



From Hominoid to Hominid Mind: What Changed and Why?*

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Abstract

The living great apes, and in particular members of the genus *Pan*, help test hypotheses regarding the cognitive skills of our extinct common ancestor. Research with chimpanzees suggests that we share some but not all of our abilities to model another's perspective in social interactions. Large-scale comparisons among human infants, bonobos, chimpanzees, and orangutans on both social and physical problem-solving tasks demonstrate that human infants are unique for their early emerging social cognitive skills, which facilitate participation in cultural interactions. Comparisons between bonobos and chimpanzees also reveal cognitive differences that are likely due to developmental shifts. These comparative studies suggest that our species' capabilities to assess the psychological states of others are built on those abilities that were present in our last common ape ancestor and were derived, in part, owing to shifts in cognitive ontogeny that likely account for species differences among other apes as well.

INTRODUCTION

It deserves notice that as soon as the progenitors of man became social (and this probably occurred at very early period), the advancement of the intellectual faculties will have been aided and modified in an important manner, of which we see only traces in the lower animals. . . .

–Darwin (1871, p. 161)

What makes human cognition so different from that of other apes? What process(es) drove the evolution of human cognition from the last ancestor we shared with bonobos and chimpanzees? Both morphological and behavioral evidence suggests that social complexity has driven the evolution of the primate brain (Humphrey 1976, Byrne & Whiten 1988, Dunbar & Shultz 2007; although see Byrne & Bates 2007). Meanwhile, observational, experimental, and theoretical analyses suggest that our species has taken primate sociality to an extreme (Richardson et al. 1998, Tomasello 1999, Spelke & Kinzler 2007). Comparative and developmental work suggests that humans have unique social cognitive skills that allow for flexible cooperation and cultural behaviors that are qualitatively different from those seen in other primates (Tomasello 1999, Tomasello et al. 2005, Herrmann et al. 2007, Hill et al. 2009, Hill 2010, Hare & Tan 2012). As a result, human society depends on people's ability to collaborate with unfamiliar or unrelated individuals as humans accumulate knowledge to build increasingly complicated technology and cultural institutions (Richerson et al. 1998, Tomasello 1999, Fehr & Fischbacher 2004, Henrich et al. 2004).

Specifically, our ability to assess the psychological states of others, known as theory of mind, is believed to underlie much of what we consider to be unique about our species. Children are largely dependent on their ability to model the psychological states of others in acquiring all types of cultural traditions unique to humans, including language (Tomasello 1999, 2003; Bloom 2000; Peterson et al. 2005; Meltzoff 2007). Therefore, it may be our

species' ability to think about the thoughts of others that provides the ontogenetic foundation to much of what is considered unique to human cognition. This article reviews comparative work with chimpanzees and bonobos that is testing the phylogenetic predictions of this hypothesis. This work is revealing that although humans are unique in the sophistication with which they can think about the thoughts of others, the human system is built on preexisting hominoid abilities. In addition, I review research that points to the early emergence of social skills in humans relative to other apes as being responsible for much of our species' unusual forms of cultural cognition. This work also suggests that developmental comparisons between bonobos and chimpanzees may be central to understanding the evolutionary processes by which such an ontogenetic shift might have occurred during human evolution.

THEORY OF MIND ABILITIES

What is theory of mind? Human social cognition is believed to be dependent on our ability to think about the thoughts of others, known as theory of mind (Premack & Woodruff 1978, Dennet 1983, Spelke & Kinzler 2007). Humans are aware that others have perceptions, intentions, and beliefs and that these psychological states can differ from our own (Wellman 1990, Perner 1991, Flavell 1999). Our species is dependent on our theory of mind for navigating through the social world (Moore & Frye 1991). For example, while interacting with others, humans constantly use cues as subtle as the smallest eye movements to make calculations about what others are thinking (i.e., if an old acquaintance gazes at your name tag, you can infer strictly from that eye movement that he or she does not know your name) (Corkum & Moore 1995). On the basis of what a person can assess from such cues about the perceptions, intentions, and beliefs of others, one can then flexibly adjust one's own behavior to communicate, teach, or even deceive social partners or competitors (Baron-Cohen 1999, Flavell 1999).

