

Theory of mind: evolutionary history of a cognitive specialization

Daniel J. Povinelli and Todd M. Preuss

Traditional analyses of the evolution of intelligence have emphasized commonality and continuity among species. However, recent research suggests that humans might have specialized in a particular kind of intelligence that is related to understanding mental states such as desires, intentions and beliefs. Data indicate that the ability to reflect on one's own mental states, as well as those of others, might be the result of evolutionary changes in the prefrontal cortex. Behavioral studies in children and chimpanzees reveal both similarities and striking differences in the developmental pathways that lead to theory-of-mind capacities. Humans and great apes share many ancient patterns of social behavior, but it is too early to be certain if they interpret them in the same manner. Humans might have evolved a cognitive specialization in theory of mind, forever altering their view of the social universe.

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IN CULTURES around the world, humans exhibit an automatic and pervasive folk psychology that interprets the behavior of the self and others in terms of inferences about unobservable mental states such as desires, intentions and beliefs¹. Premack and Woodruff² coined the term 'theory of mind' to refer to this system of inferences, noting that an ability to represent and infer mental states from the self and others 'may properly be viewed as a theory because such states are not directly observable, and the system can be used to make predictions about the behaviors of others'. This folk psychology encapsulates much of what it means to be human: our commitments to the self and others as mental agents replete with emotions, desires, beliefs, personalities and personal histories. Are humans alone in this thoroughly mentalistic interpretation of the self and others? Or did theory of mind evolve before the emergence of humans? Surely this is one of the most interesting and significant questions that we can ask about the evolution of human nature, yet it is one that has escaped empirical attention until quite recently.

This review explores the hypothesis that theory of mind is a recent evolutionary innovation. A strong version of this hypothesis is that the ability to attribute mental states, together with the specific neural organization that makes such attributions possible, is a unique specialization of the human species. This would imply that theory of mind emerged during the past several million years, after the divergence of humans and apes. An alternative hypothesis is that at least some aspects of theory of mind were already in place before the emergence of the human species, and might, therefore, be present to some extent in other primates, and most likely the great apes. Nonetheless, if this view is correct, it would mean that although for hundreds of millions of years animals have been operating on the basis of implicit 'intentions' and 'knowledge' stored in their neural circuitry, it was not until relatively recently that evolution produced animals with brains capable of rep-

resenting those mental concepts explicitly. In other words, although many organisms routinely form neural states instantiating desire, intention and belief, it is possible that only a few species (and possibly only humans) have the ability to reflect upon these states. The evolution of a psychological system that is capable of representing such mental states would not require a precise understanding of the neural architecture that encodes them. After all, even an approximation of the workings of such mental states – a theory of mind – might allow organisms to predict the behavior of their conspecifics with considerable accuracy.

The purpose of this article is twofold. First, we establish a neural and psychological framework from which to consider the evolution of theory of mind. Second, we review the evidence that concerns the development of theory of mind in human children, and what is known about its development (or lack thereof) in great apes and other non-human primates. This review makes a preliminary assessment of alternative hypotheses of the timing of the evolution of various aspects of theory of mind and, in particular, the hypothesis that theory of mind, at least in an elaborated form, is a psychological specialization of the human species.

Human brain specialization

Figure 1 depicts the evolutionary relationships among humans and our closest living relatives, the great apes. Evolutionary reconstructions of the features that were likely present in the common ancestor of great apes and humans suggest that each of its living representatives has departed in important ways from the ancestor, which was probably an arboreal ape of about 30 kg (Ref. 3). Orang-utans, for example, have become extreme arboreal specialists with important modifications that occur in the wrist, shoulder and hip to allow for more extreme suspensory postures. The African apes (chimpanzees and gorillas) have developed specializations for a distinctive form of terrestrial quadrupedalism called 'knuckle-walking', in

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which the weight of the upper body is borne on the middle phalanges of the hands. Humans have departed in an even more bizarre manner from the ancestor of the great-ape-human group, with a radical remodeling of the pelvis and lower limb to support habitual bipedalism^{4,5}.

