

Primate Neuroethology

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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. Alison 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 taxon, 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; Heyes, 1998; Tomasello & 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 reviews were written on the topic over 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., 2005; Carpenter et al., 1998; Gergely et al., 1995, 2002; Meltzoff, 1995; 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; Moll & 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 Surian 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 action, 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, 2005).² 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, 2000). 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 behavior 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

		Inferring Goals	Distinguishing Intentions	Ontogeny
Hominoids	Chimpanzees	Buttleman et al., 2007; Call et al., 2005; Horner & Whiten, 2005; Myowa-Yamakoshi & Matsuzawa, 2000; Tomasello & Carpenter, 2005; Tomasello et al., 1987; Uller, 2004; Uller & Nichols, 2000; Warneken & Tomasello, 2006; Warneken et al., 2007*;	Call & Tomasello, 1998; Call et al., 2004; Povinelli et al., 1998; Tomasello & Carpenter, 2005	Tomasello & Carpenter, 2005; Uller, 2004
	Other great apes Lesser apes		Orangutans: Call & Tomasello, 1998	
Old World monkeys	Macaques	Rhesus		
	Baboons Other			
New World monkeys	Capuchins	Brown: Kuroshima et al., 2008	Brown: Lyons & Santos, submitted; Phillips et al., 2009	
	Callitrichids Other	Cotton-top tamarins		
Strepsirrhines	Lemurs			

* Indicates that the study involved both human and conspecific social partners.

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 teasing). 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 an agent (i.e., a human hand), but 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 7.2). 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 surface 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

Table 7.2 Studies of Social-Cue Use Across Nonhuman Primate Species

	Gaze	Points and Other Gestures	Touch, Body Position, and Physical Markers	Ontogeny
Hominoids	Chimpanzees	Barth et al., 2005; Braeuer et al., 2006; Call et al., 1998, 2000; Herrmann et al., 2007; Itakura et al., 1999; Okamoto-Barth et al., 2008; Povinelli et al., 1999*	Barth et al., 2005; Braeuer et al., 2006; Hare & Tomasello, 2004,* 2006; Herrmann et al., 2007; Itakura et al., 1999*; Okamoto-Barth et al., 2008; Povinelli et al., 1990, 1997, 1999; Wood et al., 2007	Barth et al., 2005; Call et al., 2000; Herrmann et al., 2006, 2007; Itakura et al., 1999*; Okamoto-Barth et al., 2008; Tomasello & Carpenter, 2005; Tomonaga et al., 2004
	Other great apes	Bonobos: Braeuer et al., 2006 Orangutans: Herrmann et al., 2007	Bonobos: Herrmann et al., 2006 Gorillas: Herrmann et al., 2006 Orangutans: Herrmann et al., 2006, 2007	Herrmann et al., 2007 Okamoto et al., 2002; Okamoto-Barth et al., 2008; Tomasello & Carpenter, 2005; Tomonaga et al., 2004
	Lesser apes	White-handed gibbons: Inoue et al., 2004	White-handed gibbons: Inoue et al., 2004	
Old World monkeys	Macaques	Rhesus: Anderson et al., 1996; Hauser et al., 2007	Rhesus: Anderson et al., 1996; Hauser et al., 2007; Wood et al., 2007	
	Baboons	Olive: Vick & Anderson, 2003; Vick et al., 2001		
New World monkeys	Other Capuchins	Brown: Anderson et al., 1995; Vick & Anderson, 2000	Brown: Anderson et al., 1995; Vick & Anderson, 2000	
	Callitrichids	Cotton-top tamarins: Neiwirth et al., 2002 Common marmosets: Burkhardt & Heschl, 2006	Cotton-top tamarins: Neiwirth et al., 2002; Wood et al., 2007 Common marmosets: Burkhardt & Heschl, 2006	Cotton-top tamarins: Neiwirth et al., 2002 Common marmosets: Burkhardt & Heschl, 2006
	Other Lemurs			

* Indicates that the study involved both human and conspecific social partners.

