

Comparative Social Cognition

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Abstract

Theory of mind is said to be uniquely human. Is this statement justified? Thirty years of research on a variety of species has produced differences in opinion, from unequivocal positive evidence to no evidence at all for mental attribution in animals. Our review concludes that animals are excellent ethologists, but on the whole, poor psychologists. Those studies that we believe present a good case for mental attribution all possess high ecological validity, including studies on food competition by chimpanzees and cache-protection strategies by corvids. Even though the current focus of research on prediction rather than explanation may be misplaced, we believe the field is now in a strong position to discover what animals really know about their fellow beings, be it based on simple associations, behavior reading, mind reading, or something else.

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INTRODUCTION

In the 30 years since Premack & Woodruff (1978) asked the question, “Does the chimpanzee have a theory of mind?”, are we any closer to finding the answer? Indeed, is this still an important question? Although comparative social cognition has become a prominent research area within comparative psychology, it is also perhaps one of the most controversial. This is not surprising, because theory of mind (ToM) is said to be uniquely human (Penn & Povinelli 2007, Saxe 2006). In this article, we do not intend to review all that is currently known about comparative social cognition. This might be interesting from a historical perspective, but we don’t think it would get us any closer to an-

swering Premack & Woodruff’s question, for an extensive review would produce an awful lot of smoke, but very little fire based on recent assertions that there is absolutely no evidence for ToM in animals (Penn & Povinelli 2007). We therefore adopt a slightly different approach. In order to say where we think the field is going, we have to briefly describe where it’s been, discuss what the main problems and objections have been, and suggest possible ways to solve them. To do this, we agree with Penn & Povinelli (2007) that we need to think less about whether or not animals have a ToM and more about what form the underlying psychological mechanisms of social cognition take, whether they be associative, representational, symbolic, behavioral, or a mixture of different mechanisms. To this aim, we describe a number of new research paradigms based on ethological studies with high ecological validity. Thinking about why social cognition evolved and what it is used for may provide useful clues as to how we can begin to investigate the potential mechanisms of social cognition.

TRADITIONAL STUDIES OF THEORY OF MIND IN ANIMALS

Premack (1988) differentiated ToM into three classes: perceptual (the understanding of seeing and attention), motivational (the understanding of desires, goals, and intentions), and informational (the understanding of knowledge and beliefs).

Perceptual Theory of Mind

Many animals rapidly respond to eye-like shapes, which may be an antipredatory response (Burger et al. 1992, Coss 1978, Hampton 1994). However, eye gaze is also an important social signal, providing information about an individual’s perception and, subsequently, knowledge of the external world as well as their emotions and mental states (Emery 2000). Observing another move their eyes results in reflexive gaze shifts to the same point in space or object (visual co-orienting) or tracking another’s line of

sight to interesting objects in the environment (gaze following). Many species follow gaze reflexively (Anderson & Mitchell 1999, Neiworth et al. 2002) and can also follow another's direction of gaze (either head and eyes or the eyes alone) to a specific object or location (Bugnyar et al. 2004; Burkart & Heschl 2006; Emery et al. 1997; Itakura 1996; Kaminski et al. 2005; Povinelli & Eddy 1996a; Tomasello et al. 1998, 1999). Tomasello et al. (1999) also found that chimpanzees would look behind barriers of different types that an experimenter had looked behind, rather than look directly at the barrier, the first object in the line of sight (see also Okamoto-Barth et al. 2007). A similar result was also found for the other great apes (Brauer et al. 2005) and for ravens (Bugnyar et al. 2004).

Gaze may also provide a clue to another's attentional state, particularly if someone is looking at them (Gomez 1996b). If an individual's eyes are open or not covered, this implies that the individual can see things, whereas if the eyes are closed or blocked, this implies that the individual cannot see. If the eyes are averted, this implies that the individual can see some things and not others. In a series of experiments, Povinelli & Eddy (1996b) examined whether young chimpanzees would beg toward one of two experimenters: one experimenter was facing the chimpanzees, whereas the other was looking away or his eyes were closed or covered (with blindfolds, buckets, or tinted goggles), or his back was turned. The chimpanzees were rewarded if they begged toward the experimenter who could see them. The chimpanzees did not differentiate between the two experimenters based on their ability to see, except at the level of discriminating between an experimenter who was facing forward and one whose back was turned. Follow-up studies on the same chimpanzees across different ages found the same results (Reaux et al. 1999).

In a similar paradigm, which used one experimenter instead of two and recorded a variety of spontaneous behaviors oriented toward a reward, Kaminski et al. (2004) found that chimpanzees, orangutans, and bonobos produced more communicative gestures (e.g., knocking,

poking, begging, and giving) when the experimenter's face was oriented toward the subject compared to when the experimenter's back was turned, but there were no differences between the eyes-open and eyes-closed conditions. This finding suggests that apes are not responsive to the eyes (see also Tomasello et al. 2007), in contrast to capuchins in a similar task (Hattori et al. 2007).

A popular test for whether animals understand another's mental states from social cues (gaze, pointing) is the object-choice task. In this paradigm, animals are trained that food can be found under various containers, such as boxes or cups. An experimenter then baits one of two containers behind a screen, out of sight of the subject. When the screen is removed, an experimenter looks at (head and eyes or eye gaze alone) or points to the container concealing the food. The animal is then presented with a choice of the two containers to search for food. Perhaps surprisingly, primates have displayed a wide variety of responses and inconsistencies in performing this task, whereas other animals, especially domesticated animals, have had more success (Emery 2000, Miklosi & Soproni 2006).

Table 1 presents an overview of the results of these studies across a wide range of species. However, differences in experimental procedures and number of subjects and subtle differences in seemingly similar cue types do not allow for a real comparative analysis of species differences and so must be treated with some caution. For example, chimpanzees cannot use human head and eyes to locate food hidden in bowls, but they can use these cues to locate food hidden in tubes (Call et al. 1998). The addition of species-typical vocalizations to gaze cues also appeared to increase performance (Call et al. 2000), as did a simple methodological difference: the chimpanzee approaching an experimenter already providing a cue, making a choice, and then leaving the test room at the end of each trial (Barth et al. 2005). It is not clear why such subtle changes have such significant effects on performance in this task; however, it does suggest that chimpanzees' performance overall is quite poor and inflexible.

Table 1 Overview of all known object-choice tasks across a variety of mammalian and avian species

Species	TT	PP	PD	PG	HEP	HED	HT	EO	G
Ravens ¹	✓	X	X		X	X			
Jackdaw ²			✓			X		X	✓
Domestic goats ³	✓			✓	X				
Domestic horses ^{4,5}	✓	✓	✓						
Domestic dogs ⁶⁻¹²		✓		✓	✓		X	X	
Puppies ^{6,13}				✓	✓				
Wolves ¹⁴	✓	✓	✓						
Wolf cubs ¹³	✓	✓	✓						
Silver foxes ¹⁵				✓					
Domestic cats ⁸		✓	✓						
Gray seals ¹⁶			✓				X		X
Fur seals ¹⁷		✓	X	✓	✓			X	
Dolphins ^{18,19}		✓	✓		✓		✓		✓
Cotton top tamarins ²⁰	X	X			X			X	
Common marmosets ²¹	X(✓)	X(✓)	X(✓)		X(✓)			X(✓)	
Capuchins ^{22,23}	✓	✓		✓	✓(X)	✓			X
Rhesus macaques ^{24,25}	✓ ²⁴	✓ ²⁴		✓ ²⁴	X				✓ ²⁴
Orangutans ²⁶	✓			✓	✓	X		X	
Enculturated ²⁷	✓			✓	✓	✓		✓	
Gorillas ²⁸	✓	✓			✓	✓		X	
Chimpanzees ²⁹⁻³¹		✓	X		✓			X	
Enculturated ²⁷	✓			✓	✓	✓		✓	

TT, tap/touch; PP, point—proximal; PD, point—distal; PG, point + gaze; HEP, head + eyes—proximal; HED, head + eyes—distal; HT, head turning; EO, eyes only; G, glancing.