Just as in musculoskeletal structure, the brain too has undergone dramatic evolution following the divergence of the human lineage from that of the African apes, ~5–8 million years ago. The brain increased in volume by approximately threefold, and the fossil evidence indicates clearly that most of the increase occurred during the past 2 million years, long after the evolution of bipedality⁵. Not only did the volume of the brain increase during human evolution but there was also a disproportionate enlargement of the association cortex, and especially the prefrontal cortex, which occupies ~24% of the cerebral mantle in humans, compared with ~14% in great apes⁶. The expansion of the human prefrontal region might be related to the evolution of specialized neural systems that subservise distinctive human cognitive capacities⁷, including theory of mind. In a number of theoretical accounts, prefrontal cortex has been accorded a supervisory or executive role in the cognitive system, serving as the substrate by which mental representations of the state of the world exert their influence on other brain systems that control attention, memory and action^{8–10}. Moreover, what is regarded as the peculiarly adaptive or flexible character of human behavior, and the insightful, self-reflective character of human thinking, has been attributed to the action of frontal-lobe systems⁸. The ability to regulate behavior through the use of representations of the mental states of oneself and others might be a human specialization of the representational capacities present in the prefrontal cortex of other primates (compare Ref. 9). In fact, studies of autistic individuals suggest that human theory-of-mind capacities involve frontal cortex. Autistic individuals show little understanding of their own mental states, or those of others and, thus, perform very poorly on formal theory-of-mind tasks, relative to mental-age-matched controls¹¹. Autistics' lack of insight and introspection is reminiscent of deficits that result from frontal lesions, as is their stereotyped, perseverative behavior, prompting the suggestion that frontal-lobe dysfunction is an important element in autism^{12–14}. This view is supported by a recent demonstration of activation in orbital prefrontal cortex during performance of a theory-of-mind task¹⁵.

If theory of mind is an evolutionary specialization of human cognition, it should be expected that there are corresponding specializations at the level of neural systems. Unfortunately, apart from the fact that the human brain is unusually large, and the prefrontal region disproportionately so, very little is currently known about how human cerebral organization differs from that of our closest relatives. Thus, our current understanding of possible human specialization in theory of mind is based largely upon behavioral studies. Developmental psychologists have undertaken substantial research to characterize the development of theory of mind in children. Likewise, comparative psychologists are beginning to explore whether other non-human primates possess a similar 'folk psychology'.

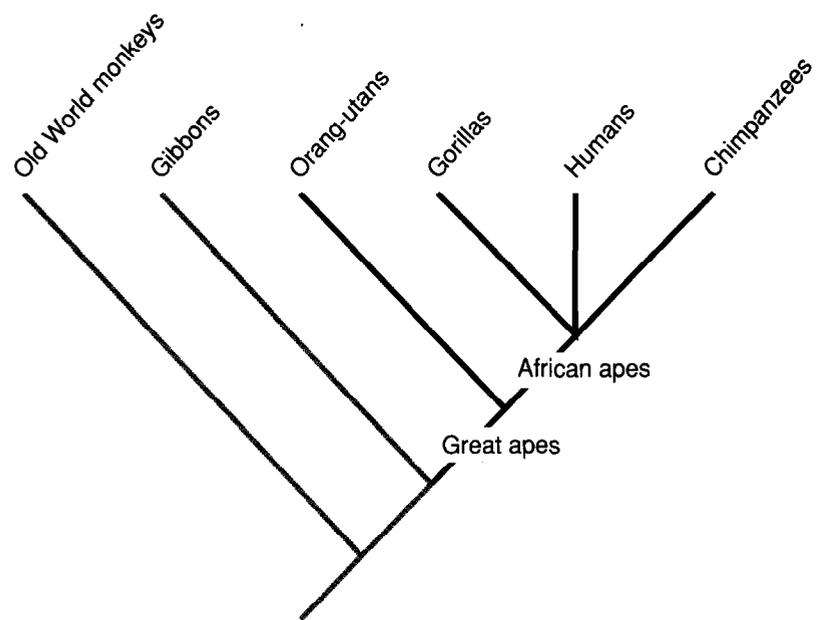


Fig. 1. *The great apes and humans share a common ancestor approximately 12–15 million years ago. Although the exact relationships among gorillas, chimpanzees and humans are still uncertain, it is widely acknowledged that the other living great ape, the orang-utan, diverged considerably earlier.*

