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## Social Knowledge

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## Abstract

The social milieus of animals can be complex, ranging from almost completely asocial to monogamous pairs (no mean feat) to entire societies. To adapt to a constantly shifting environment of individuals striving toward their own goals, animals appear to have evolved specialized cognitive abilities. As appealing and intuitive as the idea of social cognition is, just defining it is difficult. We attempted to delineate social cognition, speculate on its adaptive value, and come to an understanding of what we mean when we talk about complexity. Transitive inference was often brought up as an example of a cognitive ability that is important for social animals, though the focus of much of the discussion was on theory of mind. For some, theory of mind is something of a Holy Grail, whereas for others, it is more of a McGuffin. There are a number of challenges and debates in trying to determine what cognitive abilities different animals use to solve their social problems. This chapter discusses methodological approaches and issues that are needed to propel the future of research into social knowledge.

## Social Cognition: What Is It, and What Is It Good For?

### What Is Social Cognition?

Simply put, social cognition comprises cognitive processes that are applied to social behavior. That may sound trivially obvious; however, there are some tricky waters to be navigated in this thimble-sized definition.

What is social and what is cognition? One important issue concerns the question of whether social cognition is, indeed, special and distinct from, say, physical cognition. Examples of behaviors and capacities that are examined under the rubric of social cognition include individual recognition, social partner preferences, development and maintenance of relationships (e.g., reconciliation and alliances), triadic relationships (including transitive inference),

morality, social preferences, theory of mind, contingent social coordination, collaboration, cooperation, social executive function, synchrony in time and space, social learning (e.g., imitation), gaze following, social manipulation, deception, predicting behavior, teaching, imitation, and punishment. The challenge is to determine which cognitive processes underlie these different behaviors, as well as to analyze how different species might use different processes to achieve the same outcomes.

Behaviors are observable phenomena. We can infer from these phenomena their function, namely their adaptive value, and their underlying structure, specifically their mental processes (cognitions) and the mechanisms which underlie these (such as neurological structures and hormones, as well as associative learning mechanisms). While behavioral ecologists tend to be interested in the functions of behaviors, comparative psychologists focus more on the processes. These divergent interests are both highly informative in explaining why an animal does what it does, though disagreements do arise, in part, because specialists in these fields often talk solely about the function or the process without agreeing that they might be talking about the same phenomena. Using the same terms for these different levels of explanation (ultimate and proximate, respectively) does little to reduce the confusion, a point emphasized in our discussion of folk psychology. For cognition researchers, the functional approach to understanding behavior is very important since cognitive processes should, or at least can, be tailored to specific adaptive problems.

### **Social Cognition as Distinct from Physical Cognition**

In theory, at least, social cognition is different from physical cognition because it addresses problems linked to interactions with other agents, whereas physical cognition deals with problems linked to a relatively passive environment. Typically, the physical environment does not change rapidly, from moment to moment, as the social environment can, and thus it is more predictable: a solution which works today will likely work as well tomorrow. For example, the physics of tool use are constant, and landmarks used for orientation typically persist over long time periods. In a social environment, however, individuals pursue their own goals, and things such as rank orders and quality of relationships are subject to change. This often leads to the situation where the optimal behavior of an individual depends on how its partner(s) behaves. A partner's behavior may be variable because many behaviors are condition dependent (e.g., hungry animals behave differently from satiated ones, reproductively active animals differently from non-reproducing ones).

In terms of sociality, game theory provides a partial answer to why social cognition might be different from physical cognition. Game theory is a formal system in both behavior ecology and economics concerned with interactions between individuals and their choices. Optimality (or choice) theory provides

another modeling approach. The key difference between the two, as used in behavioral ecology (Krebs and Davies 1993), is that the optimality approach assumes that the environment is passive. Under this assumption, one best solution emerges and all animals should behave in the same way. For example, animals should only eat high quality food and ignore food of lower quality as long as the density of high quality food is above a threshold. Below that threshold, animals should eat anything they find. In the game theoretical approach, the environment is not passive but consists of other agents with their own goals. Therefore, the best behavioral strategy to adopt during an interaction often depends on what others are doing. Whether animals treat game theoretical and optimality problems differently is an open question.

### **Adaptive Value of Social Cognition**

A behavior that is specialized in one domain may be used in another domain, making it difficult to determine whether a given ability involves physical or social cognition (or some of both). Memory, for instance, is domain general, but memory for faces may build on this due to selection pressures for a specialized trait. Adaptive social behavior would come about from selective pressures in the social domain, distinct from generalized cognitive abilities or those adapted to nonsocial problems, such as foraging. (Whether predator-prey interactions count as “social” is something that is rarely considered; the emphasis is usually on conspecifics, though this need not be the case, as in, e.g., interspecific mutualisms.) Social problems include predicting the behaviors of others (animate beings), possibly manipulating them or coordinating with them, or recognizing relationships among individuals. To determine whether a given trait is specialized for the social domain, and hence is underpinned by specialized cognitive abilities, it helps to consider the trait’s adaptive function. For behaviors such as navigation, it is clear that the cognitive processes which lead to the animal getting home, for instance, are adaptive. Researchers can then manipulate components of that process and measure whether the animal achieves its goal, or not, and how it does so.

For social behavior, this can be more difficult. Consider transitive inference, inferring relationships among items. The ability to infer from one’s belief that “4 is greater than 2” and “2 is greater than 1” to the belief that “4 is greater than 1” is an ability that cuts across domains, but it might be selected for in the social realm. An animal that lives in a social group may not only have some knowledge of its own relationship to other individuals in the group, say whether it is dominant to *D* and *E* and subordinate to *A* and *B*, but it may also recognize the relationships among others in the group (e.g., that *B* is also subordinate to *A* and dominant to *D*). Although the adaptive value of a particular cognitive ability often seems to be intuitively obvious, this is usually very difficult to demonstrate empirically. We can hypothesize, for example, that

transitive inference allows animals to recognize other individuals' dominance ranks, recruit alliance partners, and assess potential rivals' fighting abilities, but it is almost impossible to assign a fitness value to these behaviors or to demonstrate any individual variation in this ability that might be related to reproductive success.

A related problem arises when we attempt to identify the mechanisms underlying a particular cognitive ability. Again, consider transitive inference. There are several ways by which an animal could infer that  $B > D$  in a sequence in which  $A > B > C > D > E$ , etc. One way is through associative strength; that is,  $B$  is valued higher than  $C$  because of its association with  $A$ , and  $C$  is valued higher than  $D$  because of its association with  $B$ . This indirect acquisition of associative strength, or "value transfer" (von Fersen et al. 1991; Shettleworth 2010b), predicts that error rates will be higher at the end of a sequence than at the beginning, such that the discriminations  $B/C$  or  $B/D$  will be more accurate than  $C/D$  or  $C/E$ . Error rates will also increase significantly if a new item appears in the sequence. By contrast, an animal that has a linear representation of the entire sequence recognizes an item's ordinal position in the list. Transitive inference through list representation is thought to be more cognitively complex than inference through associative strength. It should be equally accurate at the end of a list as at the beginning, and it should be relatively insensitive to omissions and substitutions (Bond et al. 2003; Shettleworth 2010b). A number of tests conducted on captive animals have suggested that pigeons (*Columba livia*) make transitive inferences based on associative strength, whereas monkeys represent ordinal sequences (reviewed by Shettleworth 2010b).

