CHAPTER 7
Primate Social Cognition: Thirty Years After
Premack and Woodruff

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In 1871, Darwin wrote, "The greatest difficulty which presents itself, when we are driven to the above conclusion on the origin of man (evolution through natural selection), is the high standard of intellectual power and moral disposition which he has attained." Since Darwin declared the mind as the province of biology as well as psychology, the human intellect has been a major challenge for evolutionary biologists, with some researchers emphasizing the continuity between humans and other animals and others emphasizing seemingly unique aspects of our psychological makeup. Increasing observations of nonhuman primate (hereafter, primate) behavior in both the wild and in captivity in the mid-twentieth century led to a number of proposals addressing the question of why primates seem to be so "smart." These proposals, and the comparative research they have sparked, have far-reaching implications for how we place human cognition in a broader evolutionary context—both in terms of how or to what degree humans are different from our closest relatives as well as whether broad taxonomic-level evolutionary changes in the primate lineage were necessary precursors to human evolution.

The most well-received proposal for the origin of primate intelligence argues that the social lives of primates is sufficiently complex—or predictably unpredictable—to have acted as a driving force in primate cognitive evolution. Alson Jolly (1966) set forth one of the earliest such proposals, musing on the "social use of intelligence" following her observations of wild lemurs and sifakas in Madagascar. A decade later, Nicholas Humphrey (1976) drew many of the same conclusions from watching captive rhesus monkey colonies, noting that it was navigation of the social world, rather than the physical world, that seemed to require the most complex skills. This basic thesis—that the sophisticated cognitive abilities of primates have evolved for a social function—has since taken several forms. For example, some researchers have emphasized the political maneuvering (de Waal, 1982) or "Machiavellian intelligence" (Byrne, 1988) that primates must use to succeed in their societies, while others have focused on the evolutionary arms race between intelligence and increasing social complexity (Dunbar, 2003) (for a different perspective on these issues, see Chapter 28).

The social world has therefore long been thought to be a major force shaping primate cognition—but, paradoxically, very little was known about the cognitive abilities primates actually use when interacting with other social agents. Most early proposals of the social intelligence hypothesis stemmed from observations of complex social behaviors across the primate taxonomy, but the psychological mechanisms underlying these behaviors were not well understood. For example, although human social behavior is supported by a rich belief-desire psychology through which we can represent and reason about others' subjective psychological states, it
was unknown if primates possessed any similar representational capacities. In fact, when Premack and Woodruff (Premack, 1978) first asked their big question, “Does the chimpanzee have a theory of mind?” they argued that their single test subject had shown the ability to assess the intentions of another. However, after two decades of research following this pioneering paper, several major syntheses of primate cognition weighed the evidence and concluded that although primates can use observable phenomena to make predictions about the future behaviors of others, there was no convincing evidence that any nonhuman primates represent the underlying, unobservable psychological states of others’ minds (Cheney & Seyfarth, 1990; Heres, 1998; Tomonosu & Call, 1997). Research over the past 10 years, however, has drawn this initial sweeping conclusion into question, revealing that at least some primates have some capability to assess the psychological states of others—while simultaneously showing striking differences between the social-cognitive capacities of humans and other primates (Call & Tomasello, 2008; Tomasello et al., 2003).

Here we address two aspects of primate social cognition—understanding of intentional, goal-directed action and understanding perceptions, knowledge, and beliefs—focusing on the newest comparative research since the last major review was written on the topic a decade ago. We first review evidence suggesting that diverse species of primates understand the actions of others in terms of goals and intentions, and furthermore can reason about some, but probably not all, kinds of psychological states. We then examine the hypothesis that primates show their most complex social skills in competitive contexts, and suggest that inquiry into other aspects of primate social life, such as during cooperative interactions, may prove to be the next important step for experimental inquiries into primate social-cognitive skills. Finally, we examine primate social cognition in a broader evolutionary context that may allow us to better understand both primate and human cognitive skills.

### Reasoning About Psychological States

While studies of primate social cognition have until recently made it difficult to characterize the social skills of primates with confidence, studies of human infants and toddlers have mapped out with ever-increasing resolution the fundamental changes that occur in the way young children come to think about others. This research has pointed to the importance of social-cognitive skills for the development of normal functioning adult behavior. For example, without the normal development of social-cognitive skills, children cannot participate in all forms of cultural endeavors—including language (Tomasello, 1999). Starting in the first year of life, children begin to treat other people as intentional agents and come to organize other people’s actions in terms of goals and desires (Behne et al., 2003; Carpenter et al., 1996; Gergely et al., 1995; 2002; Meltzoff, 1991; Repacholi & Gopnik, 1997; Woodward, 1998; Woodward et al., 2001). Secondly, children also come to realize that other agents will behave according to their perceptions and knowledge (Brooks & Meltzoff, 2002; Flavell, 1992; Molt & Tomasello, 2004; Phillips, 2002). By the time they are around 4 years of age, children begin to expect that another person will also act in accord with their beliefs, even when such beliefs conflict with the current state of the world (Wellman, 1990; Wimmer & Perner, 1983) (see also (Onishi & Baillargeon, 2005; Southgate et al., 2007; and Sutan et al., 2007 for possible evidence at an even earlier age).

