Cognitive Continuity in Primate Social Cognition

Vittorio Gallese* and Maria Alessandra Umiltà
Department of Neuroscience, Section of Physiology
University of Parma, Italy
vittorio.gallese@unipr.it

What are the mechanisms enabling primates to display their complex social skills? And in particular, what makes humans different? A common view prefigures a sharp distinction between humans as mind readers and all nonhuman primates species, confined to behavior reading. This distinction is held to be the result of a discontinuity in the evolution of social cognition. We challenge this view by positing that behavior reading and mind reading may not constitute two autonomous, encapsulated realms. Apparently different cognitive strategies may be underpinned by similar functional mechanisms, which in the course of evolution acquire increasing complexity and are exapted to sustain more sophisticated new cognitive skills. We discuss the role of mirror neurons in monkeys and humans in relation to the ascription of intentions to others as a paradigmatic case in support of our thesis of a cognitive continuity within the evolution of primate social cognition.

Against the "Ptolemaic" Paradigm

Primates, and particularly human beings, are social animals whose cognitive development capitalizes upon the interaction with other conspecifics (see Barrett and Henzi 2005). During social interactions we manifest our inner intentions and thoughts by means of overt behavior, while simultaneously trying to figure out what are the intentions and thoughts of others, when witnessing their behavior. Detecting another agent's intentions helps anticipating this agent's future actions, which may be cooperative, noncooperative, or even threatening. Accurate understanding and anticipation enable the observer to adjust his or her responses appropriately (see Byrne

and Whiten 1988; Byrne 1995; Whiten and Byrne 1997; de Waal 2001).

What are the mechanisms enabling us to display such complex social skills? The traditional view in the cognitive sciences holds that humans are able to understand the behavior of others in terms of their mental states—intentions, beliefs, and desires—by exploiting what is commonly designated as "folk psychology." The capacity for attributing mental states to others has been defined as Theory of Mind (ToM; Premack and Woodruff 1978). A common trend on this issue has been to emphasize that nonhuman primates, apes included, do not rely on mentally based accounts for others' behavior (see, among others, Povinelli and Eddy 1996; Heyes 1998; Povinelli et al. 2000). This view prefigures a sharp distinction between all nonhuman species, confined to behavior reading, and our species, which makes use of a different level of explanation: mind reading. It must be noted that Povinelli's reported negative evidence on the possession by chimpanzees of *any* component of human folk psychology has been challenged by the results of Hare et al. (2000).

However, here we want to make an even stronger case against the dichotomous and discontinuist view on primate social cognition. According to us, it is by no means obvious that behavior reading and mind reading constitute two autonomous, encapsulated realms. In our social transactions, we seldom engage in explicit interpretative acts. Our understanding of social situations most of the time is immediate, automatic, almost reflex-like. Therefore it seems preposterous to claim that our capacity to *reflect* on the real intentions determining others' behavior is all there is in social cognition. As it will be clarified in the next sections, it is even less obvious that while understanding the intentions of others we employ a cognitive strategy totally unrelated to predicting the consequences of their observed behavior.

As pointed out by Allen and Bekoff (1997), this "all-or-nothing" approach to social cognition, this search for a "mental Rubicon" (the wider the better) is strongly arguable. This attitude, in our opinion, constitutes a "ptolemaic paradigm" with a very strong anthropocentric aftertaste. When trying to

---

*Corresponding author.

account for our social cognitive abilities we should not forget that they are the result of a long evolutionary process. It is therefore possible that apparently different cognitive strategies may be underpinned by similar functional mechanisms, which in the course of evolution acquire increasing complexity and are exapted to sustain cognitive skills newly emerged out of the pressure exerted by changed social and/or environmental constraints (Gallese and Goldman 1998; Rizzolatti and Arbib 1998; Gallese 2003a,b; Gallese et al. 2004; Arbib 2005). Hauser (2005) recently emphasized that before drawing any firm conclusion about the mentalizing abilities of nonhuman species, methodological issues related to species-specific spontaneous abilities and environments should be carefully scrutinized.

