of these factors for the percolation of activity through networks following injury. In addition, existing drugs can inhibit proteases such as MMP9 and allow retrospective analyses of patients to determine the optimal degree of structural plasticity that balances circuit repair and stability.

Microlevel approaches: The team proposed live imaging of the distribution of matrix and glial scar cells after brain damage in mice through thinned skulls, combined with ion current visualization to track neural activity.

Societal Impact: Meeting in the Middle

The team proposed that these experiments would produce multiscale data, which could be used to computationally model how different mechanistic factors influence neural network function. Such results have the potential to reveal how the ongoing equilibria neural circuits must maintain—managing resource competition, balancing excitation and inhibition, and regulating plasticity and repair—and interact with specific genetic and physical risk factors to produce neurological disorders such as epilepsy. Understanding these chronic influences on the function of neural circuits may also enable researchers to target relevant mechanisms to prevent age-based cognitive decline.

In addition, from a purely scientific perspective, the team argued, this research strategy would allow neuroscientists to finally bridge the profound gap between human neuroimaging and the mechanisms underlying brain function.

Appendixes

List of Collective Behavior Preconference Tutorials

OVERVIEW

Tutorial Released: September 11, 2014
An Overview of Collective Behavior
Gene E. Robinson (NAS)
Director, Institute for Genomic Biology and Swanlund Chair of Entomology
University of Illinois at Urbana-Champaign

CELLS

Tutorials Released: September 25, 2014
Cell Signals
DNA Learning Center

Experiments that Point to a New Understanding of Cancer
Half the Secret of the Cell Is Outside the Cell
Mina J. Bissell (NAS/IOM)
Distinguished Scientist, Life Sciences Division
E.O. Lawrence Berkeley National Laboratory

Nerve Cells, Neuronal Circuits, and the General Organization of the Brain
Charles F. Stevens (NAS)
Professor, Molecular Neurobiology Laboratory
Salk Institute for Biological Studies

MICROBES

Tutorials Released: September 25, 2014
How Bacteria Talk
Bacteria Communication via Quorum Sensing
Bonnie l. Bassler (NAS)
Investigator, Howard Hughes Medical Institute
Chair and Squibb Professor, Department of Molecular Biology
Princeton University

SOCIAL INSECTS

Tutorials Released: October 9, 2014
The Emergent Genius of Ant Colonies
Deborah Gordon
Professor, Department of Biology
Stanford University
The Real Life of Social Insects?
Bucknell University

Ant Whisperer
Edward O. Wilson (NAS)
University Research Professor Emeritus, Museum of Comparative Zoology
Harvard University

Ants—Nature's Secret Power
Bert Hoelldobler (NAS)
Professor, Zoology Emeritus
University of Wurzburg
Regents' and Foundation Professor, School of Life Sciences
Arizona State University

Solving the Nature vs. Nurture Dilemma: Social Regulation of Behavior and Brain Gene Expression in Honey Bees
Gene E. Robinson (NAS)
Director, Institute for Genomic Biology
Swanlund Chair of Entomology
University of Illinois at Urbana-Champaign

ANIMALS

Tutorials Released: October 9, 2014
Moral Behavior in Animals
The Feelings of Animals
Frans B.M. de Waal (NAS)
C.H. Candler Professor of Primate Behavior, Psychology Department
Emory University

EVOLUTIONARY THEORIES OF COOPERATION

Tutorials Released: October 30, 2014
The New Power of Collaboration
Howard Rheingold
Digital Community Builder

Social Selection: A Primer
David C. Queller
Spencer T. Olin Professor, Department of Biology
Washington University in St. Louis

OPTMIZATION

Tutorials Released: October 30, 2014
Optimization: Genetic Algorithms
Optimization: Applications of Particle Swarm Optimization
Yahya Rahmat-Samii (NAE)
Northrop Grumman Professor, Electrical Engineering Department
University of California, Los Angeles

ROBOTS/ARTIFICIAL INTELLIGENCE

Tutorials Released: November 5, 2014
Lessons from Robots about Being Human
Ken Goldberg
Professor, Industrial Engineering and Operations Research in Robotics, Automatic and New Media
University of California, Berkeley

How Algorithms Shape our World
Kevin Slavin
Assistant Professor, Media Arts and Sciences
Benessee Career Development Professor, Media Arts and Sciences
MIT Media Lab, Massachusetts Institute of Technology

The Future of Robotics and Artificial Intelligence
Andrew Ng
Stanford University

HUMANS

Tutorials Released: November 5, 2014
Power of Networks
James Fowler
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The Hidden Influence of Social Networks
The Sociological Science Behind Social Networks of Social Influence
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Social Networks 101
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All tutorials are available at www.keckfutures.org.