Theory of mind in humans and other primates

Knowledge and belief

Large portions of the adult human theory of mind are established firmly in children between three and five years of age^{16–18}. Perhaps the quintessential achievement of the four- to five-year-old is the clear understanding that beliefs are mental representations – internal states that are formed as people interact with the world. The standard test of this achievement involves determining at what age children understand that the mind can represent incorrectly a true state of affairs in the world; in other words, when they understand the notion of false belief¹⁹. Understanding that beliefs can be false is an excellent diagnostic of theory of mind because, in this case, an organism must keep track of the divergence between the mind and the world, thus demonstrating clearly that it understands the distinction between the two. Research on children's understanding of false belief suggests that between three and five years children solidify their understanding of the mind as a mechanism that creates mental representations (and misrepresentations) of the external world¹⁸.

Four-year-olds also understand some of the ways in which belief and knowledge states arise. For example, they understand that perceptual contact with a situation or event is a sufficient (and in some cases necessary) condition for one to possess a privileged state of knowledge as compared with someone who has not had similar perceptual contact. In the case of visual perception, a four-year-old who observes someone peering into a box automatically attributes to that person knowledge of the box's contents; likewise they attribute ignorance to someone who merely touches the box²⁰. Strikingly, younger children appear unaware of this crucial aspect of acquisition of knowledge, failing to grasp that the person who did not look into the box has no way of knowing what was inside. Indeed, young three-year-olds apparently do not even know how they themselves come to know certain