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 too!") in these social cuing 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*; Neiwirth 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 (Burkhart & Heschl, 2006), while rhesus monkeys tested with a more species-specific looking gesture are better able to determine the location of hidden food (Hauser et al., 2007). Wood and colleagues (2007) further argue that cotton-top tamarins, rhesus, 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 would profit from parsing out why primates may demonstrate understanding of intentions in some contexts but not others. Taken together, then, studies of communicative gesture use 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 (1996c) taught young chimpanzees to use a visual begging gesture to obtain food from a human experimenter. 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 differed in their perceptual access to the chimpanzees: 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 can and 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 flexible 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; Tomasello et al., 1998) and the other great apes (Braeuer et al., 2005; Okamoto-Barth et al., 2007); Old World monkeys such as various macaques (rhesus: *Macaca mulatta*; stumptail: *M. arctoides*; pigtail: *M. memstrina*;

Emery et al., 1997; Tomasello et al., 1998), mangabeys (*Cercocebus atys torquatus*; Tomasello et al., 1998) and olive baboons: mangalys (*Cercocebus atys torquatus*; Tomasello et al., 1998), New World monkeys including capuchins (Vick & Anderson, 2000), cotton-top tamarins (Neiworth et al., 2002), and common marmosets (*Callithrix jacchus*; Burkhardt & Heschl, 2006); and even some lemur species (ring tailed: *Lemur catta*; brown lemurs: *Eulemur 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 (Kobayashi & Kohshima, 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 direct their own gaze in the direction of others but also follow gaze around barriers and past distracting objects that are not the target of another’s gaze, sometimes by physically reorienting their own bodies (Povinelli & Eddy, 1996a; Tomasello 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 the other’s gaze (Braeuer 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 behavior 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 (Goossens 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 their natural behaviors (Shepherd & Platt, 2008), but seem less able to follow gaze in experimental contexts (Anderson & Mitchell, 1999; but see Ruiz et al., 2009 for an experimental study using Conspecific Photographs). Thus, although behavioral co-orienting 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; Itakura 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

Table 7.3 Studies of Gaze Following Across Nonhuman Primate Species

	Follow Head Orientation	Follow Eye Orientation Alone	Follow Gaze Around Barriers	Check Back with Actor; Habituate in Absence of Target	Ontogeny
Hominoids	Chimpanzees Braeuer et al., 2005; Call et al., 1998; Herrmann et al., 2007; Itakura, 1991; Okamoto-Barth et al., 2007; Povinelli & Eddy, 1996a; Tomasello et al., 1998*, 2001, 2007	Herrmann et al., 2007; Povinelli & Eddy, 1996a; Tomasello et al., 2007	Barth et al., 2005; Braeuer et al., 2005; Okamoto-Barth et al., 2007; Povinelli & Eddy, 1996a; Tomasello et al., 1999	Braeuer et al., 2005; Call et al., 1998; Okamoto-Barth et al., 2007; Tomasello et al., 2004, 2001	Barth et al., 2005; Braeuer et al., 2005; Herrmann et al., 2007; Tomasello & Carpenter, 2005; Tomasello et al., 2001; Tomonage et al., 2004
Other great apes	Bonobos: Braeuer et al., 2005; Okamoto-Barth et al., 2007; Tomasello et al., 2007 Gorillas: Braeuer et al., 2005; Okamoto-Barth et al., 2007 Tomasello et al., 2007 Orangutans: Braeuer et al., 2005; Herrmann et al., 2007; Tomasello et al., 2007 Pileated gibbons: Horton & Caldwell, 2006 [†]	Bonobos: Tomasello et al., 2007 Gorillas: Tomasello et al., 2007 Orangutans: Herrmann et al., 2007; Tomasello et al., 2007	Bonobos: Braeuer et al., 2005; Okamoto-Barth et al., 2007 Gorillas: Braeuer et al., 2005; Okamoto-Barth et al., 2007 Orangutans: Braeuer et al., 2005; Okamoto-Barth et al., 2007	Bonobos: Braeuer et al., 2005; Okamoto-Barth et al., 2007 Gorillas: Braeuer et al., 2005; Okamoto-Barth et al., 2007 Orangutans: Braeuer et al., 2005; Okamoto-Barth et al., 2007	Bonobos: Braeuer et al., 2005 Gorillas: Braeuer et al., 2005 Orangutans: Braeuer et al., 2005