To what extent do primates share these human developmental achievements? Do they come to reason about others’ behavior in terms of internal, unobservable psychological states? Many of the abilities that are of interest to developmental psychologists have been the topic of extensive research in nonhuman primates, and often the same paradigms used with children have been directly translated into primate studies (Tables 7.1 through 7.4). Here we first review evidence addressing what various primate species understand about intentional action, and then examine what primates understand about perceptions, knowledge, and beliefs.

### Goal-directed Behavior and Intentional Action

Evidence that at least some primates treat the actions of others in terms of their underlying goals and intentions comes from several different sources (Table 7.1). Some of the earliest evidence that primates understand the goals of others emerged through studies of social learning (1). Such research has revealed that apes may represent the actions of another individual specifically in terms of that person’s goal. That is, when confronted with an individual engaging in a novel action, apes rarely engage in exact copying of that behavior, but rather are more likely to engage in behavior toward the same goal that the actor was pursuing, a process referred to as goal emulation (Tomasello, 1990; Tomasello et al., 1987). Chimpanzees (Pan troglodytes) also seem to react differentially depending on whether a human demonstrator’s actions are relevant to his or her goal. For example, when confronted with a human demonstrator performing various actions to obtain food from a causally confusing opaque puzzle box, chimpanzees faithfully imitate the actor’s complete sequence of actions. In contrast, when the box is transparent and thus the causal nature of the box and the actor’s goal are clear, chimpanzees engage in goal emulation, excluding actions that were irrelevant to the goal (Horner & Whiten, 2003). In addition to imitating only goal-relevant actions, other evidence suggests that apes are more likely to exactly copy a human demonstrator’s behavior when that demonstrator successfully completes his or her goal than when he or she fails (Call et al., 2005; Myowa-Yamakoshi & Matsuzawa, 2001). Taken together, this work suggests that apes seem to naturally parse the behavior of others in terms of goals, and will only copy the superficial behavioral when the link between the actions and goal at hand is not readily apparent, and no other

### Table 7.1 Studies of Goal and Intention Understanding Across Nonhuman Primate Species

<table>
<thead>
<tr>
<th>Inheriting Goals</th>
<th>Distinguishing Intentions</th>
<th>Ontogeny</th>
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<td>Hominoids Chimpanzees</td>
<td>Burtman et al., 2007; Call et al., 2005; Horner &amp; Whiten, 2003; Myowa-Yamakoshi &amp; Matsuzawa, 2001; Tomasello &amp; Carpenter, 2005; Tomasello et al., 1987; Ullier, 2004; Ullier &amp; Nichols, 2006; Warneken &amp; Tomasello, 2006; Warneken et al., 2007*</td>
<td>Call &amp; Tomasello, 1998; Call et al., 2004; Povinelli et al., 1998; Tomasello &amp; Carpenter, 2005; Ullier, 2004</td>
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<td>New World monkeys</td>
<td>Capuchins</td>
<td>Brown: Kunoshima et al., 2008</td>
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<td>Callitrichids</td>
<td>Other</td>
<td>Cotton-top tamarins</td>
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<td>Lemurs</td>
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* Indicates that the study involved both human and conspecific social partners.

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appropriate means is available. To our knowledge, there is only limited work testing more distantly related species on similar goal emulation tasks, with mixed results (e.g., Kuroshima et al., 2008).

A second line of evidence suggesting that primates have some understanding of others' intentional action comes from studies in which similar or identical actions are performed, but the intention underlying these actions vary. Orangutans (Pongo pygmaeus) and chimpanzees can tell whether an action is intentional versus accidental (Call & Tomasello, 1998). Importantly, this capacity is likely not limited to apes—capuchins (Cebus apella) show similar abilities (Lyons & Santos, submitted). Moreover, chimpanzees and capuchins seem to differentiate between different types of underlying intentions. When chimpanzees are confronted with a human who fails to give them food, they are more likely to produce begging and other relevant behaviors (and are less likely to leave the room) when the human is unable to give them the food (e.g., because he or she dropped it) than when the human is unwilling to give the food (e.g., because he or she is testing). That is, the chimpanzees did not react only to the superficial result of the human’s behavior—not getting any food—but also to the reason the human failed to give the food (Call et al., 2004). Capuchin monkeys also seem to discriminate between actors that are either unwilling or unable, remaining for a longer period in the testing area when a human is unable to give them food (because a second human keeps stealing it) than when a human teases them with food. Furthermore, capuchins make these distinctions specifically when the relevant actor is a human, and not when an inanimate object (e.g., a stick) enacts the same behavior (Phillips et al., 2009).