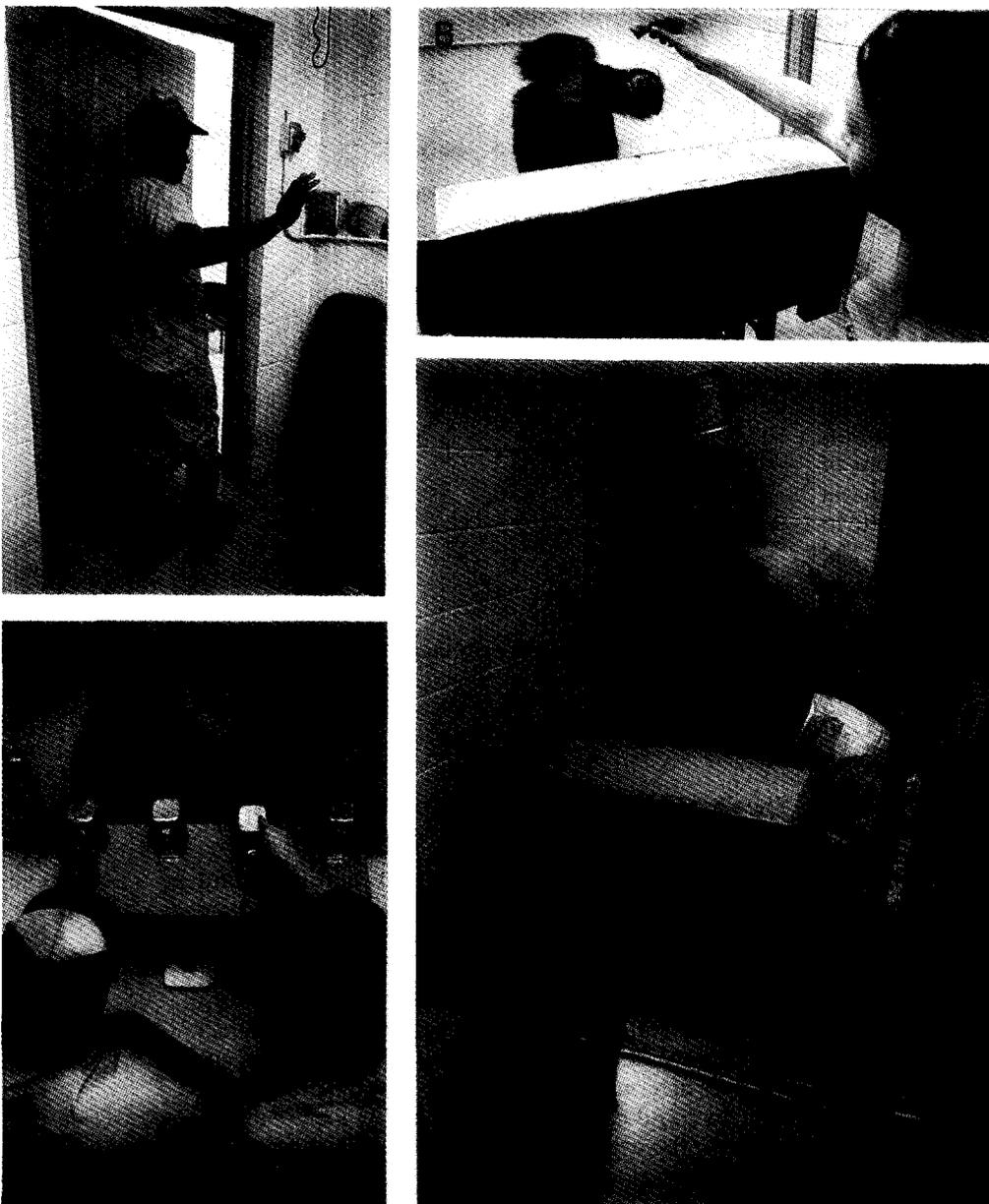


Fig. 2. By the age of four years, young children understand how the act of seeing creates internal knowledge states but it is not clear if chimpanzees ever understand this relation. The experimental procedure that is used to investigate chimpanzees' and children's understanding of the perception-knowledge relationship^{25,26}: a chimpanzee watches as one experimenter (guesser; A) leaves the room and a second experimenter (knower; B) hides food under one of several cups. (C) Both experimenters later point to different cups. (D) Transfer procedure in which logical epistemological relationships between seeing and knowing are held constant but the environmental variables that define the role of the knower and guesser are altered. With sufficient experience, chimpanzees can learn to form a discrimination between the two roles but, in their initial trials, they choose randomly. These findings raise the possibility that they solve the task by relying on learned behavioral strategies (for example, 'pick the person who stayed in the room'), rather than on mentalistic inferences about the connection between seeing and knowing. By contrast, when this same nonverbal task is administered to four-year-old children, most choose the correct person from the first trial forward; three-year-olds respond randomly²³.

facts (did you see what was in the box or did I tell you?), even in cases where their knowledge was acquired just seconds earlier²¹⁻²³. This is not to say that three-year-olds lack the concept of knowledge altogether; they might possess an earlier understanding of knowledge, perhaps one in which knowledge is conflated with desire (T.D. Lyon, PhD Thesis, Stanford University, 1993).

Do non-human primates represent the beliefs of others? To date, most research on non-human primates' understanding of belief has focused on whether they understand the perceptual basis of acquisition of knowledge. Premack²⁴, as well as

which young children use mental verbs such as 'want', 'hope', and 'wish', suggest strongly that they know that they, along with others, are 'repositories' of unobservable mental states, even if they have not yet grasped how the mind can also serve as a mechanism to copy or represent the state of affairs in the world³². Furthermore, experimental research has revealed consistently and convincingly that three-year-olds understand that people act on the basis of their desires, that they distinguish between someone thinking about something compared with someone having it, and when someone's beliefs are stipulated they can even make correct predictions about how that person will behave¹⁷. In general,

Povinelli and his colleagues^{25,26}, has explored what (if anything) chimpanzees understand about the connection between seeing and knowing. For example, in the procedure shown in Fig. 2, if chimpanzees understand the seeing-knowledge relationship, they ought to choose the 'advice' offered by the trainer who hid the food (or the person who was carefully watching while it was being hidden), as opposed to someone else who could not see the hiding event. In general, these tasks have yet to produce definitive evidence that chimpanzees, or other non-human primates, such as macaques^{27,28}, understand the perception-knowledge relationship. Finally, there are a number of observational reports of apparent deception in non-human primates (especially chimpanzees²⁹), and it is tempting to interpret them as evidence that non-human primates understand that other agents have beliefs that can be manipulated. Very little experimental work has investigated non-human primates' understanding of false belief²⁴. However, if these animals do not understand how beliefs arise (as the experimental data suggest), it seems unlikely that they could make the distinction between true and false beliefs.