A fruitful alternative strategy we fully endorse is that of framing the issue of the investigation of the *neural bases* of social cognition within an evolutionary perspective. Interindividual relations have played a fundamental role in the evolution of primate cognition. Humphrey (1978) originally suggested that the intelligence of primates primarily evolved to solve social problems. This view is supported by empirical data (see Byrne 1995; Whiten and Byrne 1997; de Waal 2001). Several studies revealed the unique capacity of nonhuman primates of understanding the quality of the relationships within their social group, not only in terms of kin, but also in terms of coalitions, friendship, and alliances. Primates can categorize and understand third-party social relationships (Tomasello and Call 1997). The evolution of this cognitive trait seems to be related to the necessity to deal with social complexities that arose when group-living individuals had to compete for scarce and patchily distributed resources.

Cognitive neuroscience has started to unveil in both monkeys and humans the neural mechanisms at the basis of the anticipation and understanding of the actions of others. The results of this ongoing research can shed light on the evolution of social cognition. The empirical data on mirror neurons in monkeys and on mirroring circuits in the human brain we briefly review in this paper suggest that some of the typically human sophisticated mentalizing skills—such as ascribing intentions to others—might be the outcome of a continuous evolutionary process, whose antecedent stages can be traced in the mirror matching system of macaque monkeys.

Empirical Evidence for the Mirror Neuron System for Actions

About 10 years ago a new class of motor neurons was discovered in the premotor cortex of the macaque monkey: mirror neurons. These neurons discharge not only when the monkey executes goal-related hand and/or mouth actions like grasping objects, but also when observing other individuals (monkeys or humans) executing similar actions (Gallese et al. 1996;

Rizzolatti et al. 1996; Ferrari et al. 2003). Neurons with similar mirroring properties, matching action observation, and execution have also been discovered in a sector of the posterior parietal cortex reciprocally connected with area F5 (PF/PG mirror neurons; see Rizzolatti et al. 2001; Gallese et al. 2002; Fogassi et al. 2005). It has been proposed that this neural matching mechanism may underpin a direct form of action understanding (Gallese et al. 1996; Rizzolatti et al. 1996, 2001; Gallese et al. 2004; Rizzolatti and Craighero 2004), by means of embodied simulation, a specific mechanism by means of which the brain/body system models its interactions with the world (Gallese 2001, 2003a,b, 2005a,b, and in press 2006).

A series of experiments by Umiltà et al. (2001) showed that F5 mirror neurons also become active during the observation of partially hidden actions, when the monkey can predict the action outcome, even in the absence of the complete visual information about it. Macaque monkeys' mirror neurons therefore represent actions made by others not exclusively on the basis of their visual description, but also on the basis of the anticipation of the final goal of the action, by means of the activation of its motor representation in the observer's premotor cortex.

In another series of experiments it has been shown that a particular class of F5 mirror neurons (audiovisual mirror neurons) respond not only when the monkey *executes* and *observes* a given hand action, but also when it just *hears* the sound typically produced by the action (Kohler et al. 2002). These neurons respond to the sound of actions and discriminate between the sounds of different actions but do not respond to other similarly interesting sounds such as arousing noises, or monkeys' and other animals' vocalizations. In sum, the different modes of presentation of events as intrinsically different as sounds, images, or willed acts of the body are nevertheless bound together within a circumscribed, informational lighter level of semantic reference, which is underpinned by the same network of audiovisual mirror neurons. The presence of such neural mechanism within a nonlinguistic species can be interpreted as the neural correlate of the dawning of a conceptualization mechanism (see Gallese 2003b; Gallese and Lakoff 2005).

Several studies using different experimental methodologies and techniques have also demonstrated in the human brain the existence of a mirror neuron system matching action perception and execution (for review, see Rizzolatti et al. 2001; Gallese 2003a and in press 2006; Gallese et al. 2004; Rizzolatti and Craighero 2004). During action observation there is a strong activation of premotor and parietal areas, the likely human homologue of the monkey areas in which mirror neurons were originally described. The mirror neuron matching system for actions in humans is somatotopically organized, with distinct cortical regions within the premotor and posterior parietal cortices being activated by the

observation/execution of mouth-, hand-, and foot-related actions (