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Social Cognition: From Behavior-Reading to Mind-Reading

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Glossary

Convergent evolution (homoplasy) – The acquisition of similar traits in unrelated lineages; that is, two lineages share a trait, but not because of common descent with shared ancestry.

Gaze-following – Looking in the direction that others are looking based on various cues including eye, head, and body position.

Mutualism – A type of cooperative interaction in which two or more individuals obtain a benefit from working together that they would not have obtained alone

Perspective-taking – The ability to reason about what others perceive, given that others may perceive aspects of the world differently than oneself. For example, an individual standing in one location may not be able to see everything that is visible to an observer in a different location.

Phylogeny – The pattern of relatedness between species and taxonomic groups, representing the evolutionary branching pattern of speciation leading to extant (living) species.

Social cognition – Processing social information. Social-cognitive skills can depend on the information provided the overt behavioral cues of others (in what direction are they looking or moving?) or depend on more mentalistic processes (what do others see or want?).

Social tolerance – A measure of how individuals in a species interact. Species with high tolerance tend to have more relaxed dominance hierarchies, and can sit in close proximity and even co-feed without much aggression. Species exhibiting less tolerance may have more 'despotic' hierarchies and show more aggression when interacting.

Theory of mind – The ability to attribute various mental states – such as beliefs, desires, and knowledge – to other individuals. Perspective-taking is one component of theory of mind.

Introduction

The social world has long been thought to be a major force shaping primate cognition: the social lives of primates are thought to be sufficiently complex to have acted as a driving force in primate cognitive evolution. This basic thesis – that the sophisticated cognitive abilities of primates have evolved for a social function – has spurred experimental and theoretical investigations for over 40 years. Although, most early proposals of the social intelligence hypothesis were inspired by observations of seemingly complex social behaviors across the primates, however, the psychological mechanisms underlying these behaviors were not well understood. It was not until relatively recently that research began to address the cognitive abilities primates actually use when interacting with others, such as whether other primates share capacities like theory of mind with humans.

In this article, we highlight a selection of complex behaviors that primates exhibit when interacting with others, with special attention to the cognitive mechanisms supporting those behaviors. Fundamental to the study of comparative cognition is the idea that many species may exhibit behaviors that appear similar, even though the psychology underlying those behaviors may differ across taxa. While this distinction may be methodologically frustrating – behavioral observations are a rich source of knowledge about animal psychology, and experimental tests of cognition may not always be viable – in fact, it is a testament to the ingenuity of evolution: the hard social problems that primates face get solved, even if the solution is not always the same! This distinction highlights the importance of thinking about primate social interactions not only in the context of behavioral evolution – the special things that primates (and humans) do – but also in terms of cognitive evolution – the special ways that primates think. We use this framework to analyze primate social behavior, and the differing psychologies underlying this behavior, in three areas: gaze-following, food competition, and mutualistic cooperation. The ultimate challenge of such analyses will be to understand why such different cognitive mechanisms have evolved across species.

Gaze-Following: Reflective Orienting or Understanding of Attention?

Imagine a small group of chimpanzees foraging in close proximity in a forest. One chimpanzee hears something in the trees, and looks up. The other chimpanzees follow suit. What cues lead the other chimpanzees to look up: the change the first chimpanzee's head position, or more

specifically a change in that chimpanzee's eye position? Did they follow gaze because they thought that the first chimpanzee had seen something, or was the process more reflexive, relying on an egocentric mechanism? Now imagine the same occurrence in a group of capuchins. Did these very different primates use the same cues as the chimpanzees? Do they understand the situation in the same way?

Gaze-following or co-orienting behaviors like this allow individuals to apprehend important objects and events that others have detected in the environment, including food sources, predators, and conspecifics. Thus, gaze-following allows individuals to exploit the information that others have acquired about the world. At the most basic level, diverse species of primates spontaneously follow the gaze (face direction) of human experimenters or conspecifics. Species including chimpanzees and the other great apes; Old World monkeys such as various macaques, mangabeys, and baboons; New World monkeys including capuchins, cotton-top tamarins, and common marmosets, and even some lemur species, all follow gaze, at least to a certain degree in some contexts.

