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Thinking About Me: How Social Awareness Evolved

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ABSTRACT—*Humans seem unique in their consideration of others' goals, motivations, intentions, and needs. But the human form of social awareness did not spring from nowhere; certain mechanisms shared across primates formed the foundation from which these processes derived. A review of recent nonhuman primate research points to particular ancestral mechanisms, including an interest in images moving in synchrony with self, a mirror neuron system that responds in the same way to actions made by the self and by others, and inherited social tolerance that provided the bases for social thinking. Still there is a gap in tracking social awareness from these basic beginnings to the ability to think about self and other with respect to intentions and goals. Comparative and clinical work will fill in this gap and will map brain processes onto social thinking.*

KEYWORDS—*social awareness; tamarins; mirror neurons; evolution*

Humans have an awareness of me and you, of mine and yours, of my actions and your actions, and of my intentions and your intentions. It is likely that this kind of thinking, especially the ability to take into account intentions and beliefs of others, enabled us to use language more deliberately and intentionally, to guide others toward a common purpose, and to conform with others to form distinct societies and traditions. It has been suggested that our complex social awareness makes us unique in our thinking. But it is likely that a uniquely human ability did not come from nowhere and that it has its foundations in brain systems that humans share with other social animals, especially nonhuman primates.

When comparisons are drawn between the social awareness of nonhuman primates and that of humans, immediately apparent are striking limits on the nonhuman primates' side, including lower rates of self-recognition; less shared attention with others; fewer face-to-face interactions; less imitation; less use of gestures and pointing; and shorter, more limited use of purposeful language. But do these limitations suggest a fundamental difference in social thinking that evolved in hominids? There is no direct way to determine what social-cognitive changes occurred in ancestral hominids, nor is it possible to assess social awareness by watching what animals do—especially if we look for human-like behaviors in nonhuman creatures rather than behaviors typical of the animal. Still, careful testing in the laboratory is starting to reveal the shared evolved social thinking of primates.

RECOGNIZING ME

One simple distinction that allows for social consideration is differentiating self from other. By 24 months, most children recognize themselves in mirrors and pass a "mark" test by touching their own head upon seeing a surprising mark on their head in the mirror. In fact, distinct brain activity corresponds with self-recognition in humans: Viewing one's own face consistently stimulates particular areas in the right frontal and right parietal lobes (Uddin, Iacoboni, Lange, & Keenan, 2007). These areas overlap with areas containing mirror neurons, which fire when one is performing an act and also when one is observing the same act performed. Mirror neurons in these areas have been noted to produce a higher rate of activation toward a mirror, most likely because one would simultaneously be both observing and making the action.

The only primates to show the proper behavior to indicate mirror-generated self-awareness through the mark test with proper controls are chimpanzees and orangutans, and this finding defines an ape–monkey fundamental split in understanding "me." There are recent documented demonstrations of self-recognition in a few other mammals (elephants and dolphins), and one example in magpies, but because many of the control conditions were not tested it is unclear whether these cases really indicate self-awareness in those species given.

In human children, the ability to recognize self emerges gradually over time, and developmental psychologists have identified self-directed behaviors in infants too young to show full-fledged mark-directed behavior. By approaching the question comparatively in the same way as it has been studied

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Fig. 1. Caitlin, an adult cotton top tamarin, looks intently at her reflection.

developmentally, recent studies have shown that two species of New World monkeys, cotton top tamarins (Neiworth, Anders, & Parsons, 2001) and brown capuchins (de Waal, Dindo, Freeman, & Hall, 2005), show a unique pattern of behaviors directed toward their reflections: (a) increased looking and more eye contact; (b) exploration of the mirror; and (c) contingency testing, or swaying back and forth in the mirror, which generates synchronous behavior in the reflection (see Fig. 1). Although one could attribute the first two behaviors to interest in a shiny object, contingency testing is a peculiar behavior only made in front of a mirror. Moreover, the behaviors the monkeys express toward strangers (taped or live) are markedly different from the behaviors they express toward a mirror. Very young humans and adult monkeys demonstrate a similar intermediate step to self-recognition. The difference between apes (including humans) and many species of monkeys, then, is not that one is aware of self and the other is not. It is that apes eventually show a causal understanding of their reflection in the mirror, with more overt control over reactions to it, while monkeys show a reactive process similar to that of young human infants—one that is automatic, attention getting, and invoked by the synchronous cues of a reflected image. Underlying all of this is likely to be a system of mirror neurons engaged by reflections, or stimuli and actions with synchronous connections to the self.