An example of the difficulty involved in determining the cognitive mechanisms subsuming transitive inference comes from a comparative study of western scrub jays (*Aphelocoma californica*) and pinyon jays (*Gymnorhinus cyanocephalus*). Western scrub jays are semi-territorial corvids, living in small family groups in some areas and conditions and territorial pairs in others. By contrast, closely related pinyon jays live in large, highly structured social groups with many individual members. Bond et al. (2003) compared transitive inference in these two bird species and hypothesized that, as a result of selection pressure favoring the ability to recognize other group members' relative dominance ranks, pinyon jays would be more accurate than scrub jays. Furthermore, pinyon jays would represent the sequence as an ordinal list, whereas scrub jays would rely on associative strength. Results provided mixed support for these predictions. Pinyon jays learned the sequences more rapidly and more accurately than scrub jays, and they showed no early-order effects. However, scrub jays also learned to rank items in the sequence, though more slowly and less accurately than pinyon jays. Results such as these highlight both the value of comparative studies and their limitations. If two species can achieve almost similar results through different means, of what benefit is it to adopt the apparently more difficult method?

### Is Social Cognition Complex?

Presumably, the more complex the problem to be solved, the more sophisticated the cognitive mechanism needed, although even this intuitive claim cannot be taken for granted since simple mechanisms can sometimes do the trick (Shettleworth 2010a). As a result, again presumably, a relatively larger and more energetically expensive brain is needed to solve more complex problems. Complexity is a scale of variability in the environment, and at least three dimensions of complexity are relevant to this issue. One aspect of complexity is the possible number of variations in the environment or states of the world. If the only possible states of the world are night and day, little variation exists, and the world is not very complex. However, increasing the number of possible states of the world increases the complexity of the environment. Possible states of the world give a maximum amount of variation in the environment. Patterns in these states may, however, exist and the predictability of the patterns may reduce complexity in the environment. For example, if an individual always attacks after giving a particular threat signal, the predictability of the situation reduces its complexity. If, however, following a threat, an animal sometimes attacks and sometimes bluffs, the situation becomes more complex. Finally, strategic elements of the environment influence its complexity. If aspects of the environment depend on an individual's behavior, this increases complexity because the states of the world are not fixed but respond to an individual's behavior. This dependency is captured by the notion of a strategic game in game theory (von Neumann and Morgenstern 1947; Maynard Smith 1982). Thus, when dependency exists, the world is a moving target depending on one's own behavior, thereby increasing the complexity of the environment.

Complexity is not just an objective, external aspect of the environment. In this sense, it can be quantified by an outside observer. Animals, however, do not necessarily have to track or respond to all of this environmental complexity. We may think of more subjective approaches to measure the complexity of the environment. Wildebeest (*Connochaetes* sp.) herds can number into the tens of thousands, but no individual uses social information on all other individuals in the group. Though the complexity exists objectively in the environment, it is not effectively relevant to the organism. Thus, it is important to make conceptual distinctions between objective and subjective aspects of complexity in the environment. For instance, the fact that a pair-bond in birds only involves two parties (when they are not "eavesdropping" on other pairs) does not necessarily mean that the complexity of the relationship is reduced compared to relationships among multiple parties in a larger social group. Indeed, there is good reason to think that individuals who form strong bonds process social information in a very complex manner, particularly when reasoning about others' mental states. By contrast, individuals in larger groups which do not form strong bonds process social information at a low level of complexity because they do not know or need to know as much information about other parties

where relationships are not as “valuable” (van Schaik and Aureli 2000). As yet, we do not have very good measures or tests for social complexity which do not rely on assumptions about the underlying cognitive abilities required when living in a pair versus a larger group. The measures or tests will need to accommodate many different forms of sociality (social system, mating system) if they are going to prove useful tools for comparative analyses.

## Complexity and the Brain

If more complex environments require more complex cognitive abilities, one would expect the brain to reflect this increase in complexity. This has been called the *social intelligence hypothesis* (Dunbar 1992, 1998a).<sup>1</sup> The suggestion is that processing nonsocial information, such as the location, state and type of food, does not depend on the same structure (or complexity) of cognitive abilities as social information does (though see the technical intelligence hypothesis; Byrne and Whiten 1997). A number of analyses found that there was a strong relationship between the relative size of the neocortex and mean group size, but not with other ecological variables, such as home range size or the amount of fruit in the diet (Dunbar 1992). In primates and carnivores, the relationship is not wholly uncontroversial, as no data were presented on the relatively solitary orangutans in the original analysis, and primates living in the largest social groups, such as baboons (*Papio* sp.) and macaques (*Macaca* sp.), do not necessarily have the largest neocortices. The relationship between social complexity and brain size varies among the extant families of mammals, with some families failing altogether to conform to predictions of the social brain hypothesis, but others conforming very well (Finarelli and Flynn 2009). Recent analyses have further confused the issue because pair-bonding also correlates with brain size in many mammals (ungulates, bats, and primates; Dunbar and Shultz 2007). Many bird species display very complex forms of social behavior, but would be predicted to demonstrate poor correlations between brain size and flock size using similar analyses performed with primates (Emery 2006). In birds, there is a strong relationship between the size of the forebrain (the best neuroanatomical data available from one source) and pair-bonding (Emery et al. 2007; Shultz and Dunbar 2010).

The main problem with the social brain hypothesis is what the two variables in the analysis actually represent. Mean group size was originally chosen as a proxy measure of social complexity or level of social information processing. For example, a species that lives in a pair ( $n = 2$ ) is more limited by the number of potential relationships ( $n = 1$ ) than is a species that lives in a larger social group (say, 5 individuals) because the number of potential relationships

<sup>1</sup> Emery and colleagues propose to apply the social brain hypothesis to prosocial behavior and the Machiavellian intelligence hypothesis to the more strategic (i.e., deceptive) aspects of social behavior.



in the larger group ( $n = 10$ ) is greater than in the dyad. The natural assumption is that the greater the amount of information that can be processed in a larger group (e.g., tracking of previous relationships, dominance hierarchies, reciprocity), the larger the processor that is required, as reflected by a larger brain (or neocortex).