Developmental psychologists have demonstrated that humans are not simply born with an adult-like theory of mind. Before an infant's second birthday, humans become expert at perceiving the intentions behind the actions and perceptions of others (Behne et al. 2005). It is at this age that infants begin to follow the gaze of others, produce and comprehend gestures, and shortly after, copy the actions of others on the basis of the others' goals (Carpenter et al. 1998, Tomasello & Carpenter 2005). Research indicates that it is this tendency to perceive others as being goal-directed that then leads to the development of increasingly complex social cognitive skills (e.g., modeling belief states, language acquisition). According to this constructivist analysis, understanding others as intentional agents is a crucial foundation on which all other social cognitive cooperative and cultural skills are built (Tomasello 2003, Wellman & Brandone 2009; for an alternative view, see Spelke & Kinzler 2007). Moreover, it is also around this same age that children begin showing motivation to participate in shared activities, to help others, and to cooperate to accomplish shared goals. As an example, without explicit rewarding, children will give their own stickers away to others or will repeatedly help an adult who dropped a pen (Warneken & Tomasello 2006, 2008; Fehr et al. 2008). Perhaps most remarkably, infants seem to integrate quickly their ability to assess the goals of others with their motivation to help others. Infants spontaneously begin to use simple pointing gestures to help others accomplish their goals or just to share an experience (Warneken et al. 2006, Liszkowski et al. 2008, Buttelmann et al. 2009). From this stage forward in infant development, there seems to be an explosion of cooperative and communicative behavior. Infants begin actively seeking out ways to interact and help others. They even use overt communication to negotiate when cooperation breaks down. For example, if a child is playing a cooperative game that is interrupted, he or she will use gestures and vocalizations in attempts to re-engage his or her partner (Warneken et al. 2006, Warneken & Tomasello 2006, Warneken & Tomasello 2007).

Developmental studies of humans suggest a revolutionary shift in how young infants view and interact with their social world. This revolution allows infants to interact with others in uniquely human ways (Tomasello et al. 2005, Wellman & Brandone 2009). This view of development predicts that human adults will have a variety of cognitive skills not possessed by other primates. It also predicts that this outcome will be due largely to children's early emerging, specialized skills for absorbing the accumulated skillful practices and knowledge of their social groups. Humans' especially powerful skills of social-cultural cognition early in ontogeny thus serve as a kind of "bootstrap" for the distinctively complex development of human cognition in general. To test this idea, researchers have used a phylogenetic and ontogenetic approach to (a) identify shared and derived features of our species' abilities to attribute psychological states to others and (b) explore whether the development of social cognitive skills in human infants has shifted from that observed in other apes.

A PHYLOGENETIC RECONSTRUCTION OF HOMINID COGNITIVE EVOLUTION

To test the central phylogenetic prediction of this developmental hypothesis, we must identify the social cognitive skills we inherited through common descent with bonobos and chimpanzees. If developmental psychologists are correct that theory of mind provides the ontogenetic foundation to much of what is considered unique to human cognition (Dennet 1983, Perner 1991, Baron-Cohen 1995, Carruthers & Smith 1996, Tomasello 1999), then human social cognition should have evolved significantly since our lineage split with our last common ape ancestor (LCA) with bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*).

Observational studies have long suggested that primates and particularly great apes might be capable of modeling others' psychological states (Byrne 1995, Russon et al. 1996).

Goodall (1971) made several intriguing observations of chimpanzees discovering previously unknown food resources and then proactively using strategies to assure that this resource remained unknown to others (e.g., leading conspecifics away from the food). These observations and others like them provide extremely valuable information about the cognitive potential of a species and when this potential might be deployed, but as is always the case with anecdotes, it is unclear how replicable they might be (Byrne & Whiten 1992). In addition, no matter how frequently one observes behavior such as that observed by Goodall (1971), there is no way to distinguish between (a) the “rich” mentalistic interpretation suggesting that the chimpanzee is manipulating what the competitor can see, having predicted his or her reaction to the sight of the food, or (b) the “lean” or more parsimonious hypothesis proposing that the chimpanzee was simply attempting to manipulate how the competitor behaved by reacting to their observable behavior (Byrne & Whiten 1992, Heyes 1993, 1998). In the first case, the animal is taking the visual perspective of his or her competitor, whereas in the latter case, the animal is using a completely egocentric strategy that does not require perspective-taking. Therefore, to demonstrate perspective-taking or other related theory-of-mind abilities, experiments must be able to show that subjects are not responding solely to another individual’s observable behavior. Instead, subjects should be able to flexibly predict or infer the future behavior of others spontaneously (i.e., without training) in a range of novel contexts. Because naturally occurring social behaviors can have multiple explanations, experimental methods are essential for presenting completely novel social problems that can test between different rich or lean mechanistic hypotheses (Shettleworth 2010).

THE NULL HYPOTHESIS: HUMAN THEORY OF MIND IS COMPLETELY DERIVED

Until ten years ago, there was no convincing experimental evidence that nonhumans,