Emotions and desires

The four-year-old's discovery that mental states such as belief are internal representations of the external world clearly unites their emerging theory of mind with our own. However, children younger than four years might already understand other, nonrepresentational mental states, and they might even possess a nonrepresentational understanding of belief^{30,31}. Two-year-olds talk extensively about certain mental states, such as emotions and desires, that are not representations of the external world but are nonetheless thoroughly mentalistic concepts.

For example, the subtle ways in

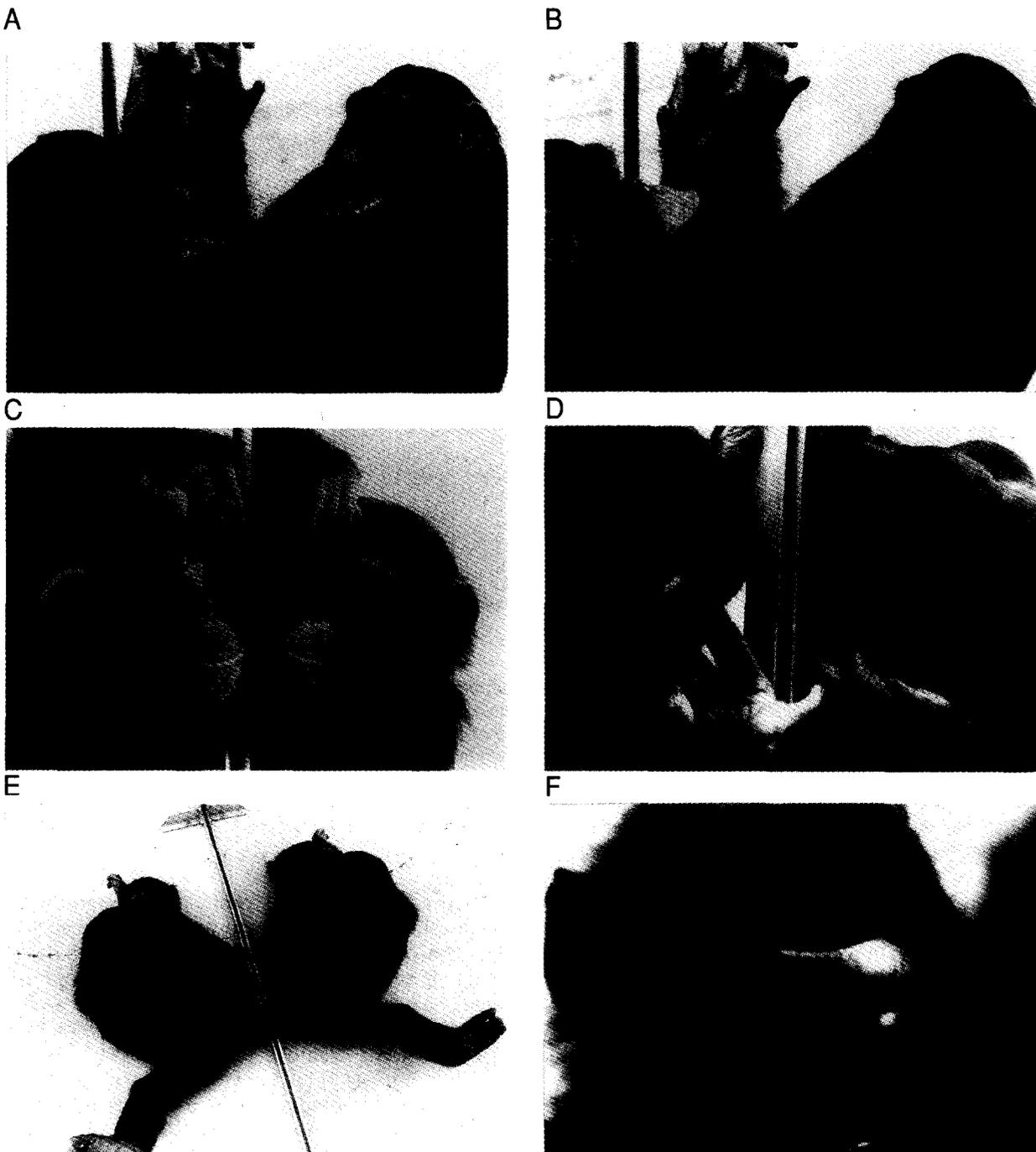


Fig. 3. *Chimpanzees and orang-utans (but not other primates) show clear evidence of recognizing themselves in mirrors. Like most animals, chimpanzees react initially to mirrors as if confronted by another member of their species, and typically engage in a variety of social behaviors. However, in as little as 5–30 min, many chimpanzees begin to engage in self-exploratory behaviors in which they use the mirror to gain access to previously unavailable information about their appearance. They use mirrors to make exaggerated facial displays (A and B), as well as groom their body, face and teeth (C–F). Many of the chimpanzees that display the types of self-exploratory behaviors that are shown in C–F also will use a mirror to locate and inspect red marks placed surreptitiously on their ears and eyebrow ridge^{47,49,50}. Organisms such as Old World monkeys, which do not display these spontaneous episodes of using the mirrors to explore their bodies, also fail to explore marks that were placed on their face by experimenters^{47,48}.*

younger children's relative ease in understanding desires, as opposed to thoughts and beliefs, has led a number of researchers to propose the existence of a specific developmental pathway in which children come to grasp nonrepresentational aspects of the mind before understanding the representational aspects, such as those tapped in false belief and knowledge-attribution tasks^{31,33}.

Given that children have a better understanding of desires before beliefs, it is reasonable to ask if chimpanzees or other non-human primates display a better understanding of desires than they do of beliefs.

Premack and Woodruff's² original investigation of theory of mind tested whether a chimpanzee could attribute desires or goals to actors who were struggling to solve staged problems. After observing videotapes of these problems, the chimpanzee correctly selected photographs that depicted solutions to the actors' implicit desires or goals, as opposed to those that depicted associated events. In a different study, Povinelli and his colleagues trained chimpanzees to co-operate with a human partner on a task that required each to perform a different action (role), in order to achieve a common goal³⁴. The crucial finding