Although gaze-following behaviors are widely shared across the primate order, the psychological basis of these co-orienting behaviors seem to vary widely, especially in how flexibly this behavior is deployed. First, different species may vary in what cues they use to follow gaze. For some species, there is evidence that individuals can successfully follow eye position alone (e.g., apes). Other species, in contrast, appear highly dependent on shifts in the position of the face, head, or even entire body (such as capuchins, tamarins, and lemurs). Interesting, this variation may be due to variation in the amount of information that the eye carries due to differences in eye morphology across different taxa.

Secondly, gaze-following appears to reflect understanding of attention in some species, but may be more of a reflexive response in others. For example, gaze-following in chimpanzees and other great apes suggests that individuals of these species follow gaze because they understand something about the nature of seeing. Apes not only direct their own gaze in the direction of others, but also follow gaze around barriers and past distracting objects that are not the target of another's gaze, sometimes by physically reorienting their own bodies. They may also check back with the actor in attempt to verify the direction of the other's gaze or quickly stop following the gaze cues when they cannot locate the target of the other's gaze. These flexible shifts in behavior across contexts suggest that apes follow the gaze of others because they expect there to be something interesting to see.

The evidence for such behaviors in more distantly related primate species is less complete, mostly because few studies have been conducted. Macaques, like apes, habituate to repeated gaze cues when they repeatedly cannot locate the target of another's gaze. However, studies of New World monkeys and lemurs suggest that the co-orienting behaviors in some of these species are more reflexive and used in more limited circumstances. For example, cotton-top tamarins will co-orient with conspecifics at high rates during natural interactions (although the cause of this co-orienting is unclear), but fail to follow the explicit gaze cues provided in controlled experimental settings. Similarly, some lemur species co-orient with conspecifics during their natural behaviors, but seem less able to follow gaze in experimental contexts. Thus, although behavioral co-orienting may be common to all primates, not all primates necessarily follow gaze because they understand that others see things. Thus, observations of different species of primates altering the direction of their gaze in response to another individual doing the same does not mean that this behavior is modulated by the same cognitive mechanism.

Competition for Food: Behavioral Predictions or Visual Perspective-Taking?

Imagine the same group of chimpanzees foraging in the forest. As most of the group is distracted, busy following the gaze of that first chimpanzee, a young male realizes that the group has come upon a fig tree with many ripe fruits. He knows that if he has to compete with more dominant individuals for this food, he will likely lose out. Luckily, he spots a large fig that is hidden behind a fallen log and thus out of sight of the others, and quickly runs to take it. What cues led him to target that piece of food, and not another in full view of the other group members? What did he think when he did so? What would it mean if a capuchin was spotted doing the same thing?

Food competition like this is an important consequence of the fact that primates are social living animals: although being gregarious has benefits, it also has costs. Dealing with competition with conspecifics is, therefore, a major problem that primates have to solve. However, there are different ways to deal with such competition that might be quite successful. One possibility is to become a skilled behaviorist, or an expert in using the actions of others in order to decide what to do. In this case, the young chimpanzee might be especially sensitive to the orientation his competitors head and body, as well as any indication that the competitor was going to approach another piece of fruit. A soon as the competitor headed one way, the male headed the other – in this case, to the fruit behind a log. An alternative strategy is to become a mentalist. Rather then depend on the actions of others when making social decisions, a mentalist might form representations of what others perceive – or even

know – and act based on this model of what is going on in the other individual's head. In this case, the male might have realized that, even though he could see the fallen fruit, the competitor could not do so from his different spatial position, and thus it was safe to take the fruit.