including bonobos or chimpanzees, were capable of modeling the psychological states of others (Cheney & Seyfarth 1990b, Tomasello & Call 1997). First, no bonobos had ever been tested. Second, initial positive results with chimpanzees were later explained by more parsimonious learning and behavior-reading explanations. Finally, many other studies simply produced negative results. Premack & Woodruff (1978) were the first to ask, “Does a chimpanzee have a theory of mind?” They reported on a chimpanzee that demonstrated an understanding of intentions by successfully pointing to pictures showing the completion of a human’s unfulfilled goal. Povinelli et al. (1990) then reported that chimpanzees could discriminate between a knowledgeable or ignorant experimenter by gesturing toward a helpful experimenter who was present when the food was hidden. However, Heyes (1993, 1998) later suggested for both pioneering studies that within the experiments subjects learned to rely on predictable and egocentric behavioral cues to make the observed discriminations. Meanwhile, Call & Tomasello (1999) developed a nonverbal false-belief task but failed to find evidence that chimpanzees can assess when a human is misinformed as they attempt to cooperate and communicate in a food-finding game. Finally, chimpanzees have shown little spontaneous skill at solving cooperative-communicative problems in which they can obtain food either by using the gestures of others to find food or by jointly solving an instrumental task (Povinelli et al. 1997, Call et al. 1998, Itakura et al. 1999). Therefore, until very recently, the overwhelming consensus has been that theory-of-mind abilities are unique to *Homo sapiens* (Savage-Rumbaugh et al. 1979; Premack 1986; Cheney & Seyfarth 1990b; Povinelli et al. 1990, 1994; Heyes 1993, 1998; Baron-Cohen 1995; Carruthers & Smith 1996; Povinelli & Eddy 1996; Hauser 1997; Call & Tomasello 1999; Call et al. 2000; Povinelli 2000). In this view, a vast qualitative gap exists between the social cognition of human and non-human apes. Theory-of-mind skills represent a completely derived feature that arose during the

Plio-Pleistocene after our lineage split from other apes.

EVOLVING EVIDENCE FOR THEORY OF MIND IN CHIMPANZEES

In the past ten years, experiments on chimpanzees and other nonhuman primates have revealed that they can reason about the actions and perceptions of others as intentional (Call 2001, Tomasello et al. 2003, Call & Tomasello 2008, Lonsdorf et al. 2010, Rosati et al. 2010; see **Table 1**). One reason for the shift came when social problems were presented to chimpanzees in a competitive context instead of a context that required cooperation and communication with humans (Hare 2001). The first set of competitive experiments controlled for low-level behavior reading and learning hypotheses while demonstrating that chimpanzees are sensitive to the visual perspective of a competitor. While competing, chimpanzees will preferentially retrieve food that is hidden from a human or conspecific, even if the action requires remembering what the competitor saw in the past (Hare et al. 2000, Hare et al. 2001, Hirata & Matsuzawa 2001, Hare & Tomasello 2004, Hare et al. 2006, Melis et al. 2006a, Braeur et al. 2007, Kaminski et al. 2008).

Hare et al. (2000, 2001) conducted a series of eight experiments that emphasized competition between conspecifics rather than cooperation and communication with humans. Hare et al. (2000) tested for visual perspective-taking abilities by arranging opaque occluders (e.g., burlap bags) such that one piece of food was visible to both competitors but a second piece of food was visible to only one of the competitors. The question in these cases was whether the subjects were sensitive to what their competitors could or could not see, and whether they adjusted their retrieval patterns on the basis of the position of the occluders and the identity of their competitors. The results showed that when individuals were subordinate and their dominant competitors could see only one of the pieces of food, the subordinates targeted the hidden

piece of food. In addition, subjects were also tested in the role of the dominant, and their subordinate competitors could again see only one of the pieces of food. In this context, subjects, as dominants, reversed their strategies. Now, instead of going directly to the hidden piece of food, they first targeted the at-risk piece of food, which their competitors could see, before then going for the hidden piece. They did this in an attempt to monopolize both.

Several control studies presented subjects with novel situations to rule out alternative explanations such as behavioral cuing and various forms of learning within the experiment. For example, tests were run to demonstrate that competitors were not basing their retrieval choices on the gaze direction or posture of their competitors (i.e., potentially viewed through the crack in the door before being released). Controls were also run to demonstrate that subjects were not simply attracted to occluders because they acted as physical barriers. Subjects approached randomly when the opaque barrier used previously was replaced with a transparent barrier. Critically, controls were run in which subordinates were released slightly before the dominant. In these controls, the dominant door remained completely shut until after the subordinate made a choice. Once the subordinate committed to approaching the food visible or hidden to the dominant, the dominant was released. Even with no “online” or observable information regarding the dominants at the moment they made their retrieval decisions, subordinates still targeted the hidden food for retrieval. This final and crucial control has subsequently been replicated in a completely naïve group of chimpanzees by a different set of experimenters (Braeur et al. 2007).