Understanding Intentional Communicative Cues

Although these findings support the idea that at least chimpanzees and capuchins perceive others’ behaviors in terms of goals and intentions, such studies have been conducted with very few species; this limitation makes it difficult to assess whether these abilities represent convergent cognitive evolution between apes and capuchins, a distantly related New World monkey, or are rather a set of abilities that are widely shared across primates. A more widely used assessment of intention understanding in primates is a method referred to as the “object-choice” paradigm, in which animals are presented with intentional communicative cues (Table 2.2). The goal of such studies is to examine whether primates can successfully use communicative gestures to locate hidden objects, typically desirable food items. In a typical version of this type of task, a human experimenter might point at one of several cups that contains a piece of food, and then allow the subject to choose between the cups (the subject only knows something is hidden but does not know where).

Many studies utilizing this sort of object-choice paradigm suggest that while apes are able to spontaneously use such gestures to find food, their performance is fragile and often only successful at the group level (see reviews of this object-choice work in Hare & Tomasello, 2005; Call & Tomasello, 2008). However, other evidence suggests that the fragility of the apes’ performance may be less because apes cannot use gestures to find food and more due to the difficulty in understanding the cooperative-communicative intentions underlying these gestures. For example, chimpanzees are more successful when a human competitor reaches for a food cup that they also want than when a human simply points to a cup in a cooperative fashion (Hare & Tomasello, 2004). Similarly, apes are more successful using prohibitive hand gestures (“Don’t touch that one!”) to find food than they are using a standard cooperative pointing cue (Herrmann & Tomasello, 2006). This is surprising given that both the reaching and prohibitive gestures have nearly identical salient features to the pointing gesture. One interpretation of this pattern of performance is that primates are more successful at using these reaching and prohibitive types of cues because apes more often compete with others over food rather than cooperatively share information about its location with others. These competitive cues may therefore be more ecologically valid, and
potentially more motivating for some apes (as reviewed in Hare, 2001; Lyons & Santos, 2006; Santos et al., 2007a). In the context of intention understanding, interpreting others’ behaviors in terms of competitive goals (“I want the food tool!”) in these social caging paradigms may be more transparent than interpreting their behavior in terms of cooperative goals (“I want to tell you where the food is for your benefit!”). In contrast to the studies with apes, however, many monkey species fail to use communicative cues in similar kinds of studies, at least in the absence of extensive training. For example, capuchins can learn to use a pointing cue to find food, but only following several dozens or even hundreds of trials (Anderson et al., 1995; Vick & Anderson, 2000). Rhesus macaques (Macaca mulatta; Anderson et al., 1996) and cotton-top tamarins (Saguinus oedipus; Neiworth et al., 2002) also perform poorly on these tasks. However, more recent evidence complicates this picture. For example, common marmosets (Callithrix jacchus) are more successful using a pointing cue on a modified version of the task (Barkhat & Heschl, 2008). While these monkeys, as with a more species-specific looking gesture are better able to locate the hidden food (Hasier et al., 2007); Wood and colleagues (2007) further suggest that cotton-top tamarins, threes, and chimpanzees are sensitive to hand gestures when such hand gestures are indicative of an intentional component of a goal-directed action plan. As it is unclear why this result is discrepant with results from past studies involving chimpanzees, further investigations could profit from parsing out why primates may demonstrate understanding of intentions in some contexts but not others. Taken together, then, studies of communicative gesture suggest that primates’ performance may be fragile and context dependent, but primates do seem to readily use information regarding another individual’s intentions and goals in more competitive paradigms.

Gaze Following and the Roots of Mind Reading

Early studies exploring what primates know about others’ visual attention suggested that primates lack even a very gross understanding of the nature of visual perceptions. For example, inspired by Premack (1988), Povinelli and Eddy (1996a) taught young chimpanzees to use a visual begging gesture to elicit gaze-following behaviors. The researchers then presented the chimpanzees with a situation in which they could choose one of two experimenters from whom to beg. The trick was that the two experimenters were in the same location and the chimpanzees chose one experimenter could see the chimpanzees, whereas the other could not for a variety of reasons. Although the chimpanzees spontaneously chose the human with visual access to their gestures in the condition involving the most contrast between the two humans (e.g., preferring to beg from a human facing them than with her back turned), they failed to discriminate between the two humans in a variety of other, more subtle situations (such as a person with her face turned away versus one oriented toward the subject or one with a blindfold over her eyes versus another with a blindfold over her mouth). Early experiments such as these seemed to provide strong evidence that primates do not understand what others cannot see.

