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From Nonhuman to Human Mind

What Changed and Why?

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ABSTRACT—Two questions regarding the human mind challenge evolutionary theory: (a) What features of human psychology have changed since humans' lineage split from that of the other apes such as chimpanzees and bonobos? And (b) what was the process by which such derived psychological features evolved (e.g., what were the selection pressures)? I review some of the latest research on chimpanzee and canine psychology that allows inferences to be made regarding these questions.

KEYWORDS—cognitive evolution; chimpanzees; dogs; social cognition; emotional reactivity

Our species' unique flexibility of behavior, which is a product of our psychology, presents evolutionary theory with its biggest challenge. The first challenge for researchers is to identify what part of the human mind is uniquely human. Cognitive psychologists have provided a relatively parsimonious hypothesis that may explain the evolution of much of what is considered unique about our species' behavioral phenotype. As humans, we are skilled at assessing the perceptions, intentions, and beliefs of others. This ability to infer other individuals' mental states allows for unprecedented flexibility in predicting behavior. As a result, individuals can adjust their behavior to effectively communicate, teach, imitate, or even deceive others (Flavell, 1999). Indeed, children must develop this ability in order to acquire all types of cultural traditions, including language. Therefore, it may be our species' ability to think about the thoughts of others, or *theory of mind*, that provides the developmental foundation for much of what is considered unique to human cognition (Tomasello, Call, & Hare, 2003). If this theory-of-mind hypothesis is correct, then other species of great apes, including chimpanzees and bonobos (*Pan troglodytes* and *Pan paniscus*), should differ in some important ways from humans in how they solve social problems—particularly in situations that might require thinking about other individuals' thoughts.

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SHARED SOCIAL-PROBLEM-SOLVING SKILLS

Within the past decade, significant progress has been made in developing methods to assess whether chimpanzees think about the thoughts of others. As a result, it is now clear that chimpanzees share with humans some abilities to assess the perceptual states of other individuals. For example, when two chimpanzees compete over two pieces of food, the subordinate chimpanzee preferentially retrieves the piece that is hidden from the dominant's view, suggesting that the subordinate knows that the dominant can see one piece but not the other (Tomasello et al., 2003). Chimpanzees also seem to know when other individuals can or cannot perceive how they are behaving. Chimpanzees spontaneously hide their approach to contested food by avoiding being seen or heard when competing against a human experimenter (Hare, Call, & Tomasello, 2006; Melis, Call, & Tomasello, 2006). Moreover, recent work suggests that chimpanzees not only take into account others' perceptual states but also recognize the intentions behind other individuals' behavior. For example, in several experiments, chimpanzees showed more frustration (by banging an object or leaving the test area) when a human intentionally interrupted a feeding session than when the interruption was accidental (Tomasello et al., 2003). Therefore, it is unlikely that the ability to assess other individuals' perceptual states as well as the intentions underlying their actions can account for the unusual behavioral flexibility observed in humans.

A Human Form of Social Problem Solving?

Although it seems that the ability to assess other individuals' psychological states did not entirely evolve only after humans split from other apes, it also seems unlikely that we inherited the full suite of our species' theory-of-mind capabilities in common with our nearest nonhuman ape relatives (Tomasello et al., 2003). For example, although chimpanzees can exploit social cues such as face orientation by following the gaze of other chimpanzees in natural settings while monitoring their group members' behavior (see Tomasello et al., 2003) or while competing for food (e.g. Hare et al., 2006), they do not show human-like flexibility in using or providing such social cues in tasks requiring communication during cooperative interactions (Tomasello et al., 2003). The most striking example of this

inflexibility is the performance of chimpanzees in the “object choice” task, in which a human experimenter indicates to an animal subject the location of hidden food by using a social cue (e.g., gaze direction or pointing; see Fig. 1). Universally, nonhuman primates, including chimpanzees, show little spontaneous skill at using such communicative cues to find the hidden food in this cooperative context. In addition, chimpanzees do not use such cues when the cues are provided by members of the same species in this same cooperative context. Moreover, once chimpanzees and other nonhuman primates learn, after dozens of trials, to use any one cue, they do not generalize this new skill when presented with a slightly modified social cue.