Hare et al. (2001) then used the same general paradigm as Hare et al. (2000) but presented more complex social problems. In this next series of studies, subordinate chimpanzees had to base their retrieval strategies on what their competitors had seen in the past as opposed to what they currently could or could not see as in Hare et al. (2000). In one experiment,

Table 1 (1) Hypotheses proposed as more parsimonious explanations of chimpanzee social problem-solving behavior that (2) rely on egocentric explanations rather than psychological state attribution (references are given in corresponding footnotes, below) and (3) evidence that has been interpreted to rule them out in favor of richer interpretations (references are given in corresponding footnotes, below)

(1) Alternative hypothesis	(2) Rationale of lean interpretation	(3) Evidence against lean interpretation of chimpanzee social skill observed in recent experiments
Learning during experiment	Repeated trials used with few subjects, making it likely that subjects simply learn the correct strategy during the experiment. This makes the learned skill unlikely to generalize or triangulate to another novel context. ^a	<ul style="list-style-type: none"> ■ Large samples of subjects are used to allow group statistics and fewer trials per individual (as in human infant research).^f ■ Experiments use nondifferential rewarding in which both correct and incorrect responses are rewarded. If a preexisting inferential bias exists it will be expressed in the experiment.^g ■ Trial one results are obtained.^h ■ Learning analysis shows no improvement of subjects within test sessions.ⁱ ■ Animals triangulate social skill in several novel testing contexts (i.e., several paradigms with several tests each).^j
Online behavior reading	Experimental and control conditions differ systematically with regard to the presence of obvious behavioral cues (e.g., direction of gaze, presence or absence of social partner). Subjects egocentrically use observable behavioral cues spontaneously or after learning within a test session. ^b	<ul style="list-style-type: none"> ■ Experiments are designed to prevent the use of online behavior reading cues (e.g., subordinates must decide approach direction before dominant competitor's door is opened).^k ■ Control experiments are run to demonstrate that subject's social inferences are not the result of reading available social cues (under door).^l ■ Subjects must make social inferences regarding human experimenters who do not provide relevant behavioral cues (i.e., either by not behaving or by closely matching behaviors between experimental and control conditions).^m ■ Imitation experiments cannot be explained by this hypothesis.ⁿ
Valence of visual social cues	Subjects learn during life to direct visual communication toward the largest frontal surface of a social partner regardless of cues to their visual attention. These large frontal aspects have the highest valence to subjects. ^c	<ul style="list-style-type: none"> ■ Chimpanzee subjects can spontaneously make calculations regarding the visual perception of humans and conspecifics when gesturing (i.e., refuting previous negative evidence).^o ■ When high- and low-valence frontal aspects of a human are put in competition, chimpanzees spontaneously use information regarding visual perception even though it is of low valence.^p ■ Chimpanzees make strategic decisions using visual perception and also by attending to others' auditory perception.^q
Attraction to physical barriers	During competition against a dominant, subjects have learned to protect themselves by remaining near physical barriers. Subjects' preferences are driven by a preference for physical barriers not visual occluders during competition. ^d	<ul style="list-style-type: none"> ■ Competing chimpanzees do not approach transparent barriers that are physical barriers but do not occlude food.^r ■ Competing chimpanzees approach food the competitor did not see, even though multiple barriers are present.^s ■ When competing in a context where no physical contact is possible, chimpanzees choose food that the dominant did not see even though multiple visual barriers are present.^t ■ Competing chimpanzees hide behind an occluding but not a nonoccluding barrier even though they are same physical size.^u

(Continued)

Table 1 (Continued)

(1) Alternative hypothesis	(2) Rationale of lean interpretation	(3) Evidence against lean interpretation of chimpanzee social skill observed in recent experiments
Statistical regularities	Inferences of others' psychological states always rely on observable statistical regularities (i.e., behavioral or contextual cues). Experiments cannot rule out egocentric decisions on the basis of observable statistical regularities alone (e.g., threat posture, eye or face direction, body position, eye direction in relation to objects in the world). ^c	<ul style="list-style-type: none"> ■ Multiple experiments have ruled out all plausible online statistical regularities previously proposed (see above).^v ■ Several third-way hypotheses have been proposed (e.g., intervening variables).^w ■ Chimpanzees rewarded for approaching food near the smaller of two nonoccluding barriers do not learn to use this statistical regularity.^x ■ Flexibility observed and controls used with chimpanzees are analogous to those used in studies of human infants when psychological state attribution is recognized.^y ■ Proposed statistical-regularity experiments are no more powerful than existing experiments.^z

References for column (2): ^aHeyes 1993, 1998; ^bHeyes 1993, 1998; Povinelli & Eddy 1996; Tomasello & Call 1997; ^cKarin-D'Arcy & Povinelli 2002, Povinelli & Eddy 1996; ^dPovinelli & Giambrone 2001; ^ePenn & Povinelli 2007, Vonk & Povinelli 2004.