However, converging evidence from many different paradigms and species now appears to refute this early view of primates’ understanding of others’ perspective. Many primates are at least behaviorally responsive to the direction of others’ gaze and attention, and there is a subset of these species that appears to have a fairly robust understanding of what others perceive. At the most basic level, diverse species of primates spontaneously follow the gaze of human experimenters or conspecifics. Gaze-following behaviors allow individuals to apprehend important objects and events that others have detected in the environment, including food sources, predators, and conspecifics. Thus, gaze following allows individuals to exploit the information that others have acquired about the world. Species including chimpanzees (Povinelli & Eddy, 1996a; Tomasoello et al., 1998) and the great apes (Brauer et al., 2005; Okamoto-Barth et al., 2007); Old World monkeys such as various macaques (rhesus; Macaca mulatta; stump-tailed; M. arctoides, pigtail; M. nemestrina; Emery et al., 1997; Tomasello et al., 1998), mangabeyes (Cercocebus atys torquatus; Tomasello et al., 1998) and olive baboons; mangalas (Cercocebus atys torquatus; Tomasello et al., 1998), New World monkeys including capuchin (Vick & Anderson, 2000), cotton-top tamarins (Neiworth et al., 2002), and common marmosets (Callithrix jacchus; Barkhat & Heschl, 2006); and even some lemur species (Ring-tailed: Lemur catta; brown lemur: Lemur fulvus; black lemurs: Eulemur macaco; Shepherd & Platt, 2008; Ruiz et al., 2009) all follow gaze, at least in some contexts. Although there is variation in the degree to which various species can successfully follow eye position alone (e.g., apes: Tomasello et al., 2007; olive baboons (e.g., apes: Tomasello et al., 2007) or rather can only follow shifts in the position of the face, head, or even entire body (e.g., capuchins: Vick & Anderson, 2000; cotton-top tamarins: Neiworth et al., 2002; ring-tailed lemurs: Shepherd & Platt, 2008), this variation may be due to variation in the amount of information that the eye carries due to differences in morphology across different taxa (Kohayashi & Kohalmina, 1997, 2001).

Although gaze-following behaviors are widely shared across the primate order, the psychological basis of these co-orienting behaviors seems to vary widely. For example, the nature of gaze following in chimpanzees and other great apes suggests that individuals of these species follow gaze because they understand something about the nature of “seeing.” Apes not only directly own their gaze in the direction of others but also follow gaze around barriers and past distracting objects that are not the target of another’s gaze, sometimes by physically reorienting their own bodies (Povinelli & Eddy, 1996a; Tomasoello et al., 1999). They may also “check back” with the actor in an attempt to verify the direction of the other’s gaze or quickly stop following the gaze cues when they cannot locate the target of another’s gaze (Brauer et al., 2005; Call & et al., 1998; Tomasello et al., 2001). These flexible shifts in behavior across contexts suggest that apes follow the gaze of others because they expect there to be something interesting to see. Interestingly, those species most closely related to humans—chimpanzees and bonobos—appear to be especially sophisticated in these contexts even compared to other great apes (Okamoto-Barth et al., 2007).

The evidence for such behaviors in more distantly related primate species is less complete, mostly because few studies have been conducted (Table 7.3). Macaques, like apes, habituate to repeated gaze cues when they repeatedly cannot locate the target of another’s gaze (Gonsos et al., 2008; Tomasello et al., 2001). However, studies of New World monkeys and lemurs suggest that the co-orienting behaviors in some of these species are more reflexive. For example, cotton-top tamarins will co-orient with conspecifics at high rates during natural interactions (although the cause of this co-orienting is unclear), but fail to follow the explicit gaze cues provided in controlled experimental settings (Neiworth et al., 2002). Similarly, some lemur species co-orient with conspecifics during natural behaviors (Shepherd & Platt, 2008), but seem less able to follow gaze in experimental contexts (Anderson et al., 1995; but see Ruiz et al., 2009 for an experimental study using Conspecfic Photographs). Thus, although monkeys tested with a gaze-context interaction may be common to all primates, not all primates necessarily follow gaze because they understand that others see things.

Using Information About Gaze and Attention

Further evidence supporting the potential distinction between apes and other species comes from social cuing (or object-choice) studies. This paradigm is similar to those involving pointing gestures, although here the experimenter’s cue involves looking at the correct option (Table 7.2). Overall, evidence suggests that apes are generally successful at spontaneously using gaze cues to find the food, although, like with gesture cues, the effects are often small (e.g. Call et al., 1998; Iikura et al., 1999). Notably, apes’ performance may change dramatically depending on the specific paradigm utilized. For example, chimpanzees are much more successful using gaze cues when the experimenter looks into an object whose contents he or she alone can see (such as a tube) than when the
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<th>Table 7.3</th>
<th>Studies of Gaze Following Across Nonhuman Primate Species</th>
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<tr>
<td><strong>Follow Head Orientation</strong></td>
<td><strong>Follow Eye Orientation Alone</strong></td>
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<td>Hominoids</td>
<td>Chimpanzees</td>
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<td>Other great apes</td>
<td>Bonobos</td>
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<td>Lesser apes</td>
<td>Pilated gibbons: Horton &amp; Caldwell, 2006*</td>
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**Old World monkeys**
- Baboons: Olive: Vick et al., 2001; Socot mangabeys: Tomasello et al., 1998*

**New World monkeys**
- Callitrichids: Cotton-top tamarins: Neiwirth et al., 2002*; Common marmosets: Burkhardt & Heschl, 2006

**Other**
- Squirrel monkey: Itakura, 1996
- Ring-tailed: Shepherd & Platt, 2008*; Black: Anderson & Mitchell, 1999; Itakura, 1996; Ruiz et al., 2009*; Brown: Itakura, 1996; Ruiz et al., 2009* |

* Indicates that the study involved conspecific social partners; unless noted, the study involved human experimenters as actors.