These two potential mechanisms might look the same in a naturalistic context, leaving even the most skilled observer of wild chimpanzees and capuchins in a tough predicament: how to determine if chimpanzees and capuchins are approaching this problem in the same way? Luckily, these different underlying psychologies predict very different outcomes in experimental manipulations. For example, a behavior-reading strategy might function perfectly well in most natural situations in which the behavior of others is readily apparent. However, this kind of cognition should break down when such behavioral cues are not available for the formation of predictions. A mentalist strategy, in contrast, should be functional in this context whenever there are cues to what another agent perceives, because a mentalistic can infer how seeing is linked to future behavior – even if the competitor has not yet undertaken any actions to observe and react to. This type of cognition, consequently, would potentially allow animals to integrate different types of behavior and contextual cues into a representation of an unobservable phenomenon – another's psychological state – without limiting behavioral predictions to only specific types of input from the environment (the current behavior of that individual, such as the direction in which they are facing at the moment).

These different hypothetical mechanisms for predicting other's behavior has been tested in chimpanzees in a situation where two chimpanzees must compete for access to food. As in the example above, the two chimpanzees had differing knowledge about the food that was available: the subordinate could see both pieces, but only one was visible to the dominant. When both individuals were released into this room, the subordinate targeted the piece that only she could see – a result that is consistent with either cognitive mechanism. Support for a mentalistic view, however, is provided by a condition where the subordinate was released before the dominant. Even though monitoring the other chimpanzee's actions would not be successful in this context, the subordinate still preferred the hidden piece. This suggests they predicted what the competitor would do, instead of simply reacting to what she was doing. A second set of studies further supported the hypothesis that chimpanzees used a mentalistic strategy. Here, both the subordinate and a dominant watched the food items being baited, but sometimes the dominant was switched with another dominant before the competition began; that is, although a dominant always saw the baiting, and a dominant always was competing for the food, sometimes the current competitor had not witnessed the baiting and thus did not know

where the food was located. The subordinates made more attempts to obtain the food when the current dominant had not been present during baiting than when no switch occurred. Thus, the chimpanzees behaved as though they understood that seeing the baiting led to knowing where the food was located – even without overt behavioral cues on the part of the dominant.

Following these initial studies, several experiments using competitive paradigms have assessed similar perspective-taking skills both in apes and monkeys. For example, when rhesus macaques can choose to steal food from one of two human experimenters, they show sensitivity to variations in visual access and prefer to approach food in front of an experimenter with limited visual access (e.g., because their eyes are covered) than food in front of an experimenter with unimpeded visual access (e.g., their mouth is covered in a similar fashion, but they still can see). Studies with chimpanzees have similarly shown that they prefer to retrieve a piece of food that a competitive human cannot see, even attempting to disguise their interest in the food as they approach. Critically, in both of these examples the experimenters provide no direct behavioral cues to what they can and cannot see, such as by touching or approaching some of the food. Rather, primates in the these studies must infer which food option is 'safe' from the direction of the humans' gaze and whether the gaze is impeded by barriers – suggesting that these primates do not simply react to the behaviors that they observe, but rather predict what others will do by reasoning about their unobservable psychological states in a flexible manner.

Moreover, some evidence suggests that the perspective-taking that chimpanzees and rhesus monkeys engage in extends to the auditory modality – providing further evidence that these species can integrate many disparate cues to reason about psychological states. For example, when rhesus macaques are confronted with a human competitor sitting in front of two boxes containing food, they preferentially steal food from the box that is silent, and do so only when the competitor cannot already see their actions. This suggests that rhesus monkeys recognize how their behavior will alter the psychological state of the human: if the human cannot see them, then the noise will alert him to their presence. If the human can already see them, then noise will have no impact on the human's knowledge about their behavior. Chimpanzees similarly prefer a silent approach over a noisy one when competing with a human over food.