References for column (3): ^fHare 2001; ^gHare 2001; ^hHare et al. 2006, Flombaum & Santos 2005; ⁱKaminski et al. 2008, Melis et al. 2006a; ^jCall et al. 2004; Hare et al. 2000, 2001, 2006; Kaminski et al. 2008; Melis et al. 2006a; ^kBraeur et al. 2007; Hare et al. 2000, 2001, 2006; Kaminski et al. 2008; Melis et al. 2006a; ^lHare et al. 2000 (experiment 4); ^mCall et al. 2004, Hare et al. 2006, Melis et al. 2006a; ⁿCall & Tomasello 2008; ^oCall & Tomasello 2007, Hostetter et al. 2001, Kaminski et al. 2004, Leavens & Hopkins 1998; ^pHare et al. 2006; ^qHostetter et al. 2001, Melis et al. 2006a; ^rHare et al. 2000, 2006; ^sHare et al. 2001, 2006; ^tKaminski et al. 2008; ^uHare et al. 2006, Melis et al. 2006a; ^vSee all previous citations; ^wCall 2001, Whiten 1996, Suddendorf & Whiten 2003; ^xHare et al. 2006; ^yCall & Tomasello 2008, Fitch et al. 2010, Rosati et al. 2010; ^zFitch et al. 2010.

a subordinate saw food hidden and it could also observe whether a dominant competitor also saw the food hidden. Subordinates were more likely to approach and obtain food in the condition in which a dominant did not see food hidden. Similarly, in a second experiment a subordinate observed as a dominant watched where food was hidden. However, whereas in one condition the subordinate was released to compete against the same dominant, in another condition the original dominant was switched for a naïve dominant who had not observed the baiting. Subordinates again were more likely to retrieve the hidden food and approach farther when their competitor was the dominant who had not seen the food hidden. Kaminski et al. (2008) subsequently has built on this initial work but tested chimpanzees in a scenario that might be characterized as “chimpanzee chess.” Two chimpanzees competed over two pieces of food that were hidden in two of three cups on a sliding tray. The subject and competitor were both allowed to see one piece of food hidden. However, only the subject saw in which cup a

second piece of food hidden and which cup was left empty. Once baited, subjects could then choose to retrieve food from under one cup each time the tray was pushed back and forth between them by an experimenter. However, they could not see each other's choice. In one condition, the subject was allowed to choose the contents of one of the cups before the competitor, whereas in the other condition the competitor was allowed to choose first. As predicted, when subjects were allowed to choose first, the subjects preferred the cup in which the competitor had seen food hidden (i.e., leaving the competitor with only a 50:50 chance to get the remaining food piece before the tray returned to the subject again). Meanwhile, when subjects chose second, they avoided this same option (i.e., knowing the competitor would have taken it over the more uncertain option). A number of controls for behavioral cuing and learning again ruled out a number of low-level explanations. Taken together, these studies suggest that chimpanzees not only understand the visual perspective of others,

but also know whether others know or do not know something, at least in some contexts.

Since these initial competitive studies were conducted, evidence continues to support the ability of chimpanzees to assess the psychological states of others in different domains. Another series of studies has subsequently shown that chimpanzees as well as other primates understand much about others' visual perception and also their auditory perception (Brosnan & de Waal 2002, Kaminski et al. 2004, Flombaum & Santos 2005, Hare et al. 2006, Hattori et al. 2006, Melis et al. 2006a, Santos et al. 2006, Call & Tomasello 2007, Phillips et al. 2009; although see Cheney & Seyfarth 1990a, Hare et al. 2003, Cheney & Seyfarth 2008). Moreover, experiments now suggest that chimpanzees are also sensitive to the intentions underlying others' actions. Chimpanzees distinguish between a human experimenter who is intentionally refusing to share food and an experimenter who is accidentally failing to share food; like children, chimpanzees are far more patient when a human is trying but failing to share (Call et al. 2004, Behne et al. 2005). In addition, preliminary evidence suggests that chimpanzees also perceive human gestures as rationale and are capable of rational imitation (Buttelmann et al. 2007, Wood et al. 2007). Finally, like human children, chimpanzees possess the basic motivation to help others. In some contexts, chimpanzees will help another for no reward (Warneken et al. 2007, Greenberg et al. 2010, Melis et al. 2010; although see Silk et al. 2005, Vonk et al. 2008). They also show evidence for contagious yawning, a form of social contagion that has been interpreted by some researchers as a rudimentary form of empathy (Anderson et al. 2004, de Waal 2008, Campbell et al. 2009). In summary, by using nonverbal tasks with chimpanzees, there is now as substantial evidence for psychological state attribution as that observed in preverbal human infants—at least in some domains. As with preverbal infants, the range of experiments conducted with nonhumans provides overwhelming evidence against a variety of

leaner interpretations of the problem-solving behavior observed in the experiments (see **Table 1**).