There is evidence that this relationship between brain size and social group size does not hold. Analysis of the vocal recognition of chacma baboons (*Papio ursinus*) and closely related geladas (*Theropithecus gelada*) found that the geladas, which live in larger social groups, did not recognize all the individuals they encounter based on their vocalizations, whereas the baboons did (Bergman 2010). This suggests that there is “missing social knowledge” in geladas, such that not all potential relationships between group members are treated equally. Thus, using mean group size as a proxy for social complexity may not be appropriate for all species. There are also intriguing data from social insects which show that, even with their very small brains (and total lack of neocortex), they can remember specific individuals and the context in which they were remembered (i.e., tracking relationships) for very long periods (Sheehan and Tibbetts 2008).

In addition, it is assumed that the brain area chosen as a variable is important to social information processing. Usually, large areas of the brain (either the forebrain or neocortex) process much more than simply social information. The neural circuitry of social behavior is being investigated in various species, including primates, to a fine level of detail, but the comparative neuroanatomical data sets have yet to catch up with current knowledge, so the same old data sets are still being used (e.g., Stephan et al. 1981). As such, there are significant issues about the quality of the neural material being used in such analyses, especially if pooled across different data sets that used different methods to prepare the material and so may not present a true representation of the actual size of the brain region under study (discussed in Healy and Rowe 2007).

### **Why Is Theory of Mind So Sexy (and Has It Screwed up Comparative Psychology)?**

Transitive inference has been discussed in the context of social complexity, with the assumption that more complex social environments will demand more complex abilities at tracking social relationships. Complex cognitive abilities do not only mean being able to track larger numbers of individuals and their relationships; knowledge of what just one other individual knows, desires, and believes is considered to be cognitively advanced, and possibly even unique to humans. The topic of “mind reading” has captivated comparative psychologists who have attempted to find this ability in other animals, but it may be that this pursuit of a cognitive “Holy Grail” may be counterproductive. Ironically, perhaps, this topic generated more discussion than any other. Below

we consider the question of why theory of mind is such a provocative research issue, the evidence for and against it, and what can be done about it. We also consider whether animals can recognize something of the emotions of others. First, however, a foray into folk psychology is needed to set the stage (for more on this topic, see Penn, this volume).

## Folk Psychology

Folk psychology is most generally defined as “our commonsense conception of psychological phenomena” (Churchland 1981:67). Minimally, folk psychology consists of “a set of attributive, explanatory, and predictive practices, and a set of notions or concepts used in these practices” (Von Eckardt 1994:300). The practices of folk psychology would include things such as predicting, explaining, justifying, evaluating, and coordinating behavior. Concepts of folk psychology include theoretical mental entities such as beliefs, desires, intentions, emotions, sensations, goals, and personality traits. These causal roles and patterns of behavior are agnostic on the question of mechanism, though it is generally assumed that the same kinds of behaviors can be implemented in very different ways, both at an algorithmic and physical level (Bickle 2008).

The use of folk psychology in animal cognition research is undeniable, but concerns arise when folk psychological terms are used that have greater connotations or causal implications than appropriate. For example, when the term “punishment” is used to describe an act of antagonism toward a rule-breaker, it may be an overattribution if this connotes a particular attitude toward the transgressor (such as a desire for rehabilitating the transgressor) rather than just retribution. Just as there are folk psychologies for humans across cultures (see Lillard 1998), there may be folk psychologies across species, and to do comparative psychology, it could be productive to look at both differences and similarities across species at the folk psychological level.

However, folk psychology can, and often is, taken as an end point, rather than a starting point. For instance, when saying that a baboon is reconciling with another baboon, can we state that “she is reestablishing cordial relationships”? Flowers will deceive insects, but not in the same sense in which people will deceive each other. Is it possible to avoid the cognitive and normative baggage attached to these words? The problem of shared vocabulary continues to vex evolutionary biologists, psychologists, and economists who use the same lay terms, such as altruism, but in subtly different ways. A philosopher would argue that the baboon example is a misuse of the term “reconcile” and that despite this, according to the folk psychological view, the term should still be used by comparative psychologists, though carefully. Folk psychology is the linguistic equivalent of giving guns to children and telling them to play carefully: misuse is inevitable. This is especially true for words in the lay vocabulary that have a rich connotation. For example, the use of the term “rape” by behavioral ecologists has been lambasted. Is “friendship” better? What about

“love”? New words can be invented for the sake of precision, just as “moron” was a term invented in 1910 to refer to people assessed with an IQ of 51–70. Once the word escaped into the open, however, it took on unintended connotations. Thus, even words invented specifically to avoid the pitfalls of folk psychology can be misused. Overfamiliarity with terms can lead to inappropriate inferential leaps, and this is as true for human psychology as comparative psychology. Although it may be useful to start with folk psychological intuitions in understanding behavior, we need to determine whether these terms are warranted in each case. As stated earlier, those intuitions must be merely starting points and open to revision during scientific investigation.

A solution to the “other minds” problem, discussed next, is not to eliminate folk psychology altogether. A possible way forward is to decide how and when the vocabulary and intuitions of commonsense psychology should be best used. For example, the use of intentional predicates (e.g., attributing mental states and representations to nonhuman animals) might be useful to comparative cognitive science. Whether any particular term (e.g., “rape,” “friendship,” “reconciliation,” “belief,” “intention”) can be appropriately applied to animals, however, is an empirical matter that must be decided on a case-by-case basis (e.g., see Silk 2002).

### Theory of Mind Defined, Narrowly and Broadly

Folk psychology is hardly the only cause of confusion and misunderstanding in comparative social cognition. Research on nonhuman social cognition has been plagued by multiple and inconsistent definitions of the term *theory of mind*. Penn (this volume) suggests that theory of mind research has been particularly susceptible to the limits of folk psychology. Psychologists have long known that commonsense views are not particularly trustworthy when it comes to our own species’ cognition; they are even less so, Penn argues, when it comes to the minds of other species. Premack and Woodruff (1978) originally coined the term “theory of mind” to refer to a human’s ability to impute mental states (e.g., goals, intentions, beliefs, and doubts) to others and to use these unobservable entities to predict and explain their own and others’ behavior. According to Premack and Woodruff, this cognitive system properly counts as a “theory” in humans because “such [mental] states are not directly observable, and the system can be used to make predictions about the behavior of others” (Premack and Woodruff 1978:515). To illustrate their point, Premack and Woodruff cited the use of propositional descriptions of the form, “Paul knows that I don’t like roses.”