Old World monkeys	Macaques	Rhesus: Emery et al., 1997*; Itakura, 1996; Tomasello et al., 1998,* 2001 Stumptail: Anderson & Mitchell, 1999; Itakura, 1996; Tomasello et al., 1998* Pigtail: Itakura, 1996; Tomasello et al., 1998* Long-tail: Goossens et al., 2008 Tonkean: Itakura, 1996 Olive: Vick et al., 2001 Sooty mangabey: Tomasello et al., 1998* Brown: Itakura, 1996; Vick & Anderson, 2000 White-faced: Itakura, 1996 Cotton-top tamarins: Neiworth et al., 2002 [†] Common marmosets: Burkhardt & Heschl, 2006	Rhesus: Tomasello et al., 2001 Long-tailed: Goossens et al., 2008	Rhesus: Tomasello et al., 2001
New World monkeys	Baboons Other Capuchins			
	Callitrichids			
	Other			
Strepsirrhines	Lemurs			

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

[†] 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: Neiwirth 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: Burkhardt & Heschl, 2006), so future research is warranted with a wider range of species and paradigms before any strong conclusions can be made about a clade-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 seeing in an experimental setting. However, other research by these researchers suggests that 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 (Tomasello et al., 2007). One possibility is that the low degree of contrast between the iris and sclera makes it difficult to discriminate eye direction in almost all primates but humans; humans also appear to be unique in

our ability to move our eyes independent of our general head direction (Kobayashi & Kohshima, 1997, 2001). For example, chimpanzees, bonobos, and orangutans spontaneously adjust their gesture frequency to the attentional state of the observer (i.e., they produce more gestures when an experimenter can see them), but they treat body and face orientation, rather than eye position, as the most relevant factors (Kaminski 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 (Liebal 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 (Liebal 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 (Scerif 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 Studies of Understanding Perceptions and Knowledge Across Nonhuman Primate Species

	Attention and Predictions About Seeing	Visual Perspective	Auditory Perspective	Deception	False Beliefs	Ontogeny	
Hominoids	Chimpanzees	Herrmann et al., 2007; Hostetter et al., 2007; Kaminski et al., 2004; Liebal et al., 2004a,* 2004b; Povinelli & Eddy, 1996b, 1996c; Povinelli et al., 1997, 2002, 2003; Reaux et al., 1999; Theall & Povinelli, 1999; Tomasello & Carpenter, 2005; Tomasello et al., 1994*	Brauer et al., 2007,*; Hare et al., 2000,* 2001,* 2006; Hirata & Matsuzawa, 2001*; Melis et al., 2006a; Povinelli & Eddy, 1996c; Povinelli et al., 1990	Brauer et al., 2007,*; Hirata & Matsuzawa, 2001*; Melis et al., 2006a	Hare et al., 2006; Hirata & Matsuzawa, 2001*; Melis et al., 2006a	Call & Tomasello, 1999; Hare et al., 2001*; Kaminski et al., 2008; Krachun et al., 2009	Herrmann et al., 2007; Povinelli et al., 2002; Reaux et al., 1999; Tomasello & Carpenter, 2005; Tomasello et al., 1994*
	Other great apes	Bonobos: Kaminski et al., 2004; Liebal et al., 2004b; Pika et al., 2005* Gorillas: Kaminski et al., 2004; Liebal et al., 2004b; Pika et al., 2003*; Poss et al., 2006 Orangutans: Herrmann et al., 2007; Kaminski et al., 2004; Liebal et al., 2004b; Poss et al., 2006 Siamangs: Liebal et al., 2003*			Orangutans: Call & Tomasello, 1999	Orangutans: Herrmann et al., 2007	
	Lesser apes	Pileated gibbons: Horton & Caldwell, 2006					

(continued)

Table 7.4 (Continued)