Derived Features of Human Theory-of-Mind Abilities

On the basis of current evidence, it now seems unlikely that our ability to assess others' psychological states evolved entirely *de novo* after humans split from other apes (Call & Tomasello 2008, Fitch et al. 2010, Rosati et al. 2010). However, the same research that reveals social cognitive flexibility in chimpanzees also reveals that it is unlikely that they have all the same capabilities as seen in humans. For example, there remains little, if any, evidence that chimpanzees can flexibly integrate cooperative and communicative skills and motivations to the degree that young human infants do (Hare 2007, Rosati et al. 2010). In addition, there is no evidence that chimpanzees (or any other animal) can reason about false beliefs in others (i.e., as tested by false-belief and appearance-reality tasks; Flavell 1999, Kaminski et al. 2008). Researchers currently hypothesize that these domains of theory of mind are major derived features of human cognitive evolution (Tomasello et al. 2005, Hare 2007, Call & Tomasello 2008; see also debates regarding empathy in chimpanzees: Preston & de Waal 2002, de Waal 2008, Silk 2008).

Recall the inability of chimpanzees to solve the initial social problems that required cooperation and communication with humans (e.g., Povinelli & Eddy 1996, Call et al. 1998, Call & Tomasello 1999). It now seems that these skills are severely constrained in the same situations where chimpanzees succeed at either cooperating or communicating. For example, although chimpanzees can exploit social cues such as face orientation by following the gaze of other chimpanzees in natural settings, they do not show human-like flexibility in using or providing such social cues in tasks requiring communication during cooperative interactions (Hare 2007, Liszkowski et al. 2009, Rosati & Hare 2009). The most striking example is

the inability of chimpanzees to use cooperative-communicative social cues spontaneously (e.g., gaze direction or pointing) that indicate the location of hidden food. This result occurs regardless of whether such cues are provided by a human or by a conspecific (Itakura et al. 1999, Hare & Tomasello 2004). Meanwhile, captive apes can slowly learn to comprehend these same social cues or even to produce gestures in a circumscribed set of cooperative-communicative situations. For example, captive chimpanzees will indicate (using an outstretched arm) to a human to retrieve food for them (Leavens & Hopkins 1998, Hostetter et al. 2001, Herrmann et al. 2007). However, there are relatively few, if any, novel experimental contexts in which chimpanzees have spontaneously comprehended or produced overt communicative strategies to solve novel cooperative problems (Melis et al. 2009, Hare & Tan 2012). Thus, human communication may have evolved to be uniquely cooperative as evidenced by our unique eye morphology (e.g., white sclera) and sensitivity to eye movements relative to other apes (Kobayashi & Kohshima 1997, Burnham & Hare 2007, Tomasello et al. 2007, Kano & Tomonaga 2009, Hattori et al. 2010, Tomonaga & Imura 2010).

Recent experiments corroborate this pattern in more natural cooperative interactions. Studies recently demonstrated that chimpanzees can spontaneously solve novel instrumental tasks requiring joint effort (Melis et al. 2006c, Hirata & Fuwa 2007). In addition, chimpanzees understand the role of their partners in solving this type of cooperative task and prefer to work with more skilled individuals, shunning those who are not skilled (Melis et al. 2006b, 2009; see also Subiaul et al. 2008). Chimpanzees will even negotiate with their partners if there is a conflict of interest over cooperative payoffs (Melis et al. 2009). However, the same chimpanzees who could collaborate and negotiate never spontaneously used any overt form of communication when solving the tasks presented. When recruiting partners, chimpanzees made no attempt to communicate in the novel test situation (Melis et al. 2006b; see also Hirata

& Fuwa 2007). Even when chimpanzees were trying to “convince” another chimpanzee to jointly obtain a payoff they wanted, they never used any form of overt communication to negotiate (Melis et al. 2009). Chimpanzees seemed particularly disadvantaged without such communicative strategies as unequal payoffs became more extreme. Lack of communication may even prevent the development of reciprocal strategies (i.e., children will use gestures to agree on taking turns receiving the highest payoff: Melis et al. 2008, 2009; Brosnan et al. 2009). Finally, when chimpanzees were tested, like children, for their ability to re-engage a partner who stopped playing his or her role in a cooperative game, they were not motivated or were unable to use vocal or gestural signals to re-engage the experimenter (Warneken et al. 2006). Overall then, although recent research suggests that chimpanzees are both skilled cooperators and communicators, they are highly constrained in their understanding of cooperative-communicative intentions. Alternatively, they at least show little motivation to communicate in order to cooperate.

There also remains no evidence that chimpanzees can reason about the false beliefs of others. In some theoretical descriptions, false-belief understanding is the sine qua non of human theory of mind (e.g., Perner 1991; although see Bloom 2000). Therefore, experimenters have attempted to present nonverbal tests of false belief to chimpanzees using methods in which they show an understanding of another’s visual perspective in other contexts. However, both Hare et al. (2001) and Kaminski et al. (2008) found little, if any, evidence to suggest that chimpanzees understand when others have a false belief. Given the relevance of this skill for advanced linguistic capabilities, this distinction could be a crucial derived feature of human cognitive evolution (Astington & Jenkins 1999, Astington 2001).