In the narrow sense, theory of mind is the attribution of propositional attitudes to predict and explain behavior. A propositional attitude is an attribution of an intentional state (e.g., belief, desire, hope, want, fear) that takes a proposition as its content (e.g., “that snow is white” or “that there is ripe fruit in the tree”). An example of a propositional attitude, then, would be: “Gojelek

hopes that there is ripe fruit in the tree.” Understood narrowly in this way, theory of mind has been of primary interest in the developmental literature, where the focus has been on discovering when children are first able to attribute false belief. The motivation behind the move to understand theory of mind (narrowly defined) as the ability to attribute false belief stemmed from the idea that to determine whether an animal knows that others have beliefs, experimenters could present it with a problem where it would have to alter its own behavior in expectation of another’s behavior (Bennett 1978; Dennett 1978; Harman 1978). Predicting that another will act the same way you do is relatively simple, but making predictions of her behavior when she would act differently from you is more of a challenge, because it requires that you infer the existence of someone else’s beliefs, something that cannot be directly observed. However, this may not always be the case. A scholar in his office would have no difficulty understanding and predicting that a baker will get up at 3 o’clock in the morning to prepare the dough, though he would have a harder time explaining why the baker appears at work at 9 a.m. like the professor. Similarly, a young chimpanzee (*Pan troglodytes*) would have little difficulty understanding why a dominant will chase away a subordinate approaching his food source and not run away, like the young chimp would, when the subordinate approaches. Generally, though, different behavior in the same environment cannot be predicted via behavioral rules, because there would be no difference in the observable stimulus. The difference in the two cases must be conceptual, rather than environmental.

Theory of mind can also be broadly construed to refer to the ability to attribute mental states more generally to engage in social behaviors, like predicting and explaining, and indeed, Premack claims that this is what he and Woodruff originally meant when they introduced the term (Premack and Premack 2003). In this sense, a theory of mind involves the attribution of a mental state—an unobservable theoretical entity that is posited by a folk psychological theory. Examples of theoretical entities are beliefs and desires, but also include emotions, perceptions, sensations, sentiments, etc. Recent research has focused on this more general question about whether conceptual (i.e., nonobservable or theoretical) mediation occurs in social cognition. Comparative cognition research into mental state understanding centers primarily around theory of mind understood broadly, including the attribution of knowledge states, goals, intentions, perceptual states, and false belief. Although some claim that there is evidence of other animals’ (or, at least, chimpanzees’) ability to attribute knowledge, goals, intentions, and perceptual states, there is no experimental evidence to suggest that chimpanzees (or any other animal, for that matter) understand false belief (Call and Tomasello 2008). However, a broad use of the term sheds little light on the important social-cognitive differences between species and obfuscates the very reason why theory of mind was initially such an interesting and distinctive research domain: Do nonhuman animals, in fact, appreciate that others have unobservable mental states that modulate

their behavior? Or are we the only species which understands that others have minds of their own?

### **Theory of Mind in Animals: Putting It into Perspective**

Why is this splitting of hairs important and how can we move forward? It might seem anthropocentric to deny mental state attribution or theory of mind (in the narrow sense) to animals other than humans. However, there are a number of reasons for continuing to challenge the evidence used in favor of theory of mind. First, it is often wondered what, if anything, mental state attributions would allow a social animal to do that other processes cannot do. To be fair, when asking the question of how theory of mind evolved in humans, it does seem reasonable to look for homologs in other species. Different answers to this question suggest various potential avenues for future research. For example, the social intelligence hypothesis, especially in its Machiavellian guises (Humphrey 1978; Byrne and Whiten 1991), suggested that the attribution of belief evolved in humans to make better predictions of behavior as well as to deceive competitors more effectively, and inspired research into theory of mind (particularly false belief attribution).

Today, almost all comparative psychologists agree that social vertebrates are quite adept at predicting the observable *behavior* of other animals, including how conspecifics are likely to behave given those specific individuals' past behavior as well as the behavior of other conspecifics under similar circumstances. For humans, predictions of behavior can be made using a number of different mechanisms. One can use behavioral rules (Povinelli and Vonk 2004; Penn and Povinelli 2007b; Perner and Roessler 2010; Andrews 2005) that generalize over the target individual's past behavior, or the past behavior of other individuals. One can use group norms (Maibom 2007; Andrews 2009; Perner and Roessler 2010) to predict that others will do what they should do. One can also appeal to unobservables such as personality traits, emotions, and sensations as well as propositional attitudes such as beliefs and desires (Andrews 2011). (Note that associative learning could play some role in any of these ways of predicting behavior.) Attempts to determine how animals predict behavior has tended to pit behavioral rules (learning) against mental state understanding (propositional attitudes). This is a false dichotomy, and pluralism suggests that additional hypotheses should be considered.

It seems clear that nonhuman animals form concrete representations of the behavior of particular conspecifics as well as abstract representations of the statistical regularities in general classes of behaviors. It also seems clear that the sophistication and flexibility of nonhuman social cognition goes far beyond the limits of purely associative learning and employs what might be properly called "inferential" mechanisms and relational representations (Penn et al. 2008). One well-documented example of such inferential reasoning is the ability to make inductive generalizations on the basis of the social relation between

conspecifics (see, e.g., Bergman et al. 2003; Seyfarth and Cheney 2003c). Indeed, the ability to reason about transitive social relationships appears to be fairly widespread in the animal kingdom (Otter et al. 1999; Grosenick and Clement 2007). Thus, the important question for future research in the “theory of mind” domain is not whether animals are capable of reasoning about others’ social relationships and behavior (they are) but whether, in addition, animals are capable of reasoning about others’ unobservable mental states and, if so, what kind, when, how, and why.

Over ten years ago, Heyes (1998) complained that comparative psychology had made little progress in answering this question, and it is far from clear whether much progress has been made since then (Penn and Povinelli 2007b). One source of difficulty today is that it is rarely clear what researchers are actually claiming when they employ folk psychological terms: “chimpanzees know what others do and do not know.” For example, does claiming that one animal “knows” what another animal “knows” mean that the subject represents and reasons about how the other agent is likely to act given the other agent’s past behavior and the state of the world? Or does it mean that the subject represents the other agent’s representation of a particular state of the world? How exactly would one tease apart this difference empirically?

The same confusion plagues terms like “intentions,” “perceptions,” and even “perspective-taking.” For some psychologists, evidence that animals reason about how others typically act toward objects or what others see is taken as evidence that they understand others’ “intentions” and “perceptions” as psychological states (Tomasello et al. 2003a, b). For other researchers, this is only evidence that those animals can reason about others’ behavioral dispositions (Povinelli and Vonk 2003). The problem with “visual perspective-taking” is twofold: one needs to distinguish between Level 1 (being able to look at some object or scene or not being able to do so) and Level 2 (seeing different things when looking at the same thing or scene; Masangkay et al. 1974), and have the ability to switch between perspectives and understand that there are two perspectives involved (Perner et al. 2002). We do think that “perspective,” when properly defined, captures the central aspect of “meta-representation” which, in our view, is required for understanding false beliefs. However, another source of difficulty in studying theory of mind may be due to false presuppositions about its adaptive value and ubiquity in human social interactions. Addressing these concerns may lead to more productive future research.