This mentalistic strategy, however, does not appear to be shared by all primates. For example, both capuchins and marmosets have been tested in versions of the conspecific competition paradigm. Subordinate capuchins are quite successful when released concurrently with the dominant: like chimpanzees, they preferentially target the hidden piece of food. However, in the critical test in

which the subordinant is given a head start and must make a decision in the absence of any behavioral cues, capuchins are flummoxed – in fact, it seems they are not sure which piece to approach until they can see the direction the dominant will take first. Similarly, marmosets target the hidden food in the basic food-competition task, but a series of additional tests suggests that they lack any real understanding of visual access, supporting the conclusion that their successful behavior when competing is due to a behavior-reading mechanism. That is, both species appear to depend heavily on the behavior of the competitor, rather then reasoning about what the competitor sees or knows, when competing for contested food.

Thus, although chimpanzees, rhesus macaques, capuchins, and marmosets all show the same complex behavior in the naturalistic context – targeting the hidden piece of food and thus successfully competing with a dominant – they appear to do so in very different ways: chimpanzees and rhesus depend on a mentalistic interpretation of the situation ('she can not see the food, thus it is safe for me to approach and take it'), whereas capuchins and marmosets depend on the behavior of their competitor to make their social decisions ('she is heading toward that piece, thus I will try to take the other').

Mutualistic Cooperation: Working Together or Working Alone In Proximity?

As the same group of chimpanzees is foraging in the forest, it becomes clear that the earlier noise in the trees was not incidental – it is a group of red colobus monkeys that have (unfortunately for them!) strolled too close to their ape predators. The chimpanzees become silent, and then a subset of the group takes off after the monkeys, some in the trees and some on the ground. After a lengthy pursuit, one of the adult males makes a kill, and later shares meat from the carcass with one of his close allies. What did the chimpanzees understand about the pursuit as it was happening, and how did they view their individual behavior in the context of the group's behavior as a whole? Why did the successful male share meat with his friend? If several capuchin monkeys are spotted chasing and catching a squirrel in a similar fashion, would such behavior be under the control of similar cognitive mechanisms as those seen in chimpanzees?

Group-level cooperative activities such as this are increasingly thought to be important for understanding human cognitive evolution: one thing that seems to distinguish us from even our closest phylogenetic relatives may be the ability to pool individual resources to reach a common goal. In many ways, the human are the ultra-social species! Consequently, examples of complex cooperation in other primates are often quite telling, giving researchers hints of what might have changed in the human lineage. Cooperation is certainly not something that is unique to the human, however – indeed, like food competition, cooperation in primate societies results from the fact that primates are gregarious. Thus, many primates have been studied in experimental paradigms that examine the cognitive abilities underlying cooperative behaviors.

Human-like cooperation seems to involve many interacting components: in cooperative situations, people typically take on different, mutually reinforcing roles (division of labor), account for what others meant to do, as opposed to what they ultimately ended up doing (attend to the intentions of others), and choose their partners based on how they acted previously in cooperative contexts (reputation and image scoring). One possibility is that some primate species might understand their particular cooperative endeavors like humans. Other primates, however, might cooperate quite successfully without possessing all those components – or, indeed, any of these components. For example, did the pursuing chimpanzees view themselves as part of a group effort to obtain meat, or did each individual have his own strategy to obtain a monkey (but happened to act simultaneously with several other individuals with the same idea?). Did the male who made the kill share meat because he understood that his friend played a crucial role in capturing the monkey, or did something else (such as a desire to prevent intrusive begging) drive his generosity?