	Attention and Predictions About Seeing	Visual Perspective	Auditory Perspective	Deception	False Beliefs	Ontogeny
Old World monkeys	Macaques	Rhesus: Flombaum & Santos, 2005; Povinelli et al., 1991 Long-tailed: Kummer et al., 1996 Olive: Vick & Anderson, 2003	Rhesus: Santos et al., 2006		Rhesus: Santos et al., 2007b	
	Baboons					
	Other	Diana monkeys: Scerif et al., 2004*				
New World monkeys	Capuchins	Brown: Anderson et al., 2004; Kuroshima et al., 2002; Kuroshima et al., 2003	Brown: Fujita et al., 2002*; Hare et al., 2003*	Brown: Fujita et al., 2002 *		
	Callitrichids	Cotton-top tamarins: Santos & Hauser, 1999 Common marmosets: Burkhardt & Heschl, 2007*	Common marmosets: Burkhardt & Heschl, 2007*			
	Other	Squirrel monkeys: Anderson et al., 2004				
Strepsirrhines	Lemurs				Black: Genty & Roeder, 2006	

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

2004). Thus, whereas there is robust evidence that apes understand something about the nature of attention, the results are more variable across monkey species, suggesting again the importance of the kind of behavioral task and context employed.

From Perspective Taking to Understanding of Knowledge and Beliefs

Together, the evidence from gesture use and looking-time work suggests that apes and possibly some monkeys may be sensitive to the visual perception of others. Perhaps the most conclusive evidence that some primates have an understanding of visual attention, however, comes from studies of perspective taking. As previously mentioned, several primate species tend to perform poorly in early studies testing their understanding of visual attention and perspective taking (e.g., Povinelli & Eddy, 1996c; Reaux et al., 1999). However, these studies typically used a cooperative-communicative paradigm in which a human experimenter shared food with the chimpanzees, a situation that may be highly unnatural or unmotivating for primates, as previously noted. Faced with this problem, researchers have more recently tried to develop more ecologically valid tests of perspective taking, ones that are designed around a context that may be more natural (and motivating) for primates: food competition. The basic setup of the original studies by Hare and colleagues (2000, 2001) using this logic involved two chimpanzees competing with each other for access to food. However, the two chimpanzees had differing knowledge about the food that was available. For example, in one series of studies, the more subordinate of the two chimpanzees could see two pieces of food, and the dominant individual could only see one (the second piece was blocked from her view). Researchers then measured which piece of food the subordinate targeted when she was released with a slight head start over the dominant. Using this technique, a series of experiments demonstrated that subordinate chimpanzees were more likely to choose the food that dominant individuals could not see. In addition, when the roles were reversed

and now a dominant could see both pieces of food and was released before a subordinate who could only see one, the dominant targeted the visible (at-risk) piece of food before taking the second piece hidden from the subordinate's view. A number of controls ruled out the possibility that such strategies were due to behavioral monitoring of the dominant individual (e.g., the subjects were forced to make a decision before they ever saw their competitor make a move; Hare et al., 2000). A second set of studies indicated that chimpanzees demonstrated these preferences because they understood something about the link between seeing and knowing: When subordinates had to decide whether or not to approach a piece of food hidden from a dominant's view, they made more attempts to obtain the food when the dominant had not been present when the food was hidden than when she had been present during the baiting (Hare et al., 2001).

Following these initial studies, several experiments using competitive paradigms have demonstrated perspective-taking skills in both apes and monkeys. For example, Flombaum and Santos (2005) developed a paradigm in which rhesus macaques could choose to steal food from one of two experimenters, and then varied the degree to which those experimenters could see the food. In many ways this setup therefore parallels the preferential begging paradigm developed by Povinelli and colleagues, except that the decision was placed in a competitive context. Rhesus monkeys showed sensitivity to a wide variety of variations in visual access, even when the manipulations involved very subtle differences in eye position. Studies with chimpanzees have similarly shown that they prefer to retrieve a piece of food that a competitive human cannot see over one he or she can, even engaging in attempts to disguise their interest in the food as they approach it (Hare et al., 2006; Melis et al., 2006a). Moreover, some evidence suggests that the perspective taking that chimpanzees and rhesus monkeys engage in extends to the auditory modality. For example, when rhesus macaques are confronted with a human competitor sitting in front of two boxes containing food where one box has functional