## Looking Ahead

In contrast to the claim that the adaptive value of theory of mind is to increase the ability to predict behavior, some might speculate that adaptive value and propositional attitude attributions are to promote social cohesion by allowing individuals to explain, justify, and evaluate abnormal or unexpected behavior (Andrews 2009; Perner 2011). For instance, when an individual witnesses



something unusual, say crippling polio in chimpanzees or lack of cooperation, does it seek more information to determine the underlying social causes for atypical behaviors? Further experiments along this line will be interesting, because theory of mind could allow individuals to more subtly infer failures on the parts of their partners, to recognize innovations such as new tools, and to intentionally teach others.

In this context, we discussed an experimental paradigm that involved training a dominant and subordinate chimpanzee to work together according to a certain rule in order to acquire a preferred food. The rule was then changed, but only the dominant was informed of the change. Further, the dominant was given the opportunity to learn that the subordinate was working with a different rule. The prediction is that if the dominant understood that the subordinates' incorrect behavior was due to a different informational state, the dominant should not behave antagonistically toward the subordinate who would not engage in the behavior necessary for gaining food. However, if the dominant did not understand why the subordinate violated the rule, then, since the violation results in the dominant not gaining food, we would expect the dominant to behave antagonistically toward the subordinate. Experiments such as this are based on the view that attributions of beliefs have been adaptive for the development of social norms.

In this discussion of the mechanisms that may underlie the ability to predict and explain another's behavior in terms of mental states (i.e., theory of mind), we did not discuss a related mechanism based on introspection. Humphrey was one of the first to suggest that "mind reading" has to be based on the ability to model another's inner states (thoughts and feelings) based on one's own inner states *in the same context* (Humphrey 1980). This last point is perhaps the most important as it forms the basis for "putting yourself in another's shoes." Whether or not this method of predicting behavior involves some form of introspection (Gordon 1995, e.g., argues that it does not), it can only be adaptive if it is based on using, remembering, or "generating" (imaginative identification) previous experiences in the same or similar situation to the agent whose mental states you are modeling. There seems to be great potential for using this model to test whether nonhuman animals are reliant on reading external behavioral cues to understand anything about another's mental states. Determining what additional causal work reading minds adds over reading behavior alone is one of the most contentious issues in comparative cognition (Penn and Povinelli 2007b; Penn, this volume; Perner 2011). Hence, focusing on simulation tests may be an empirical means for getting past the behavior-reading-mind-reading trap (see also Lurz 2010).

In her criticism of theory of mind research in animals, Heyes suggested that a task based on introspection could provide clear evidence for mind reading (Heyes 1998; Penn and Povinelli 2007b). The idea is to provide an animal (e.g., a chimpanzee) with a novel first-person experience; namely goggles, one of which is translucent, allowing the wearer to see, and the other which is

opaque. The only way to tell the goggles apart is by an arbitrary feature, such as the color of the frames. Without any behavioral cues from the wearers, but from his own experience, the animal should be able to predict that another individual wearing the opaque goggles (say, red frames) will not be able to see, whereas the one wearing the translucent goggles (yellow frames) will. In the case of chimpanzees, individuals should beg from experimenters wearing goggles with yellow frames and not from those with red-framed goggles. This task was proposed in response to a study in which chimpanzees had to beg from an experimenter who had a bucket on her shoulders versus one who covered her head with a bucket (Povinelli and Eddy 1996). Chimpanzees in this study failed, but Heyes' (1998) concern was that even if they had passed, this may have been due to prior experience in begging from people with visible eyes. The goggles task proposed by Heyes (1998) has yet to be performed in animals but has recently been tested in young children (Teufel et al. 2011; Senju et al. 2011). The only empirical evidence (we are aware of) related to this issue is that of *experience projection* in scrub jays. These food-caching corvids cache food for later consumption and protect their caches from thieving conspecifics by hiding them in places they cannot see or moving them to new places once a potential thief has left the vicinity (Clayton et al. 2007). What is of interest to the current discussion is the fact that only jays with the *specific* experience of stealing another's caches utilize the cache protection strategy of moving caches (re-caching) to a new location in private (i.e., unknown to the previously observing jay). This re-caching behavior is not seen in jays of the same age that were not given this thieving experience, even though they had experienced their own caches being stolen. Emery and Clayton suggest that the cachers "reflected" on their previous experience of being a thief and used this experience to model a potential thief's future intention to steal and, as such, move caches to a new location to protect them (Emery and Clayton 2001). Although a reasonable assumption, especially when taken together with the other cache protection strategies demonstrated by these birds, the issue of what psychological mechanisms may underlie this behavior continues to be the subject of much debate (Penn, this volume; Shettleworth 2010b).

An example of how we might demonstrate visual perspective-taking would be to use a naturally occurring behavior, such as food-caching in scrub jays. The experimental design follows the suggestion of Heyes (1998) described above: scrub jays can be given experience with two peepholes that allows them to see into an adjacent cage. They would also have experience that one peephole allows the competitor to see while the other does not, and have a blind they can draw to block the peephole. When caching, the bird should draw the blind down only if there is a competitor in the cage with the seeing peephole, blocking his visual access. If this happens in the absence of any behavioral cues or past experience, then it is plausible that there is a perceptual state attribution, though it would not offer evidence of a belief state attribution. However, one always needs first-person experience to find out what something



is, whether it is yellow, green, hard, or soft. The same holds for transparent versus opaque. Once it has been established that one peephole is transparent and the other opaque, then one need not ascribe a mental state of “seeing” to the other individual. All that is needed is an understanding that the transparent hole needs to be blocked to prevent the other from intervening. In short, even with a clever paradigm such as this, it is hard to know what can be learned about perceptual state attribution.

One might ask whether it is possible to make any progress on the theory of mind question. Many comparative researchers bemoan the attention that theory of mind has already attracted and argue that further investment would be ill-spent. It may be more productive to focus on understanding the particular mechanisms employed by particular species in their species-typical forms of social interaction rather than in making a list of nonhuman animals’ inadequacies relative to a human benchmark. A final concern is that it might not ever be possible to demonstrate this in nonlinguistic species, and that research efforts would better be directed toward more ecologically grounded pursuits.

On a positive note, the point was raised that the theory of mind approach is, in fact, a productive research paradigm that has led to the discovery of many new phenomena, whereas a “behavior rule” approach just produces post-hoc explanations of these phenomena. The question of whether nonhuman animals have human-like mentalizing abilities or tendencies makes researchers look at and try to tease out aspects of animal behavior they would not otherwise detect. However, it is a legitimate post-hoc question to ask to what degree these newly discovered aspects are the product of a theory of mind or the product of picking up mind-relevant behaviors in conjunction with behavior rules. For instance, a high sensitivity to behavior in relation to locations of desirable objects attests to the fact that animals understand *something* about the mind, even though they may not have theory of mind in the narrow sense (Perner 2010). However, being a driving force in discovering new phenomena is one thing; overinterpreting these discoveries is another.