¹Schloegl et al. 2008, 2007a; ²von Bayern & Emery, *manuscr. submitted*; ³Kaminski et al. 2005; ⁴McKinley & Sambrook 2000; ⁵Maros et al. 2008; ⁶Hare et al. 2002; ⁷Soproni et al. 2001; ⁸Miklosi et al. 2005; ⁹Hare & Tomasello 1999; ¹⁰Miklosi et al. 1998; ¹¹Agnetta et al. 2000; ¹²Soproni et al. 2002; ¹³Viranyi et al. 2008; ¹⁴Miklosi et al. 2003; ¹⁵Hare et al. 2005; ¹⁶Shapiro et al. 2003; ¹⁷Schumann & Call 2004; ¹⁸Pack & Herman 2004; ¹⁹Tschudin et al. 2001; ²⁰Neiworth et al. 2002; ²¹Burkart & Heschl 2006; ²²Itakura & Anderson 1996; ²³Anderson et al. 1995; ²⁴Hauser et al. 2007; ²⁵Anderson et al. 1996; ²⁶Byrmit 2004; ²⁷Itakura & Tanaka 1998; ²⁸Peignot & Anderson 1999; ²⁹Call et al. 1998; ³⁰Call et al. 2000; ³¹Barth et al. 2005.

The basic failure of most primates to use distal head and eye gaze cues and their general successes in using proximal head or pointing cues suggests that these species are probably using low-level, proximity-based social information, such as stimulus or local enhancement, to locate hidden food, rather than a high-level interpretation based on understanding mental states. However, this does not explain the superior performance of other animals (see below).

Motivational Theory of Mind

When Premack & Woodruff (1978) introduced the term “theory of mind,” they were refer-

ring to understanding another’s intentions or goals, so-called motivational ToM. They examined whether a symbol-trained chimpanzee, Sarah, could select the appropriate response to a scenario concerning a human actor involved in a problem, such as being trapped in a locked cage or shivering next to an unlit heater. After each sequence, Sarah was shown a number of photographs of objects, one of which could be useful in solving the problem, such as a key or a lit match. Sarah accurately chose the photograph that was most appropriate for solving the problem (e.g., key for lock), which the authors proposed as evidence that she could understand the actor’s intentions. However, she could also

have paired these items based on previous associations learned in captivity (Savage-Rumbaugh et al. 1978).

One problem with interpreting goal-directed actions in terms of intentions is the distinction between external goals (e.g., food) and internal goals or action plans that will lead to goal objects (e.g., approaching and eating food; Tomasello et al. 2005). One way around this problem is to manipulate the actions of an agent so that the goal object is the same, but the means of interacting with the goal object are different. For example, Povinelli et al. (1998) tested chimpanzees' ability to discriminate between a human trainer who accidentally spilled juice on the floor, a second trainer who deliberately poured the juice on the floor in front of them, and a third trainer who aggressively threw juice onto the floor. The chimpanzees did not discriminate between any of the trainers, suggesting that they did not understand the difference between intentional and accidental acts. Call & Tomasello (1998) tested the ability of orangutans and chimpanzees to discriminate between an experimenter who intentionally placed a marker on the top of a box containing food and an experimenter who accidentally dropped the marker onto the box. All three species chose the box that had been intentionally marked. Chimpanzees were also more likely to request food, make a noise, or leave the test room when presented with an unwilling rather than an unable experimenter (Call et al. 2004).

Gaze is a good proxy for another's interest and therefore should be a good predictor of another's future actions. Santos & Hauser (1999) tested whether cotton-top tamarins recognized the link between attention and intention using an expectancy violation paradigm. They presented the monkeys with short video sequences in which an experimenter looked at one of two objects (object A) and then reached for the same object (expected event); the experimenter then recorded the amount of time the monkeys looked at this sequence. The monkeys were then presented with an unexpected event in which the experimenter looked at object B but then reached for object A. If the ex-

perimenter's head and eyes (but not eyes alone) were oriented toward object B, but the experimenter then reached toward object A, the subjects looked longer at the screen than if the experimenter looked at and reached for the same object.

In an object choice task, cotton-top tamarins, rhesus macaques, and chimpanzees were presented with two food containers; an experimenter then performed one of two actions on one of the containers. The subjects could then choose one of the containers based on the experimenter's actions (Wood et al. 2007). One action was an intentional hand grasp (reaching toward one object with an open grip); the other action was an accidental hand flop (open hand with palm upward was flopped onto one of the containers). All three species choose the object targeted by the intentional action rather than the accidental action. In a separate experiment, the subjects observed an experimenter indicating one of the containers either with a hand-occupied or hand-empty elbow touch (i.e., held an object in both hands, and touched one of the containers with an elbow, or held an object in one hand and touched one of the containers with the elbow of the free arm). The difference between these two actions was that if the hand was occupied, the only way to indicate the location of the hidden food was to use the elbow, whereas if the hand was not occupied, perhaps the action was not intentional because the experimenter would have indicated this with the free hand. All three species did choose the container indicated by the hand-occupied elbow touch (Wood et al. 2007).

Informational Theory of Mind

The final category of mentalizing is informational ToM, which includes the mental states of knowledge and belief. Three different paradigms that have been developed to examine whether animals know that others have knowledge states that differ from their own: the Guesser-Knower, Competitive Conspecific, and Ignorant Helper paradigms. In the Guesser-Knower paradigm, a reward is hidden

in one of several containers. The subject cannot see where the food is hidden, but can see that one experimenter can see (Knower) whereas a second cannot (Guesser). Once baiting was completed, the Guesser removed the occluder (a bucket, a bag, or a blindfold) or returned to the test room, and the subjects had to beg or point to one of the experimenters, the subjects' choice suggested to be based on whether they understood that the experimenters had different knowledge states.

This paradigm has been used with various species with mixed results. Povinelli et al. (1990) found that chimpanzees pointed toward the Knower (compared to the Guesser who left the room) on the majority of the trials, but only after many (200+) trials. During a transfer phase, the Guesser remained in the test room with a bag over his head. Again, the chimpanzees pointed significantly more often toward the Knower than the Guesser, but only after the first five trials (Povinelli 1994). In a replication of this study in younger chimpanzees, all subjects failed to distinguish between the Knower and Guesser (Povinelli et al. 1994).

One potential problem with this study is that chimpanzees do not understand that humans with bags, buckets, or blindfolds on their heads cannot see (Povinelli & Eddy 1996b). Therefore, the chimpanzees' inability to discriminate between the Knower and Guesser during the first five trials of the transfer phase could be attributed to a lack of understanding at this level rather than to a failure to relate seeing to knowing. Call et al. (2000) attempted to control for this possibility by replicating this basic design, but instead of the Guesser leaving the room or remaining in the room with a bag over his head during baiting, both the Knower and the Guesser remained in the room, and the Guesser had his back turned away from the subject while the Knower faced the subject. As an additional control, either the Knower or a third experimenter baited the container with food. Only two enculturated chimpanzees chose the correct cue provided by the Knower when the Knower baited the container, but not when a third experimenter baited the container.

An additional criticism of Povinelli et al. (1990) is the fact that the chimpanzee had to be taught to make begging gestures toward a human experimenter when they wanted food. Chimpanzees very rarely beg to others in the wild, and only infants beg to their parents; chimpanzees usually fight for access to food, so perhaps it is not surprising that competition is a better paradigm than cooperation for testing ToM in this species (see below). Similarly, rhesus monkeys did not appear to discriminate between trainers who were present during baiting and those that were not present, even after extensive opportunities for learning (Povinelli et al. 1991); however, capuchins were able to learn (Kuroshima et al. 2002).

In the Competitive Conspecific paradigm, two animals compete for food: only one subject knows the location of all the rewards, and the other subject knows whether its competitor had observed baiting in the past or its competitor was different from the individual that was present at the time of baiting. This paradigm was primarily developed by Menzel (1974) to examine whether chimpanzees could use others' behavior to locate hidden food or use their own behavior to deceive others into approaching locations that do not contain food (counterdeception). However, this task has been used recently to test what chimpanzees know about what others do or do not know (Hare et al. 2001, Hirata & Matsuzawa 2001).