Although negative findings are always difficult to interpret, the findings reviewed above are particularly powerful because in all cases the chimpanzees showed skill in solving complex social problems in the same testing context

in which they did not show either cooperative-communicative skills or an understanding of others' false-belief states. Therefore, on the basis of the current evidence, it is these major components of human theory of mind that were likely derived during our species evolution after the split with our LCA.

The Cultural Intelligence Hypothesis

Between-species comparisons using a variety of different tasks have been extremely instructive in producing viable hypotheses regarding the unique nature of human development. Yet, until recently, investigators had not sought to compare systematically a representative range of cognitive skills among a single set of human and nonhuman-primate individuals. This type of large-scale comparative work is required to test the cultural intelligence hypothesis, which emphasizes the specialization of human social cognition as opposed to a more general cognitive change by which human cognition was fundamentally altered across a range of domains. The major prediction of this hypothesis indicates that human cognitive development will diverge most significantly from other apes in skills related to participating in cultural interactions.

Herrmann et al. (2007, 2010a) created and administered the primate cognition test battery to more than 100 human infants as well as 100 chimpanzees and several dozen bonobos and orangutans. The battery consisted of more than 15 tasks and was constructed using theoretical analysis that suggested social and physical cognition are distinct from each other as well as from more general-purpose psychological functions (e.g., temperament, memory, inhibitory control, etc.). According to this view, physical cognition deals with inanimate objects and their spatial-temporal-causal relations, whereas social cognition deals with other animate beings and their intentional actions, perceptions, and knowledge. Meanwhile, more general-purpose cognitive mechanisms are recruited to solve problems across domains. Results from this battery provided strong support for the evolution of a social revolution in infant

development (although see de Waal et al. 2008 and Herrmann et al. 2008). Young human children who were still several years away from literacy and formal schooling performed at a level basically equivalent to that of chimpanzees and orangutans on tasks of physical cognition and outperformed these same species on tasks of social cognition (Herrmann et al. 2007, 2010b). Moreover, a structural analysis of individual differences in the large sample of chimpanzees and human infants showed that children's performances tended to differentiate among the three cognitive domains of physical, social, and spatial cognition, whereas chimpanzees differentiated between only space and the remaining tasks. This result suggests that a unique cognitive domain of more specialized social skills develops in children but is not present in chimpanzees (Herrmann et al. 2010b).

Overall the results of these comparisons show that it is in the social domain specifically that human infants (at least from one industrialized population) seem to differ from our closest primate relatives, which suggests that humans have evolved some specialized social-cognitive skills (beyond those of other apes) for living and exchanging knowledge in cultural groups: communicating with, learning from, and assessing the psychological states of others in particularly complex ways. If correct, the challenge then becomes determining how a major shift in cognitive development might have occurred.

JUVENILIZED BONOBOS AND THE PROCESS OF SOCIAL COGNITIVE EVOLUTION

Humans have two closest living relatives: the well-known chimpanzee and the lesser-known bonobo. Both species are equal in their genetic similarity to humans, and both are genetically more similar to humans than they are to gorillas (Won & Hey 2005). However, largely owing to feasibility, most cognitive research has been conducted using comparisons between humans and chimpanzees (Hare 2009). Recent research suggests that comparisons between the development of bonobo and chimpanzee psychology

may provide a powerful tool with which to study the evolution of shifts in human development.

In many ways, the socioecologies of bonobos and chimpanzees are highly similar to each other: Both are dependent on the mother for up to five years, are largely frugivorous, and live in complex, mixed-sex fission-fusion societies (Kano 1992). These similarities might suggest that their psychologies are largely the same and that testing both species is redundant. However, in many ways each species is more similar to humans than they are to each other (e.g., bonobos are more tolerant when sharing food, whereas wild chimpanzees are prolific extractive-tool users compared with bonobos; Hare et al. 2007, Gruber et al. 2010, Herrmann et al. 2010a, Wobber et al. 2010a). Moreover, recent research has demonstrated that bonobo and chimpanzee psychologies differ in important ways (Hare 2009, Herrmann et al. 2010a). When tested for social skills related to reading the behavioral intentions of others, the temperamentally shyer bonobo is more skilled than the bolder chimpanzee, just as shyer children are more skilled at the same task than are bolder children (Herrmann et al. 2010a, Wellman et al. 2010). The gestural repertoire of bonobos may also be more variable than that of chimpanzees. An observational study suggests that bonobos show a higher level of responsiveness to combinatorial signals that utilize both facial and manual gestures (Pollick & deWaal 2007). Finally, when the two species were compared for their ability to cooperate spontaneously on a novel instrumental task, bonobos outperformed a group of highly skilled chimpanzees when the food reward was made monopolizable (Hare et al. 2007). Bonobo cooperative problem-solving abilities are less constrained by tolerance, which can even translate into voluntary food sharing with strangers (Hare & Kwetuenda 2010).