### Feeling into Others: Social Concerns

Like theory of mind, emotions are difficult to define without appealing to folk psychological terms. The issue here is not how we can assess the emotional experience of animals, but whether animals are able to do this with each other. Of particular interest to social knowledge are social concerns (also called fortunes-of-others emotions; Ortony et al. 1988).

Social concerns can either be aligned with the emotions and welfare of others, or misaligned. When aligned, the emotions of the subject match those of another individual, so that if the other individual is happy (or in happy circumstances), the subject is happy (symhedonia); if the other individual is sad (or in unfortunate circumstances), the subject is sad (empathy). Aligned emotions are positive social concerns, and it is easy to see how they can be important

sources of social knowledge (for reviews, see Silk 2007b, 2009; Jensen 2011). Empathy and symhedonia should motivate prosocial behavior such as comforting, sharing, and helping. It should be noted that empathy is more than just emotional contagion, which is the automatic “catching” of emotions from another individual’s expressions (Hatfield et al. 1994). Empathy requires affective perspective-taking, resulting in having emotions appropriate to the circumstances of another individual (e.g., Hoffman 1982). This is similar to the earlier argument for theory of mind in that affective perspective-taking, such as empathy, requires imputing the unobservable, not simply mirroring a behavior. Some researchers (de Waal and van Roosmalen 1979; Preston and de Waal 2002) defend the notion of empathy in animals, particularly chimpanzees. Their evidence comes largely from anecdotes, but also from observations of consolation and experiments in food provisioning. Anecdotal observations are notoriously difficult to interpret. As for consolation (i.e., providing comfort to another individual, such as after a conflict with a third party), this has been taken as being motivated by empathy. However, “consolation” may be directed at reducing the consoler’s stress, rather than the target’s, and it may serve the functional benefit of reducing the likelihood of redirected aggression (Koski and Sterck 2007, 2009). Consolation, then, may be motivated out of self-comfort (or self-protection), rather than out of a concern for the well-being of the recipient. Emotional contagion would produce this effect because seeing the distress of another individual would cause distress in the observers, and prompt them to seek comfort for themselves.

Affective perspective-taking, like simulation discussed earlier, involves inferences about the emotional state of others, and it can do so in the absence of emotional cues (Eisenberg et al. 1991; Hoffman 1984). This has been demonstrated in children by presenting a distressing scenario without any signs of distress in the target (Vaish et al. 2009). However, as yet, there is no evidence that, in the absence of emotional signals (but in the presence of an emotional event), animals show affective perspective-taking. This issue warrants future investigation. As for the motivations behind prosocial acts, it is difficult to determine whether empathy is the driving force, as has been suggested by de Waal et al. (2008), or whether something like empathy beyond emotional contagion is at work (Koski and Sterck 2010). The evidence for prosocial acts, in the absence of requests or distress signals, is rather uncommon in primates, the most extensively studied species so far. Chimpanzees, for instance, seem indifferent to outcomes affecting others, failing to give them food even at no real personal cost (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008), yet they will help them achieve goals when the signal is clear (Warneken and Tomasello 2006; Yamamoto et al. 2009; Melis et al. 2010). Socially tolerant cooperative breeders, such as common marmosets have been suggested as being more inclined to provide food for conspecifics in the absence of signaling (Burkart et al. 2007), but here, too, results are mixed (Cronin et al. 2010, 2009; Stevens 2010a).

Misaligned emotions occur when the emotional state of the subject is inconsistent with the target's welfare and emotions. Envy (unhappiness at the good fortunes of others) and *schadenfreude* (pleasure in the misfortunes of others) are examples of negative social concerns. While not likely to lead to prosocial acts, they are valuable sources of social knowledge, allowing individuals to gauge their outcomes relative to others and to be more motivated to compete with rivals, and to do so in a more sophisticated manner. For instance, they may motivate punishment and or spiteful behaviors, the former of which are adaptive by deterring uncooperative behavior, for instance (Clutton-Brock and Parker 1995). Spitefulness is less intuitively adaptive, but may benefit the actor indirectly by preventing others from being better off (Jensen 2010). What needs to be determined is whether animals are motivated by their own immediate (or possibly) delayed outcomes, or whether they also have the suffering of others as goals. One area where negative social concerns have been suggested to manifest themselves is in disadvantageous inequity aversion. Sensitivity to fairness—being upset at having less than others is the minimal case—has been suggested as an essential component to uniquely human cooperation (Fehr and Fischbacher 2003), hence the interest in this topic. The typical approach to studying disadvantageous inequity aversion, as pioneered by Brosnan and de Waal (2003), involves one animal handing an object it just received back to the experimenter in exchange for a piece of food. The general idea—sometimes replicated, sometimes not—is that the subject is less likely to engage in the game if the partner receives a better quality piece of food, particularly if the partner does no work (i.e., exchange an object). If animals are averse to disadvantageous inequity, one would expect them to behave spitefully, to respond to the unfair outcome, and to any unfair intention, by causing their better-off rival to experience a loss. The ultimatum game is a widely used tool used by economists to probe fairness preferences (Güth et al. 1982). One person (proposer) is given an endowment (money) which he can then share with another person. The second person (responder) can refuse the offer of the proposer, causing both individuals to gain nothing; acceptance results in both getting the proposed division. Contrary to economic predictions based on rational decision making, responders reject offers perceived as unfair and, as a result, proposers tend to make fair divisions. Emotions appear to play a result in the decision to reject unfair offers, even at a cost; unfair offers are met with anger (Knoch et al. 2006; Pillutla and Murnighan 1996). On the other hand, chimpanzees, the only animal tested thus far, do not reject unfair offers in a mini-ultimatum game (Jensen et al. 2007a), despite being angry in another paradigm in which their food is taken away by a conspecific (Jensen et al. 2007b). At present, it is difficult to say whether animals have negative social concerns, taking the suffering of others into account.

Although motivational states are known to affect social decision making in animals ranging from honey bees to humans, the role of emotion in social cognition remains a rich area for future exploration. Another promising area

for future work at the interface between social decision making and brain function will address questions regarding how social information is transduced into cellular and molecular change in the brain, and which genes are involved in the mediation of social behavior. At present, research linking genes, brain, and social behavior is at its early stages (Fischer and Hammerschmidt 2011).

### **How Do We Study Social Cognition?**

A point that becomes clear from the preceding discussion is that there is no easy way to get into the heads of other animals. Trying to understand what animals do and do not know about their social worlds, and the specific processes they use to solve their adaptive challenges, is a great challenge. In our discussions, we considered three broad paths that researchers can take: computational models, observational studies, and experiments.