The only other species to have been tested using this paradigm are domestic pigs (Held et al. 2001). The subjects were trained to locate food in one of four boxes baited by an experimenter. In nonrewarded probe tests, subjects were then tested for their ability to follow one of two pigs based on whether they had visual access to baiting (i.e., were knowledgeable or ignorant). All subjects except one failed to follow the knowledgeable conspecific. This may have been attributable to associations learned prior to the experiment. Uninformed pigs can also locate hidden food by utilizing the behavioral cues of an informed pig that had previously witnessed the food being hidden by an experimenter (Held et al. 2000); however, in this case

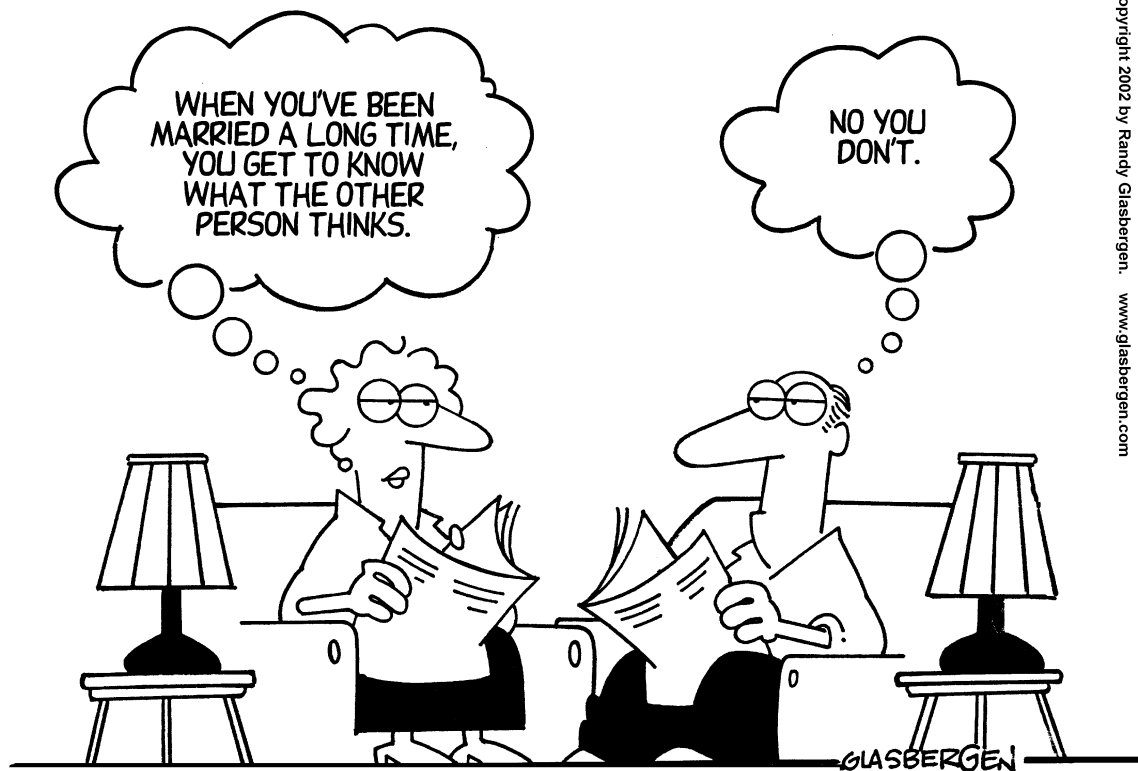


Figure 1

Mind reading and relationship intelligence. Cartoon © Randy Glasbergen. Reprinted with permission from www.glasbergen.com.

the pigs did not get to choose between a knowledgeable or an ignorant pig.

Finally, in the Informed Helper paradigm, a food item (or toy) is placed out of the subject's reach, and the subject has to indicate the location of hidden food to a human helper who is ignorant of its location. The helper also needs to use a tool to reach the food, which on some trials is also hidden from view. Whether the helper is knowledgeable or ignorant of the food, tool, or both is manipulated, and the subject's behavior differs based on how much information the experimenter possesses. This paradigm has been used with orangutans (Gomez 1996a), chimpanzees (Whiten 2000), and dogs (Viranyi et al. 2006), with differing results, suggesting that animals can signal the location of the item but not necessarily the location of the tool required to reach it.

False Belief Task

Commentators on Premack & Woodruff's (1978) paper stated that the most convincing evidence of ToM would be understanding that an agent's beliefs can differ from reality and so be counterfactual (i.e., false; Bennett 1978, Dennett 1978, Harman 1978). This form of mental attribution, so-called false belief, has been examined extensively in human children (Wimmer & Perner 1983). In the classic Sally-Anne task, a child witnesses a toy being placed into one of two containers in the presence of two dolls, Sally and Anne. An experimenter then takes Sally out of the room, and a second experimenter moves the toy from one box to the other, while Anne remains in the room. The experimenter then brings Sally back into the room, and asks the child where Sally will look for the toy. Typically, children over

3–4 years of age will say that Sally will look in the original box, because that's where she thinks the toy will be, because she didn't see the toy being moved. Children under 3–4 years, however will say Sally will look in the second box, because that's where they saw the toy last and cannot dissociate their knowledge of the toy's location from Sally's different knowledge or belief.

Language is often a fundamental feature of false belief tasks, so designing a nonverbal version has proved very challenging. However, human infants as young as 15 months old have been shown to solve a nonverbal version of the false belief task, using an expectancy violation paradigm (Onishi & Baillargeon 2005). For this and other reasons, the use of the false belief task as the standard task for determining whether an agent has a ToM has resulted in some controversy (Bloom & German 2000).

Call & Tomasello (1999) developed a nonverbal false belief task for chimpanzees, orangutans, and human children. In their design, an experimenter hid food out of the subject's view in one of two identical boxes. A second experimenter, the communicator (who had seen the baiting of the box) indicated which of the boxes contained food, and in control trials, the subjects learned to choose the box that was marked by the communicator. They also learned in additional control trials to choose the unmarked box if they saw the hider move the food from one box to another when the communicator was out of the room. Call & Tomasello (1999) suggested that if the subjects knew where the food was located (but the communicator did not), they should ignore the communicator's pointing because he had a false belief that the food remained in the box in which he had seen it placed. Only 5-year-old children passed the false belief component of this experiment, in which the hider swapped the boxes around, without showing the food, after the communicator had left the room and the communicator returned and pointed at the wrong box. The two species of apes were successful in all individual control components except false belief. This could have been because understanding false belief represents a case for third-order in-

tentionality (I know that you believe that you know X) and so may be beyond the cognitive capacities of any nonverbal creature, or because combining the individual components into one design may have been too challenging for the apes.

Problems with the Anthropocentric Approach

In her highly critical review of theory of mind research in primates, Heyes (1998) concluded that there was no evidence that chimpanzees or any other primates could represent another individual's behavior in terms of its causal structure, i.e., they lacked ToM. She provided alternative explanations for the results of the experiments, usually based on associative learning. For example, in the Guesser-Knower paradigm, the ability to choose the Knower as a means to get a reward could have been due solely to discrimination learning. The Knower was always present during baiting, and so choosing the Knower would always lead to a reward, whereas the Guesser was always absent during baiting (or their face was absent), and so choosing the Guesser would never lead to a reward. Therefore, the subject could quickly adopt a strategy based on presence or absence during baiting without recourse to explanation based on knowledge states.

An additional problem with many of the studies described in this section was their focus on proving (or disproving) whether animals have ToM. Although first tested on a chimpanzee, ToM was conceptualized as a human ability, and if by ToM we mean an all-encompassing human ToM, then surely this approach is doomed to failure. Dissociating ToM into its many constituents may be more promising; an animals' failure on a false belief task does not mean that that animal cannot reason about any mental states. We therefore advocate, along with others (Povinelli & Vonk 2003, Tomasello et al. 2003b), that the quest for ToM as a cognitive domain should be abandoned in favor of dissecting ToM into its constituent parts (i.e., mental states) and examining the conditions in

which such parts may have evolved. This is the focus of the remainder of this review.

Advocating an Alternative

When Humphrey (1976) proposed the idea that primate intelligence had evolved to solve social problems, he provided a biological platform to explain why individuals with a theory of mind would be at an advantage over those who did not have a theory of mind. The natural lives of many primates and other social animals are filled with conflict over resources, in which being one step ahead of competitors should result in early procurement of those resources and in a manner less likely to result in personal injury. Such acts of deception may indeed involve the ability to recognize what others can see, what they intend to do, and what they know (Byrne & Whiten 1988). Likewise, if one does not have the “Machiavellian smarts” to outwit competitors subtly, the alternative is to use skills in the cooperative realm, such as making friends and forming alliances, so that less-subtle means can be used to procure resources instead. For example, forming a cooperative alliance may allow individuals to access resources previously unavailable to them.