Fig. 4. Humans and chimpanzees share portions of the developmental pathway that controls the expression of gaze-following. By 18 months, human infants are capable of responding to the shift in orientation of the gaze or head posture, or both, of another by following their line of sight, including tracking this line into the space behind them⁴³. One possible interpretation of this type of behavior is that it reflects a type of 'joint-visual attention' in which the infant and adult appreciate the attentional focus of each other. That is, not only do they have a mechanism that serves joint attention⁴³, they might also appreciate that they share the same subjective attentional experience⁴⁴. (A–C) Research with chimpanzees reveals that they also display this phenomenon (as, indeed, might other social mammals)⁵⁷. However, additional research with chimpanzees (see Fig. 5) indicates that they might not represent the subjective attentional state of the other one⁵⁶. This raises the possibility of both a developmental and evolutionary dissociation between joint-visual attention and the presence of a folk psychological interpretation of visual perception as the mental state of attention.

was that the chimpanzees were able to reverse roles immediately, assuming their partner's role without explicit training. In contrast, rhesus monkeys failed the same role-reversal task³⁵. Collectively, these data suggest that chimpanzees might possess some understanding of goals or desires, although both of these studies have enough methodological limitations to warrant further research before firm conclusions are drawn.

Early-emerging knowledge of self and others

In humans, the emergence of conceptual knowledge of the self and others manifests itself at around 18–24 months in the transitional period between infancy and early childhood. Indeed, this period introduces such dramatic achievements by the child (not all limited to an understanding of mental states) that it is tempting to speculate (as did Piaget) that a fundamentally new conceptual system is emerging. Although even the very young infant has access to proprioceptive and kinesthetic information that enables it to distinguish self from the environment (self-perception), evidence for an objective understanding of the self does not begin to emerge clearly until ~18 months. At this point, children recognize themselves in mirrors, engage in symbolic play, exhibit simple acts of altruism, participate in reciprocal cooperative actions with others, produce linguistic comments about the failure of self-generated plans, display mastery smiles upon completion of a task, and use mental state terminology that refers to desires^{32,36–41}. Each of these behaviors suggests at least a limited understanding of the self and other as possessing agency, desires or internal emotional states, or both.