We distinguish two broad types of strategies from successful cooperation – recognizing, of course, that many other variants undoubtedly exist. One type of cooperation stems from high levels of inter-individual tolerance: because individuals of such species tend to be in proximity to one another, they show high rates of by-product cooperation just by virtue of time spent together in close affiliation. For example, the chimpanzees in the hunting example may like to groom and sit near each other; thus, they tend to be together when a group of colobus appears. Although their actions in the pursuit appear mutually reinforcing toward the goal of capturing the monkey, the goal is not shared from the perspective of individual chimpanzees. Rather each individual tries to catch the monkey on his own without regard for what other individuals are doing. An alternative is cognitive cooperation: species that have some understanding of the cooperative act itself and the role of their partners in that act. For example, the hunting chimpanzees might actually have realized that hunts are more likely to be successful if different individuals pursue the monkey from different directions, even playing different roles in the pursuit (e.g., one chimpanzee chasing the monkey in the clutches of another). As with gaze-following and food competition, experimental tests of cooperation can help to disentangle these two solutions to the problem of cooperation.

Tolerance appears to play a critical role in facilitating cooperative behavior across a number of species, and

variation in tolerance predicts successful outcomes in cooperative tasks both within and between species. For example, in one study, rhesus and Tonkean macaques were confronted with a problem: there was food placed under a large stone, but no single individual monkey was strong enough to move it. Two monkeys working in tandem, however, could displace the rock and access the food. Only the Tonkean macaques succeeded at doing so, however, and the cause for this differential success seems to be different levels of tolerance in these two species. Rhesus have a 'despotic' social structure with strict dominance hierarchies, whereas Tonkean macaques have a more relaxed dominance system. Higher levels of tolerance result in a higher likelihood that a pair of Tonkean macaques would sit in close proximity and attempt to move the stone in tandem. Notably, there was no evidence that the Tonkean macaques understood the problem better than did their close phylogenetic relatives; rather, the Tonkean macaques were just more likely to engage in individual attempts to move the rock at the same time that another individual was doing the same thing.

Results from other primate species confirm that cooperative success can depend heavily on the nature of the relationships that exist between individuals, rather than cognitive abilities *per se*. For example, when pairs of capuchins are presented with an apparatus in which two handles must be pulled simultaneously to acquire food, but the handles are too far apart for one individual to pull both alone, the monkeys show a high rate of success. However, an examination of what the capuchins actually did during the operation of this apparatus indicated that the individuals seemed to pull the handle without regard for what their partner was doing: that is, both pulled at a high rate and thus succeeded basically by accident, but the monkeys did not try specifically to pull in concert with their partner. Similarly, when marmosets were presented with an instrumental cooperative task in which one individual had to pull a lever so that another could grasp a bowl of food, success depended on the role that the dominant and subordinate took. Although individuals had previously shown proficiency in the components of the task when tested alone, only those pairs where the subordinate pulled the lever and the dominant took the food showed any success when working together.

Personal relationships appear to play a similar role in ape cooperation. In a series of experiments, pairs of chimpanzees were confronted with a rope attached to an out-of-reach tray of food. If two chimpanzees pulled both rope ends together, they could eat the food; if one individual tried to pull the rope alone, the rope came unthreaded. The level of tolerance between any two individuals – as measured by their ability to share food in the absence of the cooperative component – was the major determinant of whether that pair would successfully cooperate.

Similarly, bonobos – the sister species of chimpanzees with greater levels of inter-individual tolerance – appear to be more successful than chimpanzees on a version of this task. However, unlike some of the studies with monkeys described above, chimpanzees do not seem to cooperate merely as a by-product of this tolerance. While chimpanzee cooperation is constrained by personal relationships between individuals, it also has a complex cognitive component. For example, chimpanzees know that they need a partner for the cooperative task, and are more likely to recruit that partner (by unlocking a door and allowing the other individual access to the room) when the task requires two individuals than when it can be solved alone. Moreover, chimpanzees prefer to recruit partners that are more successful at the task than those that are less skilled, and recruit those that have recruited them in the past over those that have failed to do so. Thus, chimpanzees seem to remember the past cooperative behavior of others and understand how that influences their own possibility of success now. These results suggest that while tolerance does constrain chimpanzee cooperation, chimpanzees are also cognitive cooperators that understand the role their partner plays in the joint endeavor.

Conclusions: How Does Social-Cognition Evolve?