#### **Computational Models**

Computational modeling allows us to control variables selectively and observe their effects, and illustrates how relatively simple processes can produce complex outcomes. Agent-based models are particularly attractive for behavioral research.

One example of an agent-based model is GroofiWorld, which is based on the social behavior of primates (Hemelrijk, this volume). In GroofiWorld, when agents “meet,” they may “attack” the other, “groom” it, or do nothing. The model appears to reproduce many of the grooming patterns of real primates without assuming the cognitive processes usually assumed. For example, in the model the agents reciprocated grooming and reconciled fights, especially with valued partners as well as in egalitarian rather than despotic societies. Reciprocation in the model emerges because individuals have more opportunities to groom some than others. Reconciliation is statistically found in the model because former opponents are, on average, closer together after a fight than they are otherwise. Thus they have more opportunities to groom a former opponent (called reconciliation) immediately after a fight, than at other times. Thus, “reconciliation” may be in the eye of the beholder: what we observe to be “reconciliation” need not involve an underlying “conciliatory tendency.” In a similar way, “preferred reconciliation” with “valuable partners” emerges in the model without an understanding of social relationships; it emerges as a side effect of rank, because individuals in the model groom and reconcile more often with partners that are higher in rank. The model also produces a higher conciliatory tendency in egalitarian societies, because subordinates initiate interactions more often than they do in a despotic society and subordinates (compared to dominants) groom others more often. Consequently, the percentage of time spent grooming as well as the frequency of grooming immediately after

a fight (i.e., the conciliatory tendency) is higher in egalitarian than in despotic societies.

One insight is that simple behavioral rules can produce behaviors that appear complex to outside observers. Reconciliatory behavior may not require an understanding of social relationships, prosocial motivations, or anything of the sort. All that may be required is risk-sensitive aggression, grooming that reduces tension, a tendency to groom if defeat is expected, and the spatial positions of individuals.

Computational models generate an abundance of hypotheses for future investigations. The GroofiWorld model points to the importance of studying the spatial positioning of individuals in a group and their relation to dominance and grooming behavior. For example, there is less reconciliation in despotic species, such as Rhesus macaques (*Macaca mulatta*), than in more egalitarian species such as Tonkean macaques (*M. tonkeana*). This difference can be fully explained by a different spatial structure in both species.

Care is advised in how strongly one interprets findings from models like these. Just because a simple rule can explain the behavior of agents in a model does not mean that only simple rules actually apply (simple rules may also be applied only in a certain percentage of cases), or that all animals use the same rules. Mice might solve conflicts based solely on proximity rules, whereas monkeys might use an understanding of social relationships, while humans will apply norms of social conduct. The behavioral outcome might be the same in each case, but the processes governing the behaviors may be very different.

For computational models to advance research into social cognition, they must reflect the real world. In other words, the variables in the model have to be valid. In addition, models must make predictions which can later be confirmed. The DomWorld model (predecessor to GroofiWorld) satisfied these criteria. It predicted that female dominance over males was higher when aggression was fiercer and when males constituted a higher percentage in the group. Both predictions were first derived from the model and subsequently tested and confirmed with empirical data. Perhaps more importantly, some variables must be shown to work less effectively than others. For instance, in GroofiWorld, it made no difference whether dominance interactions had self-reinforcing effects or not; resemblance to grooming patterns of primates largely vanished when agents chose interaction partners at random instead of interacting with those that they met close by (thus, when the spatial effects were excluded). It is sometimes suspected that many variables and many models will produce the same, or superficially similar, outcomes (see Hemelrijk, this volume).

### Observational Studies

The best way to determine the validity of computational models is to see what animals actually *do*. Ideally, this should be done in the natural habitat using several groups of animals for as diverse a range of taxa as possible. The idea



is to build up a portrait of the behavioral repertoire. Reports of behavior of animals in the wild continue to yield surprises and insights. Observational studies from the field have revealed a fascinating array of behaviors, some very complex (Cheney and Seyfarth 1990a, 2007). For instance, spotted hyenas (*Crocuta crocuta*) often recruit conspecifics from several kilometers away with loud vocalizations (Figure 18.1); once a sufficient number of group-mates has arrived, they solicit help to mob and displace lions (*Panthera leo*) from a carcass (Figure 18.2). How hyenas assess relative group size and probability of success, how they interpret and decide to respond to recruiting signals, and how they decide with whom to form mobbing coalitions are open questions. As hyena societies are structured exactly like troops of cercopithecine primates (Holekamp 2007), priority of access to food is determined by social rank once the hyenas gain possession of the carcass from lions. Therefore, division of the spoils is never equitable among the coalition partners who mobbed and displaced the lions. This raises the question of why low-ranking hyenas cooperate in dangerous mobbing of lions if their expected rewards will be small or nil. In her chapter in this volume, Cheney suggests that monkeys might make decisions regarding whether or not to help conspecifics contingent upon earlier or anticipated behavior of group-mates, perhaps mediated by some form of long-term “emotional book-keeping.” Field studies are needed, however, to determine whether a mechanism like this might be operating among gregarious animals.

In another example, giant moray eels (*Gymnothorax javanicus*) and groupers (*Plectropomus pessuliferus*) were observed to hunt in a coordinated,



**Figure 18.1** Spotted hyenas join forces to mob a lion (photo by Stephanie M. Dloniak).

cooperative fashion reminiscent of chimpanzee hunting (Bshary et al. 2006), which raises provocative questions about the cognitive abilities used by animals. The key conclusion from the grouper-moray study is that we cannot use observations to infer the cognitive processes underlying the behavior, something that field researchers are, quite understandably, inclined to do at times, particularly when working with species that more closely resemble humans. The old idea that behaviors or patterns uniquely described in primates/chimps/humans indicate complex cognitive processes has been shattered by many studies in other taxa.

Unfortunately, field observations can obfuscate research into social cognition. Although their strength lies in describing behavioral phenomena and their adaptive functions, field observations are more opaque when it comes to inferring mental states. For example, chimpanzee hunting and border patrols have been held up as examples of a fairly sophisticated cognitive process called joint intentionality (Boesch 2005). However, coordinated behavior does not require joint intentionality; individual agents pursuing their own goals simultaneously do not have to have the goals of others in mind (Tomasello et al. 2005). Distinguishing between the two processes can only be done experimentally.

When making observations, having an open mind without preconceptions is essential, but it also helps to have expectations about what is to be observed. It may be useful to ask anthropocentric questions such as: Does the chimp intentionally deceive his opponent? Does he understand that the opponent knows where the food is? This approach goes awry, however, when the human (folk psychological) interpretation of such behavior is viewed as the only obvious and viable interpretation. Initial exploratory anthropocentric expectations need to be verified through cognitive analysis (Perner 2010). Is attribution of every element in this analysis supported by the observed behavior?