There might even be earlier manifestations of human infants' developing awareness of the subjective side of behavior. In the period leading up to 18–24 months, children begin to develop sophisticated behaviors that suggest at least an implicit awareness of the mental state of attention in themselves and others. For example, proto-declarative pointing (in which infants point to objects or events solely to draw the other's attention to them) is consolidated by about 12 months⁴², and between 12 and 18 months infants develop the ability to track another person's line of sight into space outside of their own immediate perceptual field⁴³. Some researchers have suggested that these 'joint-attention' behaviors reflect⁴⁴, or at least lay the perceptual foundations for⁴⁵, an initial understanding of the subjective attentional states of both the self and others. In an ingenious series of studies, Dare Baldwin and her colleagues have provided evidence that, by at least 18 months, infants understand that when another person looks or points at an object or event, that person becomes connected to it subjectively through the mental state of attention⁴⁶.

Do non-human primates share even these limited glimpses into the mind? Like humans, many chimpanzees and orang-utans display clear evidence of recognizing themselves in mirrors, whereas no other non-human primates have done so, despite extensive research^{47,48} (Fig. 3). The ability of these apes to recognize themselves in mirrors has been replicated many times, and there is little doubt that they display the same phenomenon of self-recognition as do 18–24-month-old children^{49,50}. Gallup's initial discovery of