Therefore, it seems that chimpanzees lack the ability or propensity to flexibly read social cues in cooperative-communicative contexts—an important skill for humans that develops as children begin acquiring language skills (Tomasello et al., 2003). The ability to use social cues in a cooperative-communicative context therefore seems to have evolved after the hominid split, and thus may play a role in explaining the unusual behavioral flexibility observed in humans. Now the challenge is to characterize the social-cognitive skills of nonhuman apes more precisely, so that robust differences, such as the relative ability of different ape species to solve cooperative-communicative problems, become increasingly apparent.

PROCESSES BY WHICH SOCIAL PROBLEM SOLVING EVOLVES

Identifying unique psychological features of our species’ evolutionary past is merely the first step in reconstructing human cognitive evolution. The second and toughest evolutionary challenge is answering the question, what selection pressures



Fig. 1. Basic test of an animal’s (in this case, a dog’s) ability to use human behavioral cues to find hidden food. An experimenter places food so that the dog sitting across from her does not know under which cup it is hidden. Then the experimenter points in the direction of the correct cup and lets the dog choose a cup. (Dogs are more skilled at this task than are chimpanzees.)

drove the evolution of human species-specific cognition, and what did selection act upon? Cases of convergent evolution potentially provide a unique opportunity for inferring how heritable traits evolve. If two distantly related species share a similar trait, it is possible that this trait arose independently due to a similar evolutionary process. Indeed, comparative work with primates and canids (wolves, dogs, and foxes) supports the hypothesis that dogs’ social skills in cooperative-communicative contexts are a case of convergent evolution with humans (Hare & Tomasello, 2005). This comparative work has begun to identify the selection pressures that drove the evolution of dogs’ social skills and suggests that similar pressures may have shaped human social skills during hominid evolution.

Domesticated Social Skills in Canids

In contrast to nonhuman primates, domestic dogs are expert at spontaneously using humans’ cooperative-communicative social cues (e.g., gaze or pointing) when searching for food in the object-choice task (Fig. 1). Dogs even have the ability to use novel and arbitrary social cues to find hidden food (e.g., a wooden marker placed on the correct location). Many dogs are skillful from the first trial, with no learning effects being observed within the experiments. Controls have ruled out the possibility that dogs use olfactory cues to find the hidden food (reviewed in Hare & Tomasello, 2005). But perhaps the most striking findings are that dogs do not require intense exposure to humans to learn these skills (e.g., kennel-reared puppies are as skillful as puppies reared with a human family) and that dogs did not simply inherit these abilities from their closest relative, the wolf (wolves perform much like nonhuman primates). Taken together, these findings suggest that dogs, unlike chimpanzees, have human-like skill at using cooperative-communicative social cues and that this skill likely evolved during domestication, as it is neither learned nor inherited through common descent (Hare, Brown, Williamson, & Tomasello, 2002; Miklosi et al., 2003).

Domestication Is Emotional Evolution

In 1959, geneticist Dmitri Belyaev began experimentally domesticating foxes on a farm in Siberia, Russia. The experimental population has now been selected for over 45 years based on the sole criterion of low levels of fear and aggression toward humans (i.e., not based on their use of human social cues or communicative gestures). Successive generations of experimental foxes increasingly began to approach humans instead of running away (the foxes now even bark and wag their tails as humans approach). This experimental population also began exhibiting a high prevalence of floppy ears, curly tails, piebald coats, less robust skeletons, and a whole suite of nonselected changes associated with domestication in dogs and other animals. In addition, the experimental foxes showed changes in the adrenal cortex and serotonergic and limbic systems (which mediate fear

and aggression) when compared to the control population of foxes that had been bred for an equal number of generations without regard to their behavior toward humans (Trut, 2001).

Like the two fox populations, humans also vary in their stress response to novel people and other discrepant events. Such variance in human temperament is, in large part, thought to be due to differences in the reactivity or “tone” of the limbic system, particularly the amygdala. Thus, it has been suggested that similar variance in emotional reactivity in the original breeding stock of experimental foxes became the incidental target of the Russian researchers’ artificial-selection regime (Kagan & Snidman, 2004).