**Figure 18.2** Collective action by spotted hyenas allows them to maintain possession of a giraffe carcass also sought by a large subadult male lion (photo by Kay Holekamp).

## Experiments

Ultimately, the best way to assess the cognitive processes of animals is to use experiments, both in the laboratory and in the field. Laboratory experiments are more prone to problems of ecological validity, whereas field experiments are more likely to suffer from problems of lack of control. A basic disconnect between the two appears to be far greater in the study of social cognition than in the study of other cognitive processes (e.g., navigation). Optimally, both approaches are needed when studying a particular species, but this is done less often than one would hope. In addition, if we want to understand the *adaptive* value of any particular aspect of social cognition, this can only be addressed in the field.

Playback experiments on free-ranging baboons have revealed that animals recognize the close associates, dominance ranks, and transient consort relationships of other individuals (reviewed by Cheney and Seyfarth 2007) and that they make use of this knowledge in their social interactions. For example, when a female baboon hears her opponent's "reconciliatory" grunt shortly after being threatened, she is more likely to approach her opponent and to tolerate her opponent's approach than after hearing no grunt or hearing the grunt of another female unrelated to her opponent (Cheney and Seyfarth 1997). In other playback experiments, Wittig et al. (2007) demonstrated that baboons also accept the grunt of a close relative of a recent opponent as a proxy for direct reconciliation with the opponent herself. After hearing the grunt of one of their opponent's close relatives, subjects were more likely to come into close proximity of their opponent. By contrast, hearing the grunt of a female from a different matriline had no effect on subjects' behavior.

These results suggest that baboons take into account a variety of information when deciding how to respond to a vocalization, including the identity of the caller, call type, the nature of recent interactions, and the relation between the caller and other recent partners or opponents. In the case of kin-mediated reconciliation, baboons seem to recognize that a grunt by the relative of an opponent serves the same function as a grunt by the opponent herself.

## Ways Forward

### A Question of Questions

There are a number of reasons to study the cognitive processes and the abilities of nonhuman animals. Our attempts to understand the processes used by animals to solve their everyday problems help us understand the evolution of such behaviors. When we see lions hunt and hyenas amass to usurp their kill, comparative psychologists and others cannot help but wonder what an animal is "thinking" or how it "knows" how to achieve its goals (though behavioral ecologists might remain agnostic on these topics). Folk psychology



may inspire our pursuit, but we must remain guarded against unbridled anthropomorphism. At the most fundamental level, we need more field studies asking what animals “know” about their social worlds, and we need to learn much more about multiple aspects of social cognition in a broader array of species than has been studied to date. Only once we understand what animals know in nature will we be able to ask how they acquire and use this knowledge to make adaptive decisions.

We are also interested in animals for what they can tell us about how humans solve their social problems. This is the reason for the theory of mind research “industry,” just as it was the basis of comparative psychology when it was called behaviorism prior to present-day neuroscience. Understanding the brains of animals helps us understand human brains; discovering the processes animals use for addressing their social problems, which have parallels with our own, can illuminate the processes we use. In addition, while this is not likely to be a popular view, seeing how difficult it is for animals to solve social problems can impress us with what might otherwise seem to be mundane cognitive feats, such as understanding that a cup at which someone is pointing contains food. On the other hand, seeing how easy it is for animals to solve other social problems may lead us to realize that humans may be using simpler cognitive mechanisms than previously assumed. Some very exciting work on animal cognition is done in parallel with developmental psychology (e.g., Krachun and Call 2009). Both young children and animals can be tested with paradigms that do not rely on language. This allows us to see behaviors that are not manifestly fully formed (and culturally biased), as they are in human adults.

### **The Future of Social Cognition**

In an ideal world, one useful approach would be to compare multiple species using the same or similar methods used by teams of researchers. Consortium-level experiments have been very fruitfully applied by Joseph Henrich and others in comparing economic game theory in human cultures around the world. Similar approaches, informed by phylogenetic relatedness, are being used to choose the species most appropriate to test specific questions, such as temperament. In this way, rather than piecemeal collections of papers using different methods on few species of variable phylogenetic relatedness, researchers could begin to construct phylogenies of cognitive traits and relate these to ecological factors. While a monumental and challenging enterprise, it would be desirable to see work of this type.

Related to the use of phylogenetically corrected methods for interspecific comparisons of social cognition will be the use of these methods to inquire about the evolutionary history of specific cognitive abilities in animals, as well as the selection pressures that shape them. In the same way that Basolo (1990, 1996) was able to demonstrate that female preferences for long tails among swordtail fish evolved before the long tails themselves, study of a wider range

of species should allow us to infer the evolutionary pathways through which specific cognitive abilities developed. To date, the majority of work on social cognition has been conducted with primates, and a number of specific abilities in the domain of social cognition were long thought to be unique to primates, including, for example, transitive inference. Recent work has, however, shown that this ability is also present in nonprimate mammals, birds, and fish (Engh et al. 2006; Grosenick and Clement 2007), suggesting either that its mediating mechanisms in the nervous system are very old or that this ability evolved convergently multiple times in response to a common suite of selection pressures.

Another approach is to integrate research methodologies. Having more information on the possible role of neurological mechanisms using noninvasive data recording and imaging techniques will allow us to infer more about the possible cognitive processes that are involved. Physiological data (e.g., heart rate and hormones) will add depth to questions such as the role of stress in grooming and reconciliation. If these can be experimentally manipulated, such as by administering oxytocin to see if it has an effect on prosocial preferences in other animals as it does in humans, then we will be able to say more about the role of emotional and executive processes, and the evolutionary implications of these.

In addition, modeling results need to be integrated as hypotheses for empirical data from free-living animals and for experimental procedures with captive ones. Models based on self-organization are particularly useful, because their results are close to natural observations (usually the same observation units and statistical methods are used in the model as in empirical studies). These models are usually based on simple behavioral rules known to exist in animals (e.g., grouping behavior, the calming effect of grooming) and thus can be used by scientists to become acquainted with the consequences of simple behavioral rules for patterns of social behavior and for types of social organization. By integrating effects of space, these models generate hypotheses which we cannot think of without these models; it appears that our mind is more prone to thinking intentionally than to integrating spatial constraints on behavioral interactions. Therefore, social-spatial structure must be investigated on a large scale in many species.

Over forty years ago, talk of animal cognition was taboo. Since then, it has been slow to gain traction as a respected research discipline (see Griffin 1984). Students of animal behavior were once taught that there was no possible way to peer inside the black box, nor was there any value in looking. This was the one—and possibly only—thing upon which ethologists, behavioral ecologists, and behaviorists could all agree.

Now, however, based on a cornucopia of impressive discoveries of the cognitive abilities of animals, new insights are available which, in turn, generates more questions and will hopefully lead to further discoveries. Although it is not possible to predict where the field will progress over the next ten years, we see great potential in future research endeavors.

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