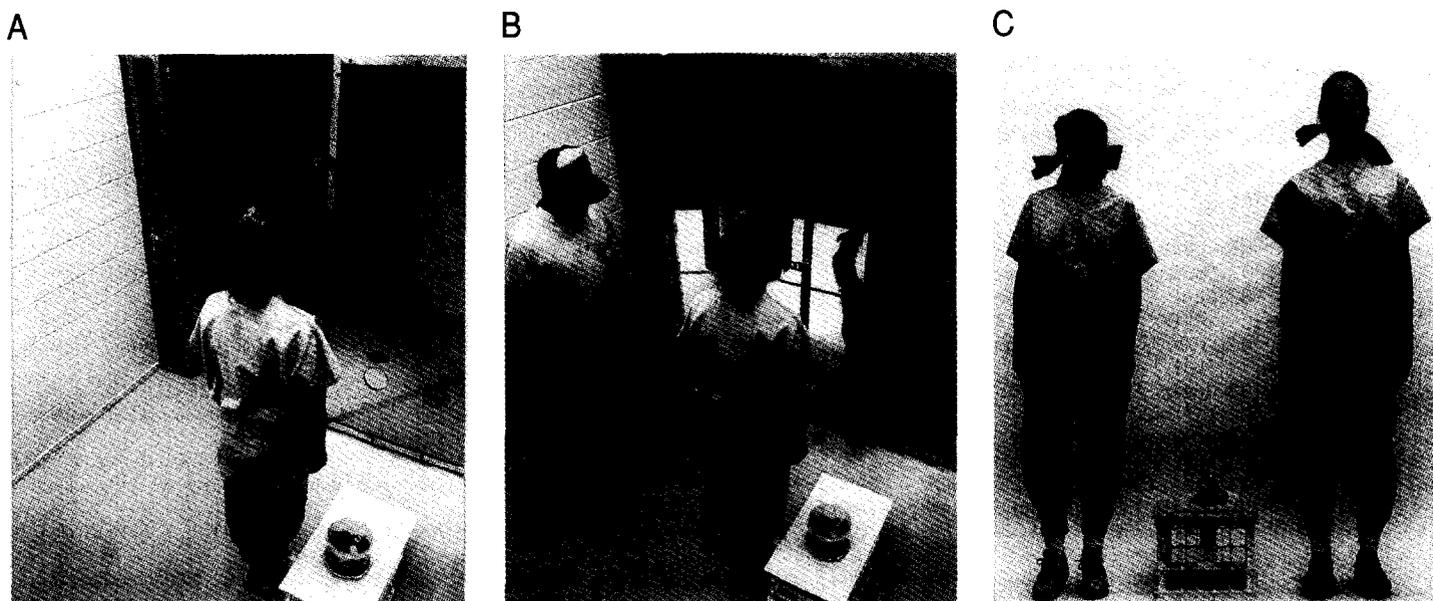


Fig. 5. Although young chimpanzees are very sensitive to the eyes of others, they do not appear to understand them as 'portals' through which the mental state of attention emanates. (A and B) Chimpanzees can be trained to use their natural begging gesture to request food from an experimenter. If an experimenter stands on the left (A and B), the chimpanzee will gesture through the hole on the left side of the partition; if she stands on the right, the subject will gesture there. However, this is no guarantee that the subjects realize that this person is subjectively linked to them via the mental state of attention. (C) When two experimenters are used, one who can see the chimpanzees and one who cannot, the chimpanzees typically respond randomly⁵⁶. They apparently fail to understand that only one of the experimenters is connected to them through the mental state of attention, perhaps because they simply cannot represent such states. Alternatively, they might simply fail to understand the specific role that eyes play in deploying attention. Young children that are tested similarly reveal an understanding of the subjective aspects of visual attention by about two and a half years of age⁵⁶.

self-recognition in chimpanzees led him to speculate that chimpanzees might possess a self-concept. Adopting a long-standing epistemological argument, he further hypothesized that perhaps their knowledge of self might enable them to make inferences about such mental states as desires and beliefs in others⁵¹. Thus, he has speculated that in organisms that are capable of self-recognition, there might be a causal connection between the onset of self-recognition and theory of mind, with the critical factor being self-awareness^{51,52}. Consistent with his predictions, some research has revealed correlations between the onset of self-recognition in infants and their capacity for altruism and the emergence of the self-conscious emotions^{53,54}. By contrast, Gallup's proposal would be in jeopardy if proto-declarative pointing and other joint-attention behaviors reflect a genuine understanding of the mental state of attention because, in humans, joint-attention behaviors typically emerge by 12 months or so, long before self-recognition in mirrors (18–24 months). At present, the paucity of research in this area (especially with non-human primates) makes a full evaluation of the proposition difficult⁵⁵.

Finally, there are some recent findings that concern joint attention in chimpanzees, and that highlight additional similarities and differences between humans and chimpanzees. On the one hand, chimpanzees do not naturally point to inform others about objects or events, nor is it clear that training them to point, or to respond to human pointing (see Fig. 2), produces an appreciation of pointing as a way of co-ordinating the mental states of self and others. On the other hand, chimpanzees do display gaze-following abilities that are as sophisticated as those of 18-month-old children^{56,57} (see Fig. 4). Although such gaze-following abilities suggest that chimpanzees might appreciate how the eyes connect someone's internal states of

attention to the world (as do children by 18–24 months), a recent extensive investigation of this question has indicated that they do not⁵⁶ (see Fig. 5). These somewhat contradictory findings raise a number of possibilities. On the one hand, it might be that limited aspects of theory of mind were present in the common ancestor of the great apes and humans, and this is reflected in chimpanzees' limited joint-attention behaviors. On the other hand, these joint-attention behaviors might have evolved for other reasons, and might be controlled by psychological mechanisms that evolved before a human specialization in theory of mind (see Fig. 4), although in humans they now function in concert with each other.

Reconstructing the evolution of theory of mind

On the surface, much of the social behavior of the great apes resembles our own so closely that it is tempting to conclude that this behavioral similarity must reflect similarity in subjective experience²⁹. But as developmental and comparative psychological research suggest, important differences in how humans, great apes and other animals interpret other organisms might lie behind these behavioral similarities⁵⁸. It is too early to be certain, but current evidence does not yet exclude the possibility that, at some point during human evolution, elements of a new psychology were incorporated into existing neural systems – a psychology which, by its very nature, imbues ancient behavioral patterns that we share with apes with meanings they did not possess originally.

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Corrigendum

In the book review by J.D. Hahn in the July issue of *TINS* (Vol. 18, p. 327), the title and the ISBN of the book are incorrect. The correct versions are shown below.

We apologize to MIT Press and to the readers for these errors.

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