bells attached to it while the other box has non-functional bells, they preferentially steal food from the box that is silent, and do so only when the competitor cannot already see their actions (Santos et al., 2006). This suggests that rhesus monkeys recognize how their behavior will alter the psychological state of the human: If the human cannot see them, then the noise will alert him or her to their presence. If the human can already see them, then noise will have no impact on the human's knowledge about their behavior. Chimpanzees also prefer a silent approach over a noisy one when competing with a human over food (Melis et al., 2006a; but see Braeuer et al., 2008). Despite these successes, other monkey species have demonstrated poor performance in similar visual perspective-taking tasks, providing further converging evidence that the psychological mechanisms supporting social interactions vary across primates. For example, both capuchins (Hare et al., 2003) and common marmosets (Burkhart & Heschl, 2007) have been tested in versions of the conspecific competition paradigm used with chimpanzees, but appear to depend heavily on the behavior of the competitor, rather than reasoning about what the competitor sees or knows, when making food choices.

The current evidence suggests that at least chimpanzees and rhesus macaques know something about what others can and cannot perceive, and use this information to guide their own behavioral decisions. However, an open question concerns the issue of what primates are actually representing when faced with these kinds of social problems. Although recent studies provide strong evidence that rhesus monkeys and chimpanzees understand something about others' perception and knowledge, thus far there is no evidence that primates go beyond a distinction between knowledge and ignorance to actually represent the false beliefs of others. For example, chimpanzees perform at chance when confronted with two humans trying to direct them to food, one of whom had seen the food being hidden and the other who had originally seen the food being hidden, but had a false belief about its location due to a subsequent switching out of her view (Call and Tomasello, 1999). Competitive versions of false-belief tasks further confirm that

chimpanzees use information about true but not false beliefs to find food hidden (Kaminski et al., 2008; Krachun et al., 2009; see also the informed-misinformed condition in Hare et al., 2001). Similarly, when tested in a looking-time violation-of-expectation false-belief test (see Onishi & Baillargeon, 2005), rhesus monkeys make correct predictions about where a human actor will search when they have a true belief about a food item's location, but make no predictions about the actor's behavior when the actor has a false belief (Santos et al., 2007b). These findings using various false-belief tasks suggest that while primates can represent whether others are knowledgeable or ignorant, they may not represent beliefs of others in cases where those beliefs conflict with the true state of the world.

Conclusions: Understanding Psychological States

Overall, research from the past decade has greatly illuminated the cognitive skills underlying the complex social behaviors of primates. First, both apes and at least some species of monkey seem to parse the actions of others in terms of underlying goals and intentions. Similarly, apes and some monkeys seem to understand something about the perspective of others. Most research addresses whether primates understand visual perspective, but other studies suggest that this capacity may also encompass perception in other modalities. These social-cognitive abilities may not be shared by all primates: Although some behaviors, such as gaze following, seem to be widely shared, some species engage in superficially similar behaviors but do not seem to understand the nature of seeing in the same way that chimpanzees and rhesus macaques do. However, the current research supports the conclusion that at least some primates understand others' behavior in terms of psychological states such as goals and knowledge, rather than merely in terms of observable behavioral features (but see Povinelli & Vonk, 2003, 2004, for alternative interpretations of these results).