Curiously, when tested with a subset of the same object-choice tasks used with dogs and chimpanzees, experimental fox kits used human social cues at the same level as did the dog puppies and at higher levels than the control kits. Because the strict experimental breeding criterion is well documented, this finding suggests that domestic dogs, like Belyaev’s foxes, use cooperative-communicative social cues as a result of selection on levels of emotional reactivity during domestication (Hare et al., 2005). That is, dogs’ specialized social-problem-solving skills may have first appeared after systems mediating fear and aggression were altered. Once this initial evolution occurred so that dogs were motivated to apply inherited cognitive abilities (i.e., “reading” behavior in other members of their species) to solve a new set of social problems involving humans, variance in these cognitive abilities could have been directly selected (e.g., in contexts, such as herding or hunting, that require cooperation and communication with humans). However, if such evolution occurred as a result of direct selection on social skill, it would not have been possible without the initial selection on systems controlling emotional reactivity, which allowed dogs to interact with humans as comfortably as with other members of their species (Hare & Tomasello, 2005).

SOCIAL EMOTIONS AND HUMAN FORMS OF SOCIAL SKILL

One hypothesis is that social skills that evolved during human evolution are in part the result of initial evolutionary changes in humans’ emotional response to others, as seems to be the case with domestic canids. One prediction of this emotional-reactivity hypothesis is that social skills in nonhuman apes, relative to those of humans, will be highly constrained by the nonhuman apes’ social emotions (i.e., emotions that are elicited in the presence of an animate being). Support for the emotional-reactivity hypothesis comes from the finding that cooperation among chimpanzees is highly constrained by levels of tolerance between individuals (i.e., likely controlled by systems mediating fear and aggression). Chimpanzees are sophisticated collaborators that are capable of identifying and then recruiting the best partner in order to spontaneously solve a novel instrumental task, such as pulling a rope simultaneously to retrieve a tray of

food (Melis, Hare, & Tomasello, 2006a). However, chimpanzees demonstrate such skills only if (a) the food is sharable, (b) the partners are out of each other’s reach while they pull, and (c) the partners have shared food previously in a similar context. If such social criteria are not met, then chimpanzees will not solve the cooperative problem presented. It seems that subordinate chimpanzees are simply not willing to risk being attacked by intolerant dominants, and dominants are not able to control their aggression toward subordinates trying to obtain food—even if it means the dominants will not receive food either (Melis, Hare, & Tomasello, 2006b). Thus, as the emotional-reactivity hypothesis predicts, chimpanzees are constrained by their social emotions in how flexibly they can solve cooperative problems.

Is it possible that, in a similar way, constraints on social emotions also prevent chimpanzees from spontaneously reading social cues in the object-choice task? Indeed, chimpanzees can spontaneously use social cues in that task as long as they believe they are competing for the food against the individual providing the cue. If chimpanzees see a competitor apparently attempting to reach hidden food, they subsequently search in that location. Moreover, chimpanzees use social cues from a human competitor as skillfully as they use cues from a chimpanzee competitor in the same task. However, if the same chimpanzees then see the previously competitive human now helpfully pointing toward the hiding location (i.e., morphologically similar to the reaching), they do not use the gesture to locate the food. Thus, it seems that chimpanzees can spontaneously use human or chimpanzee social cues when they become upset that another individual might get “their” food (Hare & Tomasello, 2004).

This finding suggests that human levels of flexibility in using others’ social cues may have evolved in the human lineage only following the emergence of species-specific social emotions that provide motivation to attend to other individuals’ behavior and, subsequently, their communicative intent during purely cooperative interactions. Taken together, the results on chimpanzee cooperation and their use of social cues support the hypothesis that evolution in human social problem solving, much like that in dog social problem solving, occurred after changes in our species’ social emotions lifted social constraints; selection then could act on variance in inherited cognitive traits that were now expressed in new social contexts facilitated by changes in emotional reactivity.