In this article, we have attempted to highlight some major social problems that primates face, as well as the potential diversity of cognitive solutions to these problems. These particular examples, however, are by no means the only social problems where primates show complex behaviors. Indeed, there are many other examples of primates being quite sophisticated in navigating their social world, in social learning, communication, deception, and knowledge of relationships. Similarly, the cognitive 'solutions' to these problems that we have highlighted are not the only ones that primates may use: research on the psychology of most primate species is extremely limited, and it is likely that the future will reveal as much wider range of cognitive mechanisms than research thus far has addressed. However, the examples discussed here serve as important reminders that behavioral complexity can be driven by a diverse set of underlying mechanisms.

In the end, two big questions remain: to what extent do humans and other primates solve social problems in a similar fashion, and why do different species (including humans) solve similar behavioral problems with different cognitive solutions? The first question is a fundamentally phylogenetic one, and research on chimpanzees and bonobos – our two closest primate relatives – have begun to pinpoint how the social cognitive abilities of these apes are shared or differ from our own. As the

studies of gaze-following, perspective-taking, and cooperation mentioned here reveal, in many ways they are surprisingly similar, challenging researchers to come up with new hypotheses about what cognitive traits are unique to our species. The second question is an evolutionary one, and may prove to be the more challenging of the two because it requires reconstructing historical events – evolutionary change and the forces the drove it – that cannot be directly observed. For this question, comparative studies of cognition like those described here, in which the performance of closely related species are examined in similar contexts, are a powerful tool. This is especially the case when such studies are conducted with a focus on the ecological or social variables that may have driven cognitive evolution across taxa.

Studies of social cognition in primates thus provide an important lesson for the cognitive sciences as a whole: there is no such thing as 'primate social cognition!' Although shared phylogenetic history and convergence does result in cognitive traits that are similar across species, comparative research has increasingly revealed the diversity of primate social psychology. Thus, in many ways it is more appropriate to talk about 'chimpanzee social cognition,' 'rhesus macaque social cognition,' or 'tufted capuchin social cognition.' Notably, this is not just true for primates: research has begun to reveal social-cognitive mechanisms in other groups of organisms as well. For example, wild spotted hyenas live in large social group with monkey-like linear dominance hierarchies and engage in cooperative hunting behaviors. Accordingly, these carnivores (but possibly not their close relatives – the relatively less social brown hyena) appear to possess sophisticated social-cognitive skills do deal with their social landscape, such as understanding of third-party relationships. Canids have emerged as an important model for the evolution of communicative gestures comprehension: in contrast to wolves, dogs are skillful at using points and gaze cues to find hidden food, possibly because of selection during domestication. The most sophisticated social-cognitive skills are found in corvids – a group including jays, ravens, and crows. Studies of these birds have revealed startling parallels with the abilities of primates. Specifically, corvids appear to employ many social cognitive skills (such as perspective-taking or encoding the 'reputation' of potential competitors) to protect their food stores when they engage in caching behaviors.

Such an emphasis on the differences between species can challenge approaches that use a few 'model' species for understanding cognitive traits. However, these instances of convergence among distantly related species, like primates and birds, provide opportunities for biologists to test evolutionary hypotheses about the function of specific social-cognitive skills. A complete understanding of the evolutionary pressures leading to complex social cognition requires that scientists look beyond primates to determine the causes and origins of complex cognition. Thus, we hope that we have piqued interest as to what the causes and origins of social cognitive mechanisms might be.

See also: Behavior Adaptation and Selection; Brain Evolution in Vertebrates; Cooperation; Emotion–Cognition Interactions; Evolution of Emotions; Evolutionary and Developmental Issues in Cognitive Neuroscience; Mirror Neuron Mechanism; Personality, Temperament, and Behavioral Syndromes; Primate Origins of Human Behavior; Social Communication; Social Competition and Conflict Resolution; Social Learning and Behavior Transmission; Social Relationships and Social Knowledge.

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