However, there are, at present, still many limitations to our understanding of primate social cognition. As mentioned previously,

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 skillful 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 payoff—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 (Braeuer 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. Researchers will therefore profit from critically considering 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 not because these tasks cooperative 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, apes 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 instrumental task requiring joint action with conspecifics that they share a tolerant relationship with, but will not cooperate with intolerant partners (Melis et al., 2006b; 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 skillful partners (Melis et al., 2006c). Correlations of natural behaviors further suggest that chimpanzees prefer to cooperate with those who have cooperated with them in the past (Mitani, 2006). Although there are several very different types of mechanisms that could underlie such behaviors (see de Waal & Luttrell, 1988), experimental evidence supports the hypothesis that chimpanzees show calculated reciprocity in grooming (Koyama et al., 2006) and collaborative (Melis 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 who to interact with (See also Subiaul et al., 2008). But primate social-cognitive skills are not limited to direct interactions with others: Some primates also seem to represent the ongoing relations of other members of their groups. For example, experiments with wild baboons suggest that this species understands not only their relations with others but also the third-party relationships between other members of their groups (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 intention reading 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 (Warneken & Tomasello, 2006; Warneken et al., 2007). Chimpanzees also use information about whether a conspecific was the cause of their losing 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 species understand the potential of using overt forms of communication to enhance success in cooperative endeavors (See Melis et al., 2009 for

Chimpanzee's lack of communication in a negotiation game). The lack of communication may suggest that there is a lack of motivation by non-human primates to assess the cooperative-communicative intent of others.

Altogether, these results suggest that many primates do engage in "cognitive" cooperation using their social-cognitive skills to engage in more efficient and more successful forms of cooperation. Critically, the payoffs of many cooperative interactions depend not only on whether two individuals act together but also on their level of skill when performing the act. That is, if one partner cannot successfully perform his or her role, both members of the pair will fail to get anything. The use of social-cognitive skills can increase the rewards associated with cooperation, so it can pay for individuals to sustain relationships with potential partners, selectively cooperate with good partners, and be adept at the mutualistic activity itself (e.g., coordinate with the partner and be sensitive to the other's intentions). Thus, future studies of the social-cognitive abilities that primates use in cooperative interactions will likely reveal that these abilities are different than those needed in cooperative interactions, but not any less complex.

THE EVOLUTION OF PRIMATE 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 unmarked). 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

references studies with a developmental component). Developmental studies have provided critical insights into human social cognition, so they could potentially do the same for nonhuman primate 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 more patchy—with only one or two relevant studies—and often nonexistent (see Tables 7.1 through 7.4; the first row lists studies with chimpanzees). This missing evidence becomes all the 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 quantifications of intelligence via 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—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

The comparative method—examining the traits of different populations or species that have been shaped by differing ecological or social forces in order to better understand how natural selection proceeded—is one of the most important

techniques in evolutionary biology (Mayr, 1982). The comparative method allows us to reconstruct a phenomenon (evolution via natural selection) that often cannot be directly observed, and therefore address not just *what* the differences are between different groups of organisms, but also *why* those differences arose. Consequently, it may be the most powerful technique we have to answer functional questions about social-cognitive abilities across primate taxa.

One such approach is to test closely related species on a battery of tests that can be used to identify whole suites of shared and derived traits across different domains of cognition (e.g., Herrmann et al., 2007). However, several more specific hypotheses about the role of social and ecological factors in the evolution of particular cognitive abilities can also be addressed with comparative data. For example, one prediction of the competition hypothesis described earlier is that there will be critical differences between the social-cognitive skills of more despotic, aggressive species compared to more egalitarian, tolerant species. Specifically, as despotic species face more intense competition for food, as well as a steeper dominance hierarchy limiting their access to that food (de Waal & Luttrell, 1989), they may more readily show sophisticated social-cognitive skills when competing with others. Conversely, more egalitarian species might show greater skills in cooperative contexts (e.g., Hare et al., 2007; Petit et al., 1992). Notably, the two species that have been successfully studied using competitive paradigms—rhesus macaques and chimpanzees—are both more despotic than closely related egalitarian sister species. Thus, comparing the social-cognitive skills of chimpanzees and rhesus to bonobos and Tonkean macaques, respectively, in a food competition paradigm would be helpful and could provide a direct test of this hypothesis.

This kind of framework raises additional issues about evolutionary interpretations of the comparative data that we do have. For example, recent studies have indicated that many of the social-cognitive abilities identified in chimpanzees, such as perspective taking and intention reading, are also present in more distantly related monkeys such as rhesus macaques and capuchins. One