1 Indicates that the study involved both human and conspecific social partners.
experimenter just looks at the external surface of a cup, an act that is divorced from actually seeing something (Call et al., 1998). In contrast to the results with apes, studies with monkeys suggest that whereas monkeys will often follow gaze, they tend not to use gaze as a social cue when searching for food in experiments. In many experiments, both Old and New World monkeys require extensive training with cues or fail to use gaze cues at all (e.g., olive baboons: Vick et al., 2001; rhesus macaques: Anderson et al., 1996; capuchins: Anderson et al., 1995; cotton-top tamarins: Neiworth et al., 2002; but see Hauser et al., 2007, for successful use of gaze cues in rhesus monkeys). This trend of failures suggests that, in contrast to apes, some monkey species may follow gaze without actually understanding anything about the nature of attention and visual perceptions. However, as mentioned previously, there is some evidence that modification of the standard two-option object-choice paradigm may improve the performance of some species (e.g., common marmosets: Burkart & Heschl, 2006), so future research is warranted with a wider range of species and paradigms before any strong conclusions can be made about a grade-level distinctions between apes and monkeys groups.

More converging evidence that apes have some understanding of the nature of visual perception comes from studies examining their gesture use in response to others who vary in attentional state. One such study (Povinelli & Eddy, 1996c, described previously) suggested that chimpanzees understand very little about the nature of being assigned to an experimental setting. However, other research by these researchers suggests chimpanzees may be sensitive to head movements and eye contact in similar contexts (Povinelli & Eddy, 1996b), although it is not clear what factors drive this sensitivity. Nonetheless, more recent research has suggested that apes may have performed poorly in these early gesture-use studies because they favor head and body orientation over eye position as cues to what others are seeing (Tomasetto et al., 2007). One possibility is that the low degree of constraint between the iris and sclera makes it difficult to discriminate eye direction in almost all primates but humans also appear to be unique in our ability to move our eyes independent of our general head direction (Kohayashi & Kohshima, 1997, 2001). For example, chimpanzees, bonobos, and orangutans spontaneously adjust their gaze frequency to the attentional state of the observer (i.e., they produce more gestures where an experimenter can see them), but they treat body and face orientation, rather than eye position, as the most relevant factors (Kiminki et al., 2004). Chimpanzees do, however, attend to whether an experimenter’s eyes are open when this is the only cue available (Hostetter et al., 2007). Furthermore, chimpanzees will adjust the location of their gesture depending on the focus of their partner’s attention (Povinelli et al., 2003), and all four species of great ape will move to face an experimenter so that they can execute their gestures in that person’s line of sight, rather than perform the gesture behind his or her back (Lieber et al., 2004b). Similar results have come from naturalistic observations of the gestures that apes use when interacting with each other; apes modulate their gesture use to the attentional state of their conspecific partner (Lieber et al., 2004a; Pika et al., 2003, 2005) and may use loud noises to attract attention before making visual gestures (Call & Tomasello, 2007; Poss et al., 2006).

Although monkey species do not produce gestures with the flexibility that apes do (Call & Tomasello, 2007), evidence that other primate species understand something about the nature of visual perception comes from studies looking at how the attentional state of others influences the predictions that monkeys make about the behavior of others after they look at an object. For example, when cotton-top tamarins saw a human actor look at one of two objects, they expected the actor to reach for and grab that object rather than another, previously unattended object, demonstrating longer looking at the unexpected outcome (Santos & Hauser, 1999). Diana monkeys seem to have similar expectations about the directed gaze of conspecifics (Serriff et al., 2004), but two other New World monkey species (tufted capuchins and squirrel monkeys) fail to demonstrate an understanding of the link between attention and behavior at least when tested using an expectancy violation looking method (Anderson et al.,...
Table 7.4 (Continued)

<table>
<thead>
<tr>
<th>Attention and Predictions About Seeing</th>
<th>Visual Perspective</th>
<th>Auditory Perspective</th>
<th>Deception</th>
<th>False Beliefs</th>
<th>Ontogeny</th>
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<td>Macaques</td>
<td>Lobo et al., 1999;  Santos, 2005; Povinelli et al., 1991</td>
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<td>Capuchins</td>
<td>Brown: Andersen et al., 2006; Kurosawa et al., 2002; Kurosawa et al., 2003</td>
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<td>Other</td>
<td>Squirrel monkeys: Anderson et al., 2004</td>
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<td>Strepsirhines</td>
<td>Lemurs</td>
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<td>Black: Genty &amp; Reeder, 2006</td>
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Note: The table continues on the next page.
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Many of the paradigms used to examine social-cognitive skills in primates have been adapted from the human developmental literature. As such, the "interesting" topics in primate social cognition tend to grow out of developmental studies of theory of mind. As there is some indication that primates look more skilled in studies involving ecologically valid paradigms, such as competition for food, directly adapting developmental paradigms for primates may not be the only productive way to study primate social cognition. Indeed, what these kinds of paradigms emphasize is that social-cognitive skills are functional, guiding effective behavior and allowing organisms to choose the most advantageous course of action. For example, a study varying the "intensity" of competition in the sort of conspecific-competition paradigm described earlier illustrates how perspective taking is an ability that chimpanzees use strategically. When chimpanzees only have time to retrieve one piece of food, perspective taking increases their payoffs—they will therefore target the piece that their competitor cannot see. However, if the physical properties of the task are altered such that chimpanzees can potentially retrieve all the food regardless of what their competitor can see, they will simply use a "fast" strategy and race to take both pieces while choosing indiscriminately (Brauer et al., 2007; see also Karin-D'Arcy & Povinelli, 2002). This finding emphasizes the importance of examining primate social-cognitive skills in a functional framework. Research will therefore need to consider the kinds of skills that might allow primates to be more effective social decision makers in their natural environments, and when it actually benefits them to use the skills they possess.