FINDING OUR MIND IN AFRICA

Now more than ever, researchers have exciting opportunities to delve deeper into the minds of our two closest living relatives, chimpanzees and bonobos (Fig. 2), to discover precisely how nonhuman apes’ minds are similar and dissimilar to those of humans. In the absence of language, how sophisticated is their ability to think about others’ thoughts? What other dimensions of humans’ cooperative-communicative skills are products of evolution since our lineage last shared an ancestor with bonobos and

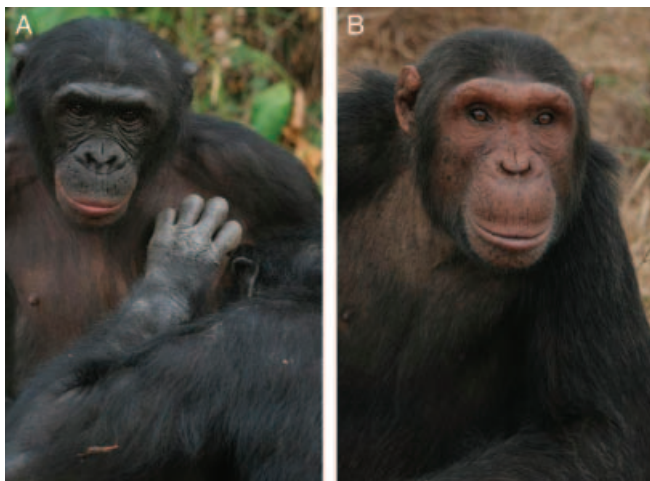


Fig. 2. Bonobos (A) and chimpanzees (B). These are humans' two closest living relatives, both sharing almost 99% of the human genome through common descent.

chimpanzees? What was the process by which selection acted on ape psychology to produce the unique behavioral flexibility of the human mind? Did it all start with selection on human social emotions, as is suggested by work with dogs and chimpanzees? The full answer to such questions will require work with bonobos, because humans and bonobos are thought to differ from chimpanzees in similar ways—particularly in cooperative-communicative behavior.

Bonobos and chimpanzees diverged from each other around 2 million years ago and differ in morphology, behavior, and perhaps even emotions and cognition in important ways. Bonobos are female dominant, with females forming tight bonds against males through same-sex socio-sexual contact that is thought to limit aggression. In the wild, they have not been seen to cooperatively hunt, use tools, or exhibit lethal aggression. Chimpanzees are male dominant, with intense aggression between different groups that can be lethal. Chimpanzees use tools, cooperatively hunt monkeys, and will even eat the infants of other chimpanzee



Fig. 3. A 40-hectare (100-acre) island sanctuary for chimpanzee orphans—a result of the illegal bushmeat trade. Ninety-five percent of the island (A) is primary tropical forest in which the chimpanzees can roam freely. A juvenile chimpanzee (B) climbs a tree before disappearing with its other 40 group members into the forest for the day. At night the sanctuary apes sleep in hammocks in large indoor enclosures (C) where they are provisioned and protected from the weather. In the morning, individuals can volunteer to play problem-solving games (D) by allowing keepers to separate them from the group, after which they are let out onto the island.

groups. Bonobos and Chimpanzees share close to 99% of their genome in common with humans, meaning that their genomes are more similar to that of humans than they are to that of gorillas. However, it may be that bonobos, whose psychology is virtually unstudied relative to that of chimpanzees, are more similar to humans than are chimpanzees in how they solve various social problems (e.g. Hare, Melis, Woods, Hastings, & Wrangham, in press). Such similarities may even be partly the result of shared and heritable neurophysiology that potentially regulates the social emotions of humans and bonobos in similar ways (Hammock & Young, 2005). Given that bonobos are thought to be more tolerant than chimpanzees, are they more human-like in their ability to cooperate flexibly with any groupmate? Or, given that bonobos show little aggression toward strangers, do they have more inhibitory control than chimpanzees?

The future of any research program with chimpanzees and bonobos will depend on the large, semicaptive populations of these apes living in sanctuaries in Africa (Fig. 3). These sanctuaries provide an unmatched resource because of the presence of dozens of infants of both species that grow up in highly enriched and natural environments (there are no bonobos and few if any infants in labs today because of the expense of breeding). Unlike lab animals, who can chronically suffer in captivity, sanctuary apes live together in large social groups in massive tracts of tropical rainforest. Semicaptive chimpanzees and bonobos can be tested in indoor enclosures similar to conventional laboratories at a fraction of the cost (e.g., Melis, Hare, et al., 2006a, 2006b; Hare et al., in press). Developing African sanctuaries as world-class resources will allow researchers to learn what changed and why during our species' evolution by allowing for tests that were not previously possible (e.g. Hare et al., in press) and will contribute to the welfare and conservation of the remaining captive and wild populations of our two closest relatives.

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