MY ACTIONS – YOUR ACTIONS

Mirror neurons were first discovered in rhesus monkeys, a variety of macaques that do not show self-awareness in the mark test (Gallup, 1977). Thus it is more likely that the mirror neuron system evolved for other uses than self-representation and may have been coopted to support that function in humans. One ability that was likely made possible by mirror neurons is crude physical imitation, or the act of copying a behavior that is being observed. Meltzoff and Moore (1977) first showed that human infants as young as 2 weeks old could imitate a mouth opening, a finger moving, or a tongue sticking out. This suggested the existence of a special mechanism, present from birth, that allows for crude imitation of others. We now know that various monkey and ape babies also imitate facial gestures and hand or paw gestures. In fact, mirror neurons in rhesus monkeys in area F5, an area of the monkey premotor cortex, and in humans in the ventral premotor cortex and the anterior inferior parietal lobe fire selectively to identical actions made by self or to the identical actions made by others, including reaching for an object or cracking a peanut (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Recently, this process has been suggested to support shared emotions and empathy—for example emotional contagion, wherein a group of babies cry once one starts, or when a single monkey's reactions spread across a group (see Decety & Jackson, 2006, for a review).

In addition to low-level imitation such as contagion, imitation can occur on a conscious level in humans when we choose between it and other strategies for success. In a recent study, McGuigan, Whiten, Flynn, and Horner (2007) found that children aged 3 and 5 will copy the exact actions of a model who demonstrates how to open a box to obtain a treat, even when some of the actions are irrelevant to the goal; thus children are choosing to copy exactly as a strategy. Adult chimpanzees, in contrast, delete needless behavioral steps if they are not causally related to obtaining the goal, and thus show "emulation" rather than imitation (Horner & Whiten, 2005). Even when chimpanzees watch other chimpanzees, they do not copy their actions exactly; rather, they select observed behaviors that are more likely to solve the problem. There is a social crux to chimpanzee emulation, though: If a hidden experimenter shows the way to open a box via a transparent string—and thus there is no animate social agent present—a chimpanzee is less likely to utilize the actions observed (see Whiten, 2008, for a brief review).

Monkeys also profit from watching others. They show higher frequencies of certain responses when they observe others perform them, relative to the rate they would emit those responses otherwise; they also pay more attention to particular objects that they have observed other individuals interacting with, although they do not copy others' exact actions to achieve goals (for a review, see Tomasello & Call, 1997). In sum, there is a low-level mechanism in primates for copying automatically, which may explain contagion and a directed focus toward certain areas and objects and responses, and this mechanism is most likely linked to the mirror neuron system. But the process of overt imitation as a chosen strategy to solve certain problems is not shared. In nonhuman primates, independent work toward the goal is more often the rule than is purposeful imitation. In humans, imitation of the exact behaviors is selected if copying will lead quickly to success.

MINE, YOURS, AND OURS: COOPERATION

How social awareness and other forms of social thinking including altruism and cooperation evolved is hard to fathom, since survival seems intricately tied to individual survival. However, in recent years there has been renewed interest in the concept of evolution by group selection (Wilson & Wilson, 2007): Both within- and between-group selection occurs in nature, and individuals may pass on traits that benefit the group even if those traits do not literally support individual survival. Traits that help the group as a whole help survival between groups at the expense of certain individuals.

Is there evidence for inherited mechanisms that lead to cooperation? Within monkey species, the likelihood of cooperating, or working together toward a common goal, seems predicted by the inherited social tolerance of the species. Cotton top tamarins and marmosets are cooperative breeders that need help from others for rearing offspring, and they readily cooperate to get food in laboratory experiments (Snowdon & Cronin, 2007). In fact, Burkart, Fehr, Efferson, and van Schaik (2007) found that marmosets pulled forward a tray to help a partner to obtain food even when the helper did not get rewarded, and Cronin and Snowdon (2008) found similar altruistic behavior in cotton top tamarins. In contrast, more competitive and antagonistic species who are not cooperative breeders, like Guinea baboons and rhesus and Japanese macaques, fail to work together to find food. It is possible that cooperation emerged in species like tamarins, marmosets, and humans that breed cooperatively.