In the previous section, we discussed some of the reasons for why studies on whether animals have a theory of mind may have failed to produce unambiguous results or results that are not prone to alternative interpretations (Heyes 1998). One additional reason not discussed by Heyes (1998), but raised by some commentators to her article (Matheson et al. 1998, Purdy & Domjan 1998), is the lack of any ecological validity in their design. Examples include using conspecifics as stimuli or protagonists, or basing studies on an animal’s species-specific behavioral repertoire (Emery & Clayton 2004, Hare 2001). The following section reviews modern studies on comparative social cognition designed to approach the problem of understanding other minds from a biological and evolutionary perspective—what advantages does possessing a theory of mind have over not hav-

ing a theory of mind, and why did the ability evolve?

THE BIOLOGY OF SOCIAL COGNITION

In this section, we discuss three programs of research into the biology of social cognition across a wide range of species: competition over food, cooperation and relationship intelligence, and domestication.

Food Competition in Chimpanzees

Chimpanzees tend to compete over food. Only in limited contexts does food sharing occur; either food is given from mother to infant, or close associates will share a bounty that cannot be monopolized by an individual, such as monkey prey killed during a cooperative hunt. Hare (2001) suggested that many of the earlier studies of chimpanzee social cognition, such as begging to request food from an experimenter that can see you, do not reflect the natural behavior of chimpanzees. Although they can be trained to beg to humans, it is not part of a wild chimp’s behavioral repertoire. Hare and colleagues therefore designed a more naturalistic, ecologically valid test for visual perspective taking based on food competition rather than food sharing (Hare et al. 2000). In this paradigm, a subordinate and a dominant chimp were allowed access to an arena where food had previously been hidden. The subordinate chimp could see both pieces of food, whereas the dominant chimp could only see one. As dominant chimpanzees will monopolize all the food they can, the only way that the subordinate chimp could gain any of the food was to approach the hidden piece first. As the dominant could only see one piece, it was predicted that they should approach the visible piece first. Therefore, the subordinate’s decision about which piece to approach first should have been dictated by their understanding of what the dominant could or could not see. When the chimps were released into the arena together, the subordinate chimp

tended to get the hidden piece. To eliminate the possibility that the subordinate was only responding to the approach behavior or gaze direction of the dominant, the subordinate was released a few seconds before the dominant. As before, the subordinate tended to retrieve the hidden food. The same paradigm has also been used with capuchins and goats, which both act differently from chimpanzees. Capuchin subordinates will also approach the hidden piece first, but not when they are given a head start, a finding that suggests that they were using the dominant's behavior to guide their decision (Hare et al. 2003). Goats will also approach the hidden piece first, but only if they had received aggression from the dominant in the past. If they have received no aggression, they approached the visible piece first and so could maximize their return by getting both pieces (Kaminski et al. 2006).

Karin-D'Arcy & Povinelli (2002) suggested an alternative account of the chimpanzees' behavior, namely that because most animals prefer to feed at the periphery of a clearing to avoid potential predation, any preference for feeding behind a barrier may have been due solely to fear of eating in the open rather than an appreciation of another's line of sight (peripheral feeding hypothesis). Second, because dominants will always go for the piece of food that is in view, the subordinate must go for the food that only they can see, but to be successful the subordinate must also understand that it is only the food that is reached first that is important. In a replication of Hare's study, Karin-D'Arcy & Povinelli (2002) found that although the subordinate chimpanzees tended to retrieve the hidden food rather than the visible, they did not selectively reach or move toward the hidden piece of food first. Similarly, Brauer et al. (2007) found that subordinate chimps did not reach for the hidden food first unless the barriers, and thereby the food, were located closer to the dominants than the subordinates. It is far from clear that the chimpanzees do understand what others can and cannot see/know (Penn & Povinelli 2007, Povinelli & Vonk 2004).

Although controversial, this paradigm has been used with different levels of success in other species and often with modified designs. For example, subordinate capuchin monkeys prefer to approach the hidden piece of food, but not when they are given a head start. This suggests that their decision is based on the behavior of the dominant, not on their mental state (Hare et al. 2003). Similarly, domestic goats will also take the hidden piece of food, but only if they had received aggression from the dominant in the past (Kaminski et al. 2006). If they had never received aggression from this individual, they chose the visible piece. Again, these results suggest that the goats were basing their decisions on reading behavior (avoid approach of aggressive dominant) or conditional rules (if paired with aggressive *X*, go to the food by a barrier; if paired with nonaggressive *Y*, forage in the open).

Flombaum & Santos (2005) used humans as stimuli in a different competitive paradigm for semi-free-ranging macaques on Cayo Santiago. Here, a piece of food was located in front of each of two experimenters. The assumption was that the experimenter would be seen as a threat, and so food choice should have been dictated by understanding the attentional state of each experimenter, choosing the piece in front of the person with their attention directed away from the food. Flombaum & Santos (2005) found that more monkeys took the food placed in front of the experimenter whose attention was averted from the food than from the experimenter who was looking at the food. The monkeys appeared to make this discrimination when the person's back was turned, their face was in profile, their eyes were closed, they had a large card placed in front of their face and upper body, or they had a small card placed over their eyes. These results have been suggested as strong evidence for ToM in monkeys (Lyons & Santos 2006); however, a simpler explanation is that the monkeys avoided approaching the face with two eyes open and directed toward the food. These results are also slightly at odds with a recent study on the same population of rhesus macaques (described above), which suggested that they could

use human gestural information (e.g., pointing, eye gaze) to locate hidden food (Hauser et al. 2007). It makes sense for the monkeys on this island to have become attuned to human social cues, especially communicative cues related to the presence of food, because this population of monkeys is food provisioned. Why the monkeys should also be wary of humans, when humans give them food, needs further investigation.

Santos et al. (2006), using the same competitive paradigm, extended their studies of what others can or cannot see to what they can or cannot hear. In this experiment, rhesus monkeys were confronted with one experimenter whose attention was directed elsewhere. Behind the experimenter were two containers, each holding a grape. One container made a noise when touched; the other container was silent. When the experimenter's back was turned, the subjects tended to take the food from the silent container, but when the experimenter was looking at the food, the monkeys did not discriminate between containers. This suggests that the monkeys discriminated between containers based on whether they would alert the experimenter that food was being taken. Perhaps the monkeys were displaying an aversive response to the container that made the sound; however, this does not explain why they did not discriminate between containers when the experimenter was looking at them. The experiments are intriguing, but difficult to interpret particularly because nothing is known about the monkeys' experimental history or background.

In some competitive situations, chimpanzees also seem to appreciate that others can perceive noise. If subjects could choose to steal food from an experimenter either by approaching via a tunnel that made a noise when opened or a tunnel that was silent when opened, they tended to choose the silent tunnel (Melis et al. 2006a). By contrast, chimpanzees competing with conspecifics in an arena did not appear to take into account whether the competitor had heard a container being baited noisily compared to one that they could not hear being baited. If the chimpanzees had understood that others

can also hear some things and not hear others, they should have approached the silent container rather than the noisy container; however, they did not discriminate between them (Brauer et al. 2008). But, why were results from Melis et al. (2006a) so different? Brauer et al. (2008) suggested three potential reasons: The subjects experienced noise rather than caused the noise themselves, there was a delay between hearing the noise and the food competition (i.e., had to keep in mind that the competitor had also heard a noise), and other chimpanzees were used instead of humans. This final suggestion seems rather odd, as this paradigm has been touted as having high ecological validity. We would like to suggest an alternative explanation for the differences. In the visual domain, there are cues to whether another is attending to a visual stimulus, whereas there are no such cues to determine whether another is listening to an auditory stimulus, especially when that individual is out of view. Even if the subordinate could have watched the dominant during baiting, we do not believe that chimpanzees "prick up their ears" in order to orient toward the source of a sound.