FROM COMPETITION TO COOPERATION

Competition is just one example of an ecologically relevant domain—primates certainly do not spend all their time competing with others for food! Rather, primate social life is a complex patchwork of both competition and cooperation—but these two opposing forces may come into play in different contexts and differentially impact different kinds of social interactions. To take one example, wild-living male chimpanzees engage in several complex cooperative behaviors (Muller & Mitani, 2005), including meat sharing (Mitani & Watts, 2001), group hunting (Boesch & Boesch, 1989), coalitionary mate guarding (Watts, 1998), and territorial boundary patrols (Watts & Mitani, 2001). Other primates also have complex patterns of cooperation and alliance formation (e.g., de Waal, 1996; Kappeler & van Schaik, 2006). As such, primates may possess sophisticated social-cognitive skills to deal with both competitive and cooperative interactions, but the kinds of skills they use may be very different in these disparate contexts. Indeed, the cooperative-communicative paradigms (such as object-choice) used so often in primate research may fail to demonstrate robust social-cognitive abilities in various species because these tasks require cooperation per se, but because they utilize specific forms of cooperation (sharing information or sharing food) that may not be a part of species-typical social interactions. In fact, studies of human cooperation suggest many ways to approach the problem in nonhuman primates that might lead to a better understanding of breadth of possible social-cognitive skills beyond the competitive contexts studied thus far. A variety of social-cognitive skills play important roles in shaping human cooperation, including knowledge about the intentions of others, the social relationship between cooperative partners, and reputation management (see reviews in Gintis et al., 2005).

Do similar social-cognitive mechanisms underlie the cooperative behaviors of nonhuman primates? Increasing evidence suggests that they do, at least in some species and contexts. For example, some species appear to have some knowledge of the quality of the relationships they share with social partners as well as being able to remember how those partners behaved in past cooperative interactions. chimpanzees will spontaneously cooperate to acquire food in an instrument task requiring joint action, competencies that they share a tolerant relationship with, but will not cooperate with intolerant partners (Meltz et al., 2000b; see Hare et al.,...
2007, for a comparison of chimpanzees and bonobos in a similar task), and will also preferentially choose to cooperate with more skillful partners over less skilled partners (Mills et al., 2006c). Correlations of natural behaviors further suggest that chimpanzees prefer to cooperate with those who have cooperated with them in the past (Milani, 2011). Although there are several very different types of mechanisms that could underlie such behaviors (see de Waal & Lutek, 1988), experimental evidence supports the hypothesis that chimpanzees show calculated reciprocity in grooming (Koyama et al., 2006) and collaborative (Mills et al., 2008) contexts. Together, these results suggest that apes remember something about the behavior of others and use this information when making social decisions—that is, they are guided by something like direct reputation when deciding whether to interact with (see also Subiaud et al., 2008). But primate social-cognitive skills are not limited to direct interactions with other primates; some primates also seem to represent the ongoing relations of other members of their community. For example, experiments with wild baboons suggest that this species understands not only their interactions with other baboons but also the third-party relationships between other members of their community (see Cheney & Seyfarth, 2007), an ability that may function as a precursor to indirect reputation formation.

There is also evidence that primates use social-cognitive skills such as reputation learning in cooperative contexts. For example, chimpanzees use their understanding of both humans’ and conspecifics’ goals to help them when they fail to reach those goals (Warkes & Tomadeso, 2006; Warkes et al., 2007). Chimpanzees also use information about whether a conspecific was the cause of their loss of access to food when deciding whether to punish that individual (Jensen et al., 2007), which may involve some form of intention reading. If this is so, chimpanzees then possess an ability thought to be an important mechanism for sustaining cooperation across repeated interactions. Notably, however, there is little evidence from any of this work that chimpanzees or other animals understand the potential of using overt forms of communication to enhance success in cooperative endeavors (see Mills et al., 2009 for references studies with a developmental component). Developmental studies have provided critical insights into human social cognition, so they could provide crucial information for understanding chimpanzee social cognition. For example, divergent developmental trajectories may be evidence of different underlying psychological mechanisms across species, even when adult behaviors appear similar (e.g., see Tomasello et al., 2001 for a developmental comparison of rhesus and chimpanzees). But perhaps the most salient limitation of current research into primate social cognition is the one easiest to remedy: whereas almost every major category of social-cognitive research has several studies examining that ability in chimpanzees, the existing data across other taxa are much more patchy—though only one or two relevant studies—and often nonconsistent (see Tables 7.1 through 7.4; the first row lists studies with chimpanzees). This missing evidence becomes even more striking for tasks that do not involve gaze-following paradigms. The consequence of this imbalance is that most of what we know about “primate social cognition” is really “chimpanzee social cognition.” This paucity of data on the social-cognitive skills of the vast majority of the Primate Order makes it difficult to draw any broad conclusions about either the social-cognitive skills of nonhuman primates or the evolutionary pressures shaping these skills. Consequently, many empirical tests of these models involve very rough generalizations about intelligence—morphological correlates such as brain size (Dunbar, 1992), making it difficult to assess the very evolutionary hypotheses that originally spurred interest in primate social cognition. However, several new approaches to the study of primate social cognition are emerging, including comparisons between closely related species and studies of convergence with other taxa—have begun to tackle this problem.