Cooperation has been demonstrated in the lab in certain primates that are noncooperative breeders (including capuchins and chimpanzees), but there may be limits to their use of it. For instance, chimpanzees can successfully pull ropes together to move boxes to obtain food, but only after training (for example, with various lengths of rope so that they learn that they need to pull simultaneously to meet the goal; Hirata & Fuwa, 2007). And chimpanzees have shown an indifference to helping partners to acquire rewards (Silk et al., 2005). It seems likely that chimpanzees cooperate spontaneously when the behavior is part of a reciprocal exchange, as happens in the wild with cooperative hunting, but they do not readily apply it in other circumstances. Cooperation in this species may have emerged due to other pressures, such as competition over resources. Something completely different may be true in cotton top tamarins; in a recent study in our lab (Greenberg & Neiworth, 2008), cotton top tamarins were found to cooperate to pull felt ropes together to move an apparatus to obtain a cereal treat (see Fig. 2), but the rate at which they cooperated actually decreased significantly when competition was introduced (for example, when other unrelated tamarins were close to them, or worse, when other unrelated tamarins could participate in the same task by pulling the apparatus toward them and away from the other group). In competitive circumstances, cotton top tamarins were not motivated to cooperate. They cooperated more readily in noncompetitive or prosocial circumstances.

Fig. 2. Wizard, an adult cotton top tamarin, looks for her partner before starting to pull a felt rope in a cooperation task.

Cooperation may also spring from variations in gene expression in mammals. Hammock and Young (2005) studied two species of a rodent, prairie and montane voles, and found that a long allele in a repetitive DNA sequence in the prairie vole's vasopressin receptor gene *avpr1a* correlated with an increase in social behaviors and tolerance in males in particular, including more grooming of the young, more tolerance of others' scents, and a stronger partner attachment. In contrast, the montane vole male does not pair bond, does not contribute to parenting, and does not differentiate partners well, and it has a very short version of the genetic expression of the vasopressin 1a receptor. The authors found that a similar sequence that appears in humans in the *avpr1a* gene sequence is deleted in chimpanzees, suggesting a biological difference that may lead to differences in social tolerance and prosocial behaviors like cooperation between chimpanzees and humans.

SUMMARY AND FUTURE DIRECTIONS

It turns out that no primate is an island entire of itself. But to understand the influence of others on primates and their thinking, we need to determine the relative contribution of thinking about me and you, mine and yours, and our intentions and goals. Research suggests shared ancestral processes that set the stage for different levels of social awareness: (a) interest in images that move synchronously with one's own body, demonstrated in various New World monkey species as well as apes; (b) crude imitation found in primates, presumably supported by mirror neurons; (c) cooperative breeding, which correlates well with cooperation and altruism in a few New World monkey species

and in humans; (d) competition over resources and group dynamics, which may lead to limited uses of cooperation by species such as brown capuchins and chimpanzees; and (e) social tolerance, supported by particular gene expression that may lead to increased social behaviors in various mammals. Each of these processes demands further study in primates, to clarify the influence of each on social thinking. The five components identified here suggest evolved social awareness in a variety of primate species, based on particular neural mechanisms, and passed on due to different group pressures. How then did we humans evolve to experience full-blown expressions of self-awareness, of overt imitation, and of intentional cooperation? Are we unique in showing all five of these components and coopting other cognitive processes to make subjective sense of them?

With the precursors to these processes slowly becoming known, we should soon be able to piece together how social awareness evolved and how it is supported by various brain processes. Animal models of social thinking are just recently illuminating how particular clinical syndromes with social deficits may have come to be. For example, Khaitovich et al. (2008) examined changes that occurred across various primates and found that the expression levels of many genes and metabolites that are altered in schizophrenia also changed rapidly during evolution. This suggests that schizophrenia may be a by-product of increased metabolic demands on the brain as it evolved. It is increasingly becoming clear that autistic humans perceive faces in a more piecemeal fashion and perceive objects less globally, or less by overall shape; they also rely less on cues for the grouping of features, such as similarity and proximity. These idiosyncracies seem similar to the perception of certain species of nonhuman primates (Neiworth, Gleichman, Olinick, & Lamp, 2006). This connection with a primate model suggests that the perceptual and social deficits of autism may be a cost of diminished connectivity among brain systems, which occurred in some primate species when evolution favored more modular brain processing. A focus on the study of autism and models of autism in primates should help to illuminate neural processing that allows for social thinking. By tracking social processes like these biologically, comparatively, and clinically, a brain model of human social thinking should emerge.

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