A similar food competition paradigm has also been used to investigate what chimpanzees may know about what other chimpanzees know, particularly in their recent past (Hare et al. 2001). Again, a subordinate and dominant chimpanzee faced one another on opposite sides of an arena containing two cloth bags, one with a piece of food, the other empty. In competition tests, (a) the dominants were informed of the food's location, or their view was blocked during baiting (uninformed), or they had seen the food being hidden but it was subsequently moved out of sight (misinformed), or (b) the dominants had seen the food being hidden, but they were switched for a second dominant who had not seen the food being hidden. By contrast, the subordinate always saw where the food was hidden. As before, the subordinate was released first. However, rather than recording reaching behavior, investigators recorded only the number of pieces gained and the number of trials in which the subordinate failed to approach the food. In each case, the subordinate gained more

pieces and failed to approach more often in the trials in which the dominant was ignorant of the food's location. In a final experiment, both bags contained food, but the dominant had only witnessed one bag being baited with food. In this case, the subordinate did not retrieve more food when the dominant was ignorant of the pieces' location.

Although these results have been proposed as evidence of ToM in chimpanzees (but not by the studies' authors, we might add), they must be handled carefully. Indeed, as we discussed above, we should cease treating ToM as a homologous collection of processes that are all intimately linked, and so if we find good evidence for one domain of ToM (e.g., seeing), we should not necessarily state that we have evidence for understanding in all domains of ToM (e.g., knowing, believing, or even hearing).

Cache Protection Strategies of Corvids

Chimpanzees and other primates are not the only species that compete over food. Many birds and mammals hide (cache) food for future consumption (Vander Wall 1990). The only benefit to caching food now is if it can be retrieved in the future. This not only requires a fully functioning memory to be able to recover those caches successfully and efficiently, but it also requires strategies to reduce the probability that caches are stolen by others (Dally et al. 2006a).

For most caching animals, cache loss through pilferage is an unavoidable problem unless the cachers are present at the time of theft to defend their caches aggressively. For corvids (crow family), the situation is different because thieves can use observational spatial memory to observe another's caches and then accurately locate those caches at a later time (Bednekoff & Balda 1996a,b; Bugnyar & Kotrschal 2002; Clayton et al. 2001), even if they were made from a completely different perspective (Watanabe & Clayton 2007). As such, cachers have to develop increasingly sophisticated cache-protection strategies not only

to hide their caches from view of an observer or reduce the amount and type of visual information available to an observer during caching, but also to move their caches from places observed by a potential thief to places they have not observed. These strategies, on the surface, would appear to require some understanding of another's behavior and possibly their mental states, from both the cacher's and thief's perspective, such as what another can or cannot see, what they have or haven't seen (knowledge), as well as installing false beliefs (that a cache remains in location A, when it has actually moved to location B). However, only experimental studies have the power to truly test whether caching animals process information about thieves' mental states rather than just their behavior.

Experiments on the social cognition of cache protection have been performed with two species of corvids, western scrub-jays (reviewed in Clayton et al. 2007) and ravens (reviewed in Bugnyar 2007). Corvids naturally cache in the laboratory and appear to make caching decisions based on the presence or absence of a conspecific competitor. If a competitor is not present, there is no need to protect caches in relation to what another can or cannot see. The only requirement is that caches are hidden completely from sight and can be recovered by the cache owner. If a conspecific is watching during caching, it makes sense to try to reduce the amount of information available to observers so that they find it difficult to locate the caches once the caching bird has left the scene. Cachers appear to do this by caching in places that either are difficult for the observer to see or where the information of cache location is visually degraded.

For example, when scrub-jays in the laboratory were allowed to cache in trays either near to or far from an observing conspecific, they chose to cache in locations far from the conspecific; however, they did not discriminate between cache sites when they cached in private (Dally et al. 2005a). When the scrub-jays were presented with a choice of caching either behind a barrier or out in the open (distance

was now no longer a relevant factor), the jays chose to cache in locations out of sight of the observer (Dally et al. 2005a). This was not the result of the jays being fearful of the presence of another jay and so ceasing to cache or eat in the open, because the jays did not discriminate between caching locations when they were given only powdered (i.e., noncacheable) food. If the scrub-jays were given the choice of caching in a tray that was in the shade (i.e., in a darkened corner of the cage) or a tray that was in the light (i.e., a well-lit corner of the cage), they chose to cache in the shaded tray, but only when they were observed caching. If they cached in private, they did not discriminate between the two trays (Dally et al. 2004). Similarly, ravens observed caching in a more naturalistic arena appeared to choose cache sites that were out of view and as far as possible from potential pilferers (Bugnyar & Kotrschal 2002). Other strategies employed during caching include making false caches (stones, small objects; Clayton et al. 1996, Heinrich 1999) as well as going through the actions of caching but not leaving a food item in the cache site (Heinrich 1999). Some caching animals will either scatter food so that pilferers will find only a small amount of their caches (Clarkson et al. 1986), whereas others will switch from scatter storing to storing their food in a larder, enabling them to aggressively defend their caches (Preston & Jacobs 2001).

Cache protection may also occur at the time of cache recovery. If the cacher was observed during caching, then any food that was not to be eaten should be rehidden, in which case it makes sense to move the cache to a new location unbeknown to the previous observer. However, if no other bird was present to see the original location of the cache site, then unless the cache was recovered to be eaten, the cacher should leave it in the original cache site. Emery & Clayton (2001) examined whether scrub-jays would treat their caches differently depending on whether they had cached in view of a conspecific or whether they had been cached when the observer's view was occluded (i.e., the cacher was in private). To distinguish between responses based on the observer's mental states,

rather than learning a simple behavioral cue, the birds always recovered their caches in private. If an observer had watched the cacher making caches, then the cacher recovered and rehid their caches in new places unbeknown to the observer. By contrast, they performed very little or no recaching when they had previously cached in private and recached indiscriminately. The jays also recached in new sites when the observed and in-private caching trials were interleaved, i.e., cached when observed in tray A and then cached in private in tray B and vice versa. This scenario produced exactly the same results (Emery & Clayton 2001), demonstrating that the jays were not just responding to the presence of another jay during the last caching event (as the last caching event may have been in private). These results suggest that the jays understood that the observer knew the location of their caches, and therefore when they return to the cache sites, they should protect them by moving them to new places, whereas if the bird could not observe them during caching because their view was blocked (in-private condition), they would be ignorant of the caches' location and so recaching would not be required.

Subsequent studies addressed the question of whether the jays could also appreciate the different knowledge states of particular observers. A cacher was allowed to hide food in tray A in the presence of observer A with a second tray (B) present, but covered so that caching in tray B was not possible. After a short delay, the same cacher was allowed to cache in tray B in front of observer B, with tray A now covered. After three hours, the cacher was given the opportunity to recover their caches from both trays in one of four conditions: to recover in the presence of observer A, or in the presence of observer B, or in front of a naïve bird (C) that had not witnessed caching in either tray, or to recover in private.

During the recovery period, the birds specifically recovered the caches that observers had seen them make. For example, cachers selectively recached items from tray A when recovering in the presence of observer A, but did not recache any items from tray B (which

observer A had not witnessed being made and so would be ignorant of their location). Similarly, cachers selectively recached items from tray B when recovering in the presence of observer B but not from tray A. Observer B had not witnessed caches being made in tray A. By contrast, cachers did not recache items from either tray when recovering in the presence of the naïve bird, suggesting possible attribution of ignorance. Recaching in front of the naïve bird would have provided information they previously did not have. Finally, the cachers recached items from both trays when they recovered in private, as observers A and B had seen caches being made in these trays, so recaching them in private would move the caches to new places that potential pilferers had not seen. This replicates earlier studies of recaching in private when previously cached observed (Emery & Clayton 2001; Emery et al. 2004).

Recaching in front of another bird does not appear, on the surface, to be a particularly sensible strategy to protect caches. Indeed, dominant birds may not need to recache at all because they can defend caches aggressively (Dally et al. 2005b). However, lower-status birds should move their caches if they had been observed because of the threat provided by a pilferer with observational spatial memory. But, moving caches in front of another bird should provide new information of any new cache site. It appears that cachers did not just move their caches only one time if observed recaching, they moved them up to six times, whereas they only moved caches once if they recovered in private. Most surprisingly, when the cachers moved their caches around multiple times, they did not necessarily leave the food in the last location into which they made a bill probe. Many caches were left in earlier locations, but the scrub-jays continued to probe a few times afterward. These probes could be interpreted as pretending to cache (Dally et al. 2006b).