Perhaps most importantly, there is significant evidence for developmental differences in bonobos and chimpanzees (Wrangham & Pilbeam 2001). In many domains, bonobos appear to show evidence of developmental delay relative to chimpanzees (the one exception

being bonobo sexual development; Woods & Hare 2010). Bonobo infants are more socially dependent: nursing for longer, grooming more social partners earlier in life, and spending more time in closer proximity to their mothers than same-age chimpanzees (De Lathouwers & van Elsacker 2006, Kuroda 1989). Bonobos retain juvenile levels of play and socio-sexual behavior into adulthood, as well as behaviors suspected of facilitating tolerance when sharing food or when cooperating to solve social problems (Palagi 2006, 2008). Even the morphology of bonobos suggests shifts in their brain development because the cranium of the bonobo appears to develop through paedomorphosis, or retention of juvenile morphology into adulthood (Lieberman et al. 2007). Wobber et al. (2010c) recently tested the prediction that the increased tolerance observed in bonobos relative to chimpanzees is a result of developmental differences in the two species. When comparing levels of cofeeding behavior in a large sample of age- and sex-matched juvenile bonobos and chimpanzees, both species were very tolerant. Meanwhile, adult chimpanzees became increasingly intolerant with age, and adult bonobos maintained juvenile levels of cofeeding. This led Wobber et al. (2010a) to predict that even though the two species have similar inhibitory control skills in solving physical problems (i.e., detour tasks; Vlammings et al. 2010), bonobos would be developmentally delayed in tasks requiring social inhibition (i.e., chimpanzee infants must quickly learn to avoid dominance transgressions, whereas bonobos do not). In two different tasks, a large sample of age- and sex-matched bonobos showed delayed development relative to chimpanzees in social tasks requiring them to inhibit begging for food from certain social partners but not other partners. Moreover, the performance of adult bonobos more closely resembled that of juvenile bonobos than that of adult chimpanzees.

With evidence suggesting evolution in the ontogeny of the two *Pan* species, it is likely that previously observed developmental differences that exist between infant chimpanzees and

humans (i.e., Tomasello & Carpenter 2005, Matsuzawa et al. 2006) will not always generalize to bonobos. Differences between the development of bonobos and that of humans may not exist or may be even more extreme than those observed between humans and chimpanzees. Moreover, because bonobos and chimpanzees differ genetically by only a few tenths of a percentage (Won & Hey 2005), any developmental differences observed between the two *Pan* species may be easier to associate with specific genetic systems (e.g., regulatory genes or differential gene expression) than with differences between either species and humans. If comparisons of the bonobo and chimpanzee genome allow for links between behavioral or cognitive differences detected in their development, we may also be able to test hypotheses regarding the evolution of human development. An understanding of how the evolution of bonobo and chimpanzee development occurred will likely allow for strong inferences regarding the processes and mechanisms by which major shifts in human development evolved (Wobber et al. 2010b).

CONCLUDING REMARKS

Some researchers have suggested that extant species of apes can tell us little about our species psychological evolution: “Comparing ourselves to our closest kin, it is somewhat sobering that the hominid path led to cognition whereas that leading to *Pan*, our closest living relatives, did not, despite the near-synonymy of our genomes” (Lovejoy 2009, p. 74e7). As reviewed here, bonobos and chimpanzees are richly cognitive, and they offer us the most powerful way to test hypotheses regarding the evolution of human cognition. In directly comparing the cognitive skills of human infants to those of bonobos and chimpanzees, we are

identifying which aspects of our own cognition are derived and likely have led to much of what we consider to be uniquely human. Initial attempts to study psychological state attribution in chimpanzees failed even to show that chimpanzees could use cues to others’ visual perception that are required to understand visual perspective-taking (e.g., Povinelli & Eddy 1996). However, recent studies have repeatedly demonstrated that chimpanzees are extremely flexible in their use of this same social information and use it spontaneously to make strategic social decisions (e.g., Hare et al. 2006, Kaminski et al. 2004). The debate has now largely shifted away from whether chimpanzees can assess the psychological states of others toward identifying the constraints on their social problem-solving skills that might suggest derived forms of psychological state attribution in our own lineage (Call & Tomasello 2008, Rosati et al. 2010; **Table 1**). Moreover, large-scale comparisons between human infants and multiple species of nonhuman apes suggest that the development of human social cognition has evolved since our lineage split from the other apes. Early emerging social skills are believed to facilitate the participation in culture, giving infants access to the knowledge of generations at an extremely early age (Herrmann et al. 2007, 2010). Comparisons between bonobos and chimpanzees have also revealed that humans may not be the only ape species showing evidence of shifts in social skill development. Thus, understanding how developmental shifts affected the cognitive evolution of our two closest living relatives may also allow for inferences regarding the evolution of development in human psychology (Wobber et al. 2010b). Ultimately, comparative and developmental studies of living apes should reveal much about how and why a hominoid mind evolved into the human mind.

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