Agenda

Thursday, November 13, 2014

7:45 a.m.	Bus Pickup: Attendees are asked to allow ample time for breakfast at the Beckman Center; no food or drinks are allowed in the auditorium, which is where the welcome and opening remarks take place at 9:30.
8:30 a.m.	Registration (not necessary for individuals who attended Welcome Reception) Poster Session A Setup
8:30–9:30 a.m.	Breakfast
9:30–9:45 a.m.	**Welcome and Opening Remarks** Bruce B. Darling, NAS/NRC Executive Officer Gene E. Robinson, Chair NAKFI Steering Committee on Social Behaviors; Director, Institute for Genomic Biology and Swanlund Chair of Entomology, University of Illinois at Urbana-Champaign

9:45–10:45 a.m.	**Keynote Address** Joan E. Strassmann, Professor, Biology, Washington University
10:45–11:00 a.m.	**Interdisciplinary Research (IDR) Team Challenge and Grant Program Overview** Gene E. Robinson, Chair, NAKFI Steering Committee on Social Behavior
	Overview of W.M. Keck Foundation Grant Programs Maria Pellegrini, Executive Director of Programs, W.M. Keck Foundation
11:00 a.m.–12:45 p.m.	Break/Poster Session A
12:45–2:00 p.m.	Lunch
2:00–5:30 p.m.	IDR Team Challenge Session 1
3:00–3:30 p.m.	Break
	Poster Session B Setup
5:30–7:00 p.m.	Reception/Poster Session B
7:00 p.m.	Bus Pickup: Attendees brought back to hotel

Friday, November 14, 2014

7:45 a.m.	Bus Pickup
8:15–9:00 a.m.	Breakfast
9:00–11:00 a.m.	IDR Team Challenge Session 2
11:00–11:30 a.m.	Break
11:30 a.m.–1:00 p.m.	IDR Team Challenge Preliminary Reports (5 to 6 minutes per group)

1:00–2:30 p.m.	Lunch
2:30–3:30 p.m.	**What's your big iDEA? (inter-disciplinary, enthusiastic, actionable, suggestions)** Attendees give 2-minute pitches for IDR Team Challenge ideas to be explored with interested attendees
3:30–3:45 p.m.	Attendees sign up for iDEA groups
3:45–5:30 p.m.	IDR Team Challenge Session 3 Drop off final presentations at registration desk at 5:30 p.m.
5:30–8:00 p.m.	iDEA groups meet over dinner to explore challenges. (Meeting location assignments available at registration desk)
8:00 p.m.	Bus Pickup

Saturday, November 15, 2014

7:45 a.m.	Bus Pickup: Attendees who are departing for the airport directly from the Beckman Center are asked to bring their luggage to the Beckman Center. Storage space is available.
8:15–9:00 a.m.	Breakfast
8:15 a.m.	IDR Team Challenge Final Presentation Drop-Off: IDR Teams to drop off presentations at information/registration desk. Taxi Reservations: Attendees are asked to stop by the information/registration **only if you need to change your transportation (as listed on the back of your name badge).**

9:00–10:30 a.m.	IDR Team Challenge Final Reports (8 to 10 minutes per group)
10:30–11:00 a.m.	Break
11:00 a.m.–12:30 p.m.	IDR Team Challenge Final Reports (continued) (8 to 10 minutes per group)
	Q&A Across All Groups
12:30–2:00 p.m.	**Working Lunch/NAKFI inMotion**: Build on the momentum put in motion at the conference. Continue work on iDEA groups, regroup with assigned IDR Team, meet with others from like teams. Open forum session in Auditorium. Grant proposal brainstorm sessions. Staff on hand to answer questions about grant proposal process.
	Lunch will be provided.

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