Ravens have also been tested for their ability to discriminate between competitors (human and conspecific) based on their knowledge states (Bugnyar & Heinrich 2005). Ravens were

allowed to cache in a small arena, either in the presence of subordinate observers or in private. A third subordinate was located in an adjacent viewing area but its view of caching was blocked. The cacher was then given the opportunity to recover its caches either in private or in the presence of the subordinate that had witnessed caching (knowledgeable) or in the presence of the third (ignorant) subordinate. Cachers recovered more caches in the presence of the previous observer than the nonobserver, especially when they approached the caches within two minutes. Bugnyar & Heinrich (2005) suggest that their results provide evidence that the raven cachers were discriminating conspecifics on the basis of their state of knowledge; however, a simpler explanation, especially based on the fact that the “storers’ response was exhibited only when the observers were moving toward the caches” (p. 1643), is that the cachers were using the competitor’s approach as a predictive cue, despite the authors’ paradoxical conclusion that “the present results provide little support for the hypothesis that approach patterns of potential pilferers allow storers to distinguish knowledgeable from ignorant competitors” (p. 1643). Bugnyar & Heinrich (2005) were careful to record various behaviors of the observer and nonobserver that may have been used to distinguish between them (in relation to the caches), such as latency to approach, time spent searching for caches, and number of places visited; however, the differences were only found in the in-private condition. This finding perhaps suggests that these behaviors were not appropriate indices of the competitor’s intent to pilfer, or the differences were too subtle to differentiate.

In a similar experiment, humans hid food in the arena, with the focal observer either in the presence of a dominant nonobserver (whose view of caching was blocked) or a dominant or a subordinate observer (both whose view of caching was unfettered). Bugnyar & Heinrich (2005) predicted that if the focal was released into the arena with a dominant nonobserver, then the focal should delay retrieving the cache until the competitor was some distance from

the cache site. However, if the focal was released with either a dominant or subordinate observer, the focal should move rapidly to the cache site in order to successfully pilfer the cache. Indeed, the focal subjects were often the first to the cache site when paired with an observer, but almost never when paired with a nonobserver. Unfortunately, it was impossible to control for a behavior-reading account, as both observers would have made a direct approach to the cache in order to reach the cache site before the focal subject.

In an extension of the previous experiment, ravens cached in the arena, observed by the focal subject and a nonstoring competitor (observer). The focal subject was then released into the arena, with the original storer, or with the observing nonstorer, or in private. The latency to the first pilfer attempt was significantly higher when the focal was released with the storer than with the nonstorer or in private. Surprisingly, there was no difference in the latency to pilfer between the storer and the nonstorer, suggesting that the storer was perhaps withholding information on the location of the caches (Bugnyar & Heinrich 2006).

There are three potential explanations for these results: a low-level explanation based on associative learning, a mid-level explanation based on sophisticated behavior-reading but with no understanding of mental states, and a high-level explanation based on the attribution of knowledge. The low-level interpretation suggests that the birds associated the action of specific caching events with the presence or absence of a specific individual (see also Heyes 1998). At recovery, the presence of that specific individual would trigger the recovery of caching. The mid-level explanation suggests that the storers read behavioral cues produced by the observers, such as spending more time attending to the tray they had cached in, compared to behavioral cues produced by nonobservers, such as lack of attention or interest in any cache site or failure to approach a cache site. By contrast, the high-level interpretation suggests that the storers remembered who was watching which specific caching event

and therefore attribute different mental states to these individuals based on their presence (knowledge) or absence (ignorance). For the Dally et al. (2006b) study, this level of interpretation would need to be quite sophisticated, as both individuals were both knowledgeable of some caching events and ignorant of others. For example, observer A had witnessed caching in tray A but not tray B, whereas observer B had witnessed caching in tray B but not tray A.

Is there any credence for the lower-level interpretations of these experiments? Heyes (1998), for example, stated that discrimination learning (presence versus absence) explained the results of earlier experiments on knowledge attribution in chimpanzees by Povinelli and colleagues (1990). This simpler explanation could also explain the ravens' and scrub-jays' behavior, but it would need to be more sophisticated and would need to be based on integrating information from the past (social context during caching) with planning for the future (potential pilfering by the observer). Note, however, that in these studies there was often only one caching and recovery trial for each condition, thereby minimizing the potential effects of learning.

We stated above that there is an alternative mid-level explanation, in which the storers' re-caching behavior may have been controlled by the observer's behavior rather than their mental states. For the raven studies, Bugnyar & Heinrich (2005, 2006) attempted to control for this mid-level behavior-reading account by recording various approach and attention behaviors of the observers and nonobservers. Although the control is useful, unfortunately its success depends on recording the right behaviors, and important behaviors for the birds may not be important behaviors for humans. A less ambiguous approach is to design control procedures in an attempt to eliminate alternative behavior-reading explanations. Dally et al. (2006b) designed such a control experiment. The cacher was presented with two caching trays (A and B). Cachers could store in tray A only in the presence of observer A, and could store in tray B only in the presence of observer B, because in each case the other tray (A or B)

was covered. The trays were then removed and presented to a second cacher (bird C), who was allowed to cache in either other original trays in the presence of an additional observer D. Then, at recovery, both trays were returned to the original cacher and they were allowed to recover caches, in the presence of either the two original observers (A or B) or the new cacher (D). If the cachers based their recaching decisions on the behavior of the observer bird, independent of whether they were present when caching in a particular tray, then the cacher should have recached items equally from both the observed tray and the other tray because observer D had witnessed caching in both trays (although by a different cacher, C). Observer D should therefore have attended to both trays equally, and so both trays would be equally at risk. By contrast, if the storers were attributing knowledge to the observer, they should have only recached items from the observed tray. Indeed, this is exactly what the cachers did (Dally et al. 2006b), suggesting that it is unlikely that the storers were using behavioral cues from observer D to influence their recaching decisions.

Bugnyar & Kotrschal (2002) suggested that cache-protection strategies and pilfering tactics may be an example of an arms race, leading to the development of increasingly complex strategies for hiding food from competitors from the perspective of the cacher and increasingly complex strategies for stealing caches without aggressive retaliation from the perspective of the pilferer (see also Emery et al. 2004). As individuals can simultaneously be both cachers and pilferers, even at the same point in time albeit with different caches, individuals not only have to keep track of their own caches but others' caches as well, also keeping in mind the social context during specific caching and pilfering events. It is therefore easy to envisage in such scenario the benefits to both caching and pilfering strategies of being able to read and predict another's behavior.

It has been suggested that because corvids cache inedible objects, such as twigs and stones, often in front of conspecifics, this form of social play may provide an opportunity to learn

about others' pilfering intentions or pilfering techniques. Bugnyar et al. (2007), therefore, allowed ravens to cache small plastic objects and then to observe what either a pilfering (P) or an onlooker (O) human did with their caches. P always stole the caches, whereas O inspected the objects but never stole them. After this experience, the ravens were then allowed to cache food in front of either P or O. The ravens started caching food more quickly in the presence of P than O; ravens also tended to cache behind obstructions and took longer to cover caches with snow. This pattern was not repeated with objects. Bugnyar et al. (2007) suggested that the caching of objects might be a tool to learn about an individual's propensity to steal food.

How do such strategies develop? Western scrub-jays readily use cache-protection strategies in a rational manner, i.e., when the strategies are most likely to result in the maximum rate of cache return (Clayton et al. 2006). However, not all scrub-jays use cache-protection strategies; their implementation depends on experience, specifically experience of stealing another's caches. Whereas scrub-jays with previous experience of being a thief will recache food items to new sites when previously observed caching, scrub-jays with no previous experience of being a thief will not recache (Emery & Clayton 2001) and do not use distance as a caching strategy (Dally et al. 2006b). We have previously suggested that the fact that pilferers may use their past experience to guide their current caching and recaching decisions, in order to protect their caches from future cache theft, may be an example of experience projection, a form of simulation theory of mind or introspection (Clayton et al. 2007; Emery & Clayton 2004, 2008).

Cooperation and Relationship Intelligence

Although the competitive hypothesis explains some aspects of chimpanzee social cognition, several questions remain. For example, what of the sociocognitive abilities of dominants?

And although chimpanzees certainly compete, they do also cooperate—from hunting colobus monkeys (Boesch 1994) to developing short-term coalitions and long-term alliances with others (de Waal 1982). Chimpanzees have also recently been demonstrated to cooperate on artificial, instrumental tasks in the laboratory, either learning to cooperate with humans (Hirata & Fuwa 2007) or spontaneously cooperating with conspecifics (Melis et al. 2006c). This recent task requires the two subjects to pull simultaneously on either end of a rope looped through hoops attached to a weighted platform with food placed on top. If one subject does not pull at the same time as their partner, the rope will pass through the hoops and will no longer be of use in pulling in the platform. Chimpanzees have also been found to recognize the need for a partner and so release them from a locked compartment, as well as to choose the most appropriate partner, i.e., the one who has been the most successful with the task in the past (Melis et al. 2006b). Bonobos are more successful than chimpanzees at this task, possibly because bonobos are more tolerant of social partners and share food more frequently with a partner (Hare et al. 2007).

In contrast to these results, studies from the same lab (and others) have found that chimpanzees also fail to perform actions that would benefit a conspecific, even at no cost to themselves, with subjects taking into account only their own self-interests (Jensen et al. 2006, 2007; Silk et al. 2005). It is not yet clear why chimpanzees will cooperate in some prosocial situations but not in others. We certainly agree that the level of tolerance and intensity of the social relationship may be critical in this regard (Hare 2007).

Corvids also form alliances, which take the form of a close relationship between two birds based on high levels of affiliative behavior, such as preening, food sharing, and social support, including support after fights (Emery et al. 2007, Seed et al. 2007). When alliances are also mated pairs, cooperation takes the form of building nests, defending the nest from conspecifics and predators, and raising offspring

(coordinating specific roles, such as foraging, feeding, and defending chicks). These joint actions could be construed as examples of shared intentionality, in which the focus of the pair is directed toward the same goal (nest, offspring, food, object, or conspecific). As with chimpanzees, rooks have been found to cooperate on a rope-pulling task requiring coordination within a pair (Seed et al. 2008). Like bonobos, rook pairs displayed great tolerance even between nonpartners, and the actions of both individuals were tightly coordinated in time. Such close coordination requires that the individuals within a pair attend to one another and to their actions. We suggest that being in a long-term relationship, such as a life-long pair bond, may afford the individuals within the pair enhanced sociocognitive skills in reading their partner's behavior and possibly their mental states. We have termed this "relationship intelligence" (Emery et al. 2007).

Domestication, Enculturation, and Socialization

We have already described the poor abilities of apes to use others' social cues to locate hidden food or to discriminate between the different attentional states of a human experimenter, except in a competitive context. Indeed, recent studies have perhaps surprisingly found that domestic dogs are superior to apes in these tasks. Dogs can use human social cues, such as head and eye direction and pointing (including cross-body pointing) to locate hidden food (Hare & Tomasello 1999; McKinley & Sambrook 2000; Miklosi et al. 1998; Soproni et al. 2001, 2002); use novel cues, such as markers, to find food (Agnetta et al. 2000); use conspecific cues (Hare & Tomasello 1999); and direct humans' searches for hidden food (Hare et al. 1998). In contrast to apes, dogs are also skilled in discriminating between different human attentional states (Call et al. 2003, Gacsi et al. 2004, Schwab & Huber 2006, Viranyi et al. 2004); however, the tests administered to dogs tend to be based on situations that often occur in the natural day-to-day lives of dogs

living in human homes, such as obeying or disobeying commands given when the owner can or cannot see the dog, or forbidding the dog to take food when the owner can or cannot see it. Recently, Hare et al. (2002) found that when compared directly on the same object-choice task, dogs outperform chimpanzees, with 9 of 11 dogs choosing correctly compared with 2 of 11 chimpanzees.

Dogs have also demonstrated an understanding of the relationship between seeing and knowing in the Guesser-Knower paradigm (Cooper et al. 2003) and the Ignorant Helper paradigm (Viranyi et al. 2006); the performance of dogs is similar to that of apes. Hare & Tomasello (2005) have suggested that the long domestication of dogs by humans has selected for this skill in using human social cues (see also Miklosi 2008, Miklosi et al. 2004). Because these paradigms are dependent on reading cooperative signals produced by humans, we might predict that all animals that have been selected for their close relationship to humans should also show these skills, in direct contrast to primates, which have not been selected for these skills. Some findings suggest that working dogs that have been directly bred to understand human gestures or to produce gestures that are comprehensible to humans (for example, gestures used during sheep herding and pointing toward a kill during a shoot) perform better in social cognition experiments than do other dogs (Hare et al. 2002, McKinley & Sambrook 2000, Miklosi et al. 2003). In addition, other domesticated animals, such as horses, goats, and cats, can use a variety of human social cues in object choice tasks (Kaminski et al. 2005, McKinley & Sambrook 2000, Miklosi et al. 2005).

In a direct test of the domestication of social cognition hypothesis, Hare et al. (2002) compared domestic dogs and wolves on the same tasks. In the object-choice task, dogs located food correctly when provided with Gaze + Point + Tap, Gaze + Point, and Point cues, whereas wolves were correct only when using the Gaze + Point cue. On a nonsocial food-finding study that was not dependent on the use of human social cues, there was no difference

in the performance of dogs and wolves. Finally, dog puppies at different ages (9–12 weeks, 13–16 weeks, and 17–26 weeks old) and with different rearing histories (litter-reared or human-reared) were tested on the object-choice task using Gaze and Gaze + Point cues. There was no difference between the litter-reared and the human-reared puppies, and no difference between the three age groups in their use of human social cues. This final result suggests that there was no effect of age or experience of humans in the use of human attention cues, therefore reinforcing the premise that the process of domestication was the key to the enhancement of sociocognitive abilities in domestic dogs.

Some problems exist with this hypothesis. First, Miklosi et al. (2003) performed experiments similar to those of Hare and colleagues (although focusing only on comprehension of human pointing) in dogs and socialized wolves and found that some of the socialized wolves could learn to use some human gestures. In two further, nonsocial tasks used to gain access to food, a rope-pulling task and a bin-opening task, there were no differences in the ability of wolves and dogs to solve this task. When the tasks were then made insolvable, i.e., the bin was locked so the food could not be reached or the rope was tied to a post rather than to the food, the dogs, but not the wolves, looked back at their owner and spent more time gazing at their owner than did the wolves. Miklosi et al. (2003) suggested that the dogs were looking back at their owners either in an attempt to communicate with them that the food was not accessible or to derive information from their owners about how to solve the task (see also Gomez 1991).

A second issue is that general domesticity is often confounded with specific use as a working animal. Currently, the majority of dogs are kept as pets; however, throughout most of the period of domesticity, dogs were kept and trained as working animals (Miklosi 2008). Interestingly, another domestic working animal, the horse, has demonstrated some basic understanding of human-given social cues to locate food (McKinley & Sambrook 2000);

however, other domestic nonworking animals (cats, goats) and other nondomestic animals (seals, dolphins) have also demonstrated some proficiency in using human social cues.

A recent experiment on hand-raised jackdaws is interesting in this regard. Jackdaws were presented with a competitive attentional state test similar in design to the test of Flombaum & Santos (2005), in which a preferred wax worm was placed between an unknown human experimenter and the jackdaw, and the latency for the jackdaw to take the worm was recorded while the experimenter was either looking at the worm or looking away (e.g., back turned, head in profile, eyes averted, eyes closed, head in profile with eyes oriented toward the worm, and one eye open while the other was closed). The shortest latencies were recorded when the experimenter's attention was directed away from the worm, but only when the experimenter was unknown to the subject; with the caregiver, the jackdaws rapidly took the worm independent of the experimenter's attentional state (A.M.P. von Bayern & N.J. Emery, manuscript submitted). In a second experiment, the ability of hand-raised jackdaws to locate hidden food using human gestures was examined using an object-choice task. The experimenter either indicated the location of the food through communicative gestures (gaze alternation or cross-body distal pointing) or static attentional states (head and eye gaze or eyes only). The jackdaws could use the communicative gestures but not the attentional states to locate the food significantly above chance (A.M.P. von Bayern & N.J. Emery, manuscript submitted). These jackdaws were not domesticated or enculturated but were hand-fed by a human during their early socialization period until they became nutritionally independent. It is also worth noting that jackdaws have a very distinctive contrast between their light-colored iris and pupil, and they frequently focus on the eye region during social interactions. These factors probably provided these hand-raised jackdaws with the ability to attend to social information from the eyes and use it in functional ways. These experiments also suggest that interaction with humans dur-

ing a critical socialization period may result in similar social skills in animals that have not been explicitly trained and have not been enculturated or selected to live with humans.