The Comparative Method: Identifying the Forces Shaping Social Cognition

Despite the major inroads that research examining primate social cognition have made in the last decade, there are still some major limitations to current research. First of all, although we began by asserting that we would review the cognitive skills that primates use during social interactions, it is notable that the vast majority of studies we have reviewed involve primates interacting with humans (Tables 7.1 through 7.4; studies that involve conspecifics are marked studies with human partners are underlined). Consequently, while we know a lot about the cognitive skills primates can utilize, we are less sure about when and how primates actually use these skills when interacting with conspecifics in natural contexts. Similarly, few studies have examined the ontogenetic development of these skills (Tables 7.1 through 7.4; the last column in each category techniques in evolutionary biology (Mayr, 1982). The comparative method allows us to reconstruct a phenomenon (evolution via natural selection) that often cannot be observed directly and to foretell the effects of different treatments on the observed differences. Consequently, it may be just as powerful a technique for the functional questions about social-cognitive abilities of birth.
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interpretation of these data are that such mechanisms are quite evolutionarily ancient, extending back to approximately 40 Ma (Steiper & Young, 2016) when the primate lineage leading to New World monkeys such as capuchins split from the lineage leading to Old World monkeys and apes. However, another possibility is that these similar behaviors actually represent instances of social-cognitive convergence, or parallel evolution, in different lineages. Capuchins—who engage in both sophisticated tool use (Visalberghi, 1990; see Chapter 29), and hunting behavior (Rose, 1997)—are often considered behaviorally convergent with chimpanzees (Premack, 1966). Similarly, if food competition is a critical selective force driving the evolution of perspective-taking, then these—with their highly despotic social system (de Waal & Luttbeg, 1989)—might also represent a case of convergence. However, such instances of possible convergence are certainly not a problem for studies of social cognition—in fact, they provide a critical method for testing how and why these abilities evolve. Indeed, some of the strongest tests of the evolutionary forces driving social-cognitive evolution come from outside the primates.

Using Convergence in Other Taxa as a Model for Primate Evolution

Studies of social-cognitive evolution in primates face two major problems. Often the critical taxa are extinct (e.g., cases in which we compare humans to other hominid species to identify uniquely human cognitive traits) or most primates share the feature in question (e.g., most anthropoids are highly social to some degree, so it is difficult to use monkeys to address coarse-grained evolutionary questions about how the presence or absence of sociality impacts social cognition). Luckily, evolution has provided an alternative route—studies of convergence in other taxa can often remedy these kinds of difficulties that arise when working within primates. Such studies also provide a critical check to primate-centric views of social-cognitive evolution, as some “general” principles of social-cognitive evolution do not seem to hold up very well in other taxa (e.g., Dunbar & Schultz, 2007).

For example, primates seem to be relatively unskilled at interpreting communicative behavior—making it difficult to assess how such abilities arose in humans. Consequently, some researchers have begun to use dogs and wolves as helpful models for understanding the evolution of communicative gestures such as pointing and gaze cues. Whereas wolves are not very successful at using pointing or gaze cues in the absence of extensive experience with humans, dogs from a very young age appear to be highly tuned to human communication, following such cues spontaneously (Hare et al., 2002; Riedel et al., 2007; Visalberghi et al., 2008). These differences suggest that the changes that occurred during domestication may be important for some kinds of social cognition, and many psychological mechanisms have been proposed for the behavioral changes that resulted from this selection, including increased attention to faces of humans (Miklósik et al., 2003) and reduced fear responses (Hare & Tomasello, 2005). Studies of other domesticated species, such as an experimental population of domesticated foxes (Hare et al., 2003), domestic goats (Kaminski et al., 2005, 2006b), and cats (Miklósik, 2003) further support the possibility that domestication can influence some forms of social-cognitive abilities. These findings suggest that interspecies tolerance may be a critical prerequisite for some kinds of human-like social-cognitive skills, particularly those involving cooperation (Melis et al., 2006b).