SO, WHAT DO ANIMALS KNOW (IF ANYTHING) ABOUT OTHER MINDS?

In this survey of comparative social cognition, what conclusions can we draw, if any, as to whether any nonhuman animal can think about another's mental states? Based on the evidence to date, whether one believes that animal's reason about others' behavior in terms of the underlying unobservable mental states may be a matter of faith. Some researchers believe that there is good evidence that some animals, specifically primates, do have a theory of mind (Santos et al. 2007); others suggest that some animals can read some mental states, such as seeing and knowing, but not others, such as false beliefs (Call 2001, Clayton et al. 2007, Tomasello et al. 2003a); and other investigators suggest that animals are restricted to thinking about another's behavior, but nothing more (Heyes 1998, Penn & Povinelli 2007, Povinelli & Vonk 2004). Povinelli, for example, has recently taken a position similar to that of Heyes (1998), suggesting that although chimpanzees and other animals are excellent readers of others' behavior, there is no evidence that they need to read others' mental states, and most current experiments do not allow for such an interpretation (Penn & Povinelli 2007, Povinelli & Vonk 2004).

Behavioral cues may be sufficient for predicting a novel individual's future actions but not for explaining their previous behavior, particularly when individuals have personality, past history, and experiences that contribute to their unique behavioral profile. Computing the statistical regularities of behavior when referred to patterns of behavior (e.g., behavior X leads to outcome Y) that are species-specific can act as simple heuristics, but it is less useful when taking into consideration the effects of context, personality, past history, etc. We suggest that

compiling and updating a database on every individual that is encountered would be extremely inefficient, except in the case of tracking close relationships (see above). We are not implying that reasoning about mental states is more efficient, only that it may have greater flexibility when dealing with novel individuals or familiar individuals in novel situations.

Povinelli concedes that most of human social cognition probably does not involve recognizing unobservable mental states either, and perhaps our ToM may only be used for explaining “why” rather than predicting “what” (see also Andrews 2005). Indeed, the ability to predict another’s future actions does not require the ability to attribute mental states; following the line of another’s sight or the trajectory of the walk, especially in relation to a goal object, should be sufficient. By comparison, paradigms based on explaining why others did what they did may be better placed to produce evidence for reasoning about mental states rather than behavior alone (in human and non-human animals). One such paradigm could be to present subjects with an anomalous behavior and then to record their responses (Andrews 2005). For example, subjects may look longer at a sequence in which reaching to object B does not follow looking at object A (Santos & Hauser 1999), or subjects may look back to the face of the experimenter when the subjects follow the experimenter’s gaze and do not find anything interesting in view (Tomasello & Call 2006; see also Povinelli & Dunphy-Lelii 2001).

Andrews (2005) suggested two additional heuristics that animals may use in social situations that are less dependent on reading behavior: trait attribution and inductive generalization. For trait attribution, one may respond to another individual in a particular way because the individual possesses a particular attribute that may be predictive of behavior. For example, dominant chimpanzees may be larger than subordinates and may adopt a particular posture. A subordinate that sees a dominant will respond in a species-specific manner—because dominants tend to be aggressive—so the subordinate should avoid competing for food in the

presence of a dominant. In this scenario, a dominant does not need to act toward the food to initiate changes in the subordinate’s behavior; its posture is sufficient.

For inductive generalization, one may respond to a particular individual in a specific way because the individual has always behaved in the same way in this context. Consider the following hypothetical scenario with food-caching scrub-jays: Public Enemy Number One is alpha and so always aggressively steals others’ caches without any need to implement subtle pilfering techniques. Public Enemy Number One always looks intently at the caches being made and does not attempt to hide his looking behavior. By contrast, Jack the Lad is mid-ranking and will pilfer when given the opportunity, but only when the dominant cacher has left the scene; to do so he relies on having a good observational spatial memory. When Jack the Lad observes caching by another, his behavior is dependent on whether the cacher is dominant or subordinate to him. He always turns away from the cacher or hides if the cacher is dominant. But when caching in front of Sweetie-Pie, who is more subordinate to him, he behaves just as Public Enemy Number One behaved in front of him. The point is that the caching tactics are modulated by context (whether another is watching or not), and by prior knowledge of who is currently dominant over whom. Consequently, the cacher only needs to recognize these individuals to implement appropriate cache-protection strategies based on their previous interactions.

In view of these considerations, we believe the field is now in a strong position to discover what animals do really know about their fellow beings and the extent to which this knowledge is acquired through simple associations, behavior reading, mind reading, or something else.

SUMMARY AND FUTURE ISSUES

Research into animal ToM has focused on three different categories of mental states: perceptual (e.g., seeing or hearing), motivational (e.g., desires and intentions), and informational (e.g.,

knowledge and beliefs). As part of perceptual ToM, many animals can follow another's gaze or pointing cues, will look around a barrier to see what another is looking at, and will look back to the experimenter if they do not find anything interesting in their line of sight; however, only enculturated, domesticated, or human socialized (e.g., hand-reared) animals can use social cues to find hidden food. Studies with a high ecological validity, such as food competition in chimpanzees and cache-protection strategies in corvids, have provided good evidence for understanding both seeing and knowledge in others, whereas previous studies of comparative social cognition have been explained using simple associative mechanisms, such as discrimination learning. Although the false belief task has been suggested to be the benchmark test for ToM in humans, there is no evidence that any animal has passed this test. Experience projection (predicting or explaining another's behavior in relation to experiences a subject has had in the same situation) has been described for western scrub-jays and may be a useful paradigm for testing what animals know about other minds. However, explaining why other individuals acted as they did, rather than predicting their intentions, may be the only unambiguous way to provide evidence for recognizing unobservable mental states.

We have several recommendations for the future of comparative social cognition. First, comparative social cognition needs to become more comparative. At present, most of the tests have been performed on chimpanzees, and occasionally the other great apes, monkeys, dogs and corvids, but there are few studies on other taxonomic groups. Where comparisons between species can be made—for example, with the object-choice task—care needs to be taken to standardize the methodology in order to be truly comparative. Second, paradigms

with high ecological validity have been very productive in revealing what animals may know about conspecifics. As such, proposing why social cognition evolved may also perform a useful function in the design of experiments. Such theoretical considerations should focus not only on species' similarities but also on species' differences, for example, whether differences in mating system and other socioecological factors predict why corvids and apes have convergently evolved complex social networks, alliances, and postconflict tactics yet differ in whether they reconcile after a fight (Seed et al. 2007) and in the complexity of their cooperative understanding (Seed et al. 2008).

Third, future research needs to focus on determining whether animals represent individual mental states (or mental states in combination, such as seeing and knowing) rather than focus on investigating whether animals have a theory of mind. Furthermore, experiments need to be conducted to assess the relative contributions of the different psychological mechanisms that may contribute to social cognition (associative learning, behavior reading, concepts, or mental attribution). Fourth, the development of social cognition in human infants is an active and productive area of research. It will be equally important to determine how social cognition develops in non-human animals. To our knowledge, this question has so far been addressed only in young chimpanzees (Reaux et al. 1999, Tomasello & Carpenter 2005, Tomonaga et al. 2004) and ravens (Schloegl et al. 2007b). Finally, research needs to include other theoretical perspectives aside from the traditional theory-theory approach, such as introspection and simulation theory. The development of these perspectives will have important implications for how our sense of self develops with our sense of other agents.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

First to report the use of the object-choice task to test for perspective taking in animals.

Provides an adjunct to Povinelli's arguments by suggesting that experiments should focus on explanation rather than on prediction.

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An influential study with high ecological validity investigating perspective taking in a food competition paradigm.

A second influential study with high ecological validity investigating perspective taking in a food competition paradigm.

An important review resulting in rethinking how comparative ToM experiments should be interpreted.

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A classic study on whether chimpanzees can infer intentions and knowledge in a foraging paradigm.

Presents a convincing argument that animals only represent behavior, not mental, states.

The original study of ToM in chimpanzees, which started the field of comparative social cognition.

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