Studies of convergence can also illuminate the evolution of social traits that likely emerged in basal primate groups, such as in catarrhines, and thus are widely shared across large taxonomic spaces. For example, wild spotted hyenas (Crocuta crocuta) live in large social groups with Old World primate-like linear dominance hierarchies and engage in cooperative hunting behaviors (Holekamp et al., 2007). This suggests that these social mammals may possess sophisticated social-cognitive skills to deal with their social landscape much like those observed in some monkey species (e.g., Drea & Carter, 2009). As spotted hyenas have two closely related relatives that share significant variation in their social structure—striped hyenas (Parahyaena brunnea) appear to be solitary, and brown hyenas (Parahyaena hamina) live in smaller, less gregarious social groups (Watts & Holekamp, 2007)—comparative studies of these species with an eye to variation in their natural environments could illuminate why such complex abilities emerge.

Arguably, the most sophisticated social-cognitive skills are actually found outside mammals—in corvids, a taxa that includes jays, ravens, and crows. Studies of these birds have revealed startling parallels with the abilities of primates (Emery & Clayton, 2004). Specifically, crows appear to use many primate-like social-cognitive skills (such as perspective taking) to protect their food stores when they engage in caching behavior. For example, ravens and jays employ protective strategies when they cache (Emery & Clayton, 2001), and seem to use information about the visual perspective of others when doing so (Bugnyar & Kotschka, 2002; Dally et al., 2004; Heinrich & Pepper, 1998). Furthermore, they not only respond to the behavior of competitors but also seem to differentiate between some kinds of knowledge states, much like chimpanzees and rhesus macaques (Bugnyar & Heinrich, 2005; Dally et al., 2006). Ravens even appear to predict how humans will behave in a caching context based on their past interactions with the humans in a non-caching context, suggesting they represent the “reputation” of social partners (Bugnyar et al., 2007). Some corvids even make social inferences from watching third-party interactions (Piu et al., 2016), suggesting that some of their social-cognitive skills are also employed outside of caching contexts. Taken together, comparative work examining social cognition in other taxa makes it clear that a complete understanding of the evolutionary pressures that led to the development of primate social cognition will require a more thorough understanding of the mechanisms in similarly sophisticated social cognition in distinctly related taxa as well.

Human Evolution and Social Cognition

A final limitation of present work on the nature of primate social cognition involves what is perhaps the least studied of all—the question that Darwin (1871) defined as “the greatest difficulty” facing anyone interested in the evolution of human social cognition. Namely, what aspects of primate social cognition are truly unique to our own species? In recent years, primate researchers have gained some new traction on this question. Recent findings using more ecologically relevant tasks have led to a growing consensus that humans and at least some other primates share the capacity to represent the intentions, perceptions, and knowledge of others. Thus, several new or more specific hypotheses have arisen that attempt to pinpoint the major social-cognitive differences between humans and other primates. For example, there is currently little evidence that primates share the capacity to reason about others’ belief states; indeed, there is some evidence that primates fail to reason about others’ belief states even when tested using a variety of different methodologies (Call & Tomasello, 1999; Kaminski et al., 2006a; Krachan et al., 2007; Santos et al., 2007) which suggests that representing others’ beliefs might be a capacity specific to our own species (e.g., Povinelli & Giambrone, 2001). Other proposals have focused on other aspects of intentionality, such as the ability to represent (and the motivation to share) joint goals and shared intentions (Tomasello et al., 2005). This proposal highlights that many human-unique behaviors, such as participation in cultural endeavors, are fundamentally collaborative in nature. Although the available work to date suggests that some species perform very differently than human children on collaborative tasks with shared goals (e.g., Tomasello et al., 2005), more work is needed to directly test both this hypothesis and the belief representation hypothesis. Indeed, such work will allow us to not only gain insight into socio-cognitive capacities that might be unique to humans but also discover why these purportedly unique capacities evolved in the first place.

Conclusions

The past decade has produced significant advances in our understanding of primate social cognition. The development of novel experimental methodologies has led to...
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increasing evidence that some primates can assess the psychological states of others in some contexts. Thus, while human social-cognitive abilities may still be outstanding, they nonetheless appear to have deep evolutionary roots. However, researchers still have a multitude of fascinating questions to attack in the future, as research has suggested that even very superficially similar social behaviors (such as gaze following) can be supported by very different underlying psychologies. The question has therefore shifted from not just if the sophisticated social behaviors of primates are the consequences of sophisticated cognitive skills, but why they might be so. With increasing comparative data, researchers can begin to address the ultimate causes that shape social cognition in both humans and nonhuman primates. Armed with a new appreciation of the importance of ecologically relevant tasks that can be used across species, the stage is now set for primate cognition researchers to answer Darwin's question.

ACKNOWLEDGMENTS

We thank Felix Warneken for comments on an earlier draft of the manuscript.

NOTE

1. Note that a complete review of the vast literature on social learning in primates is outside the scope of this chapter (see Tomasello & Call, 1997, for a review of this extensive work).

2. Interestingly, chimpanzees' goal emulation differs from the performance of children in this task, who faithfully imitate all of the actions of a human actor even when some of those actions are clearly irrelevant to obtaining the goal (e.g., Gergely, et al., 2002; Heron & Whiten, 2005; Metzolf, 1995; Nogil, et al., 1995; see Lyons & Keil, 2007, for a discussion of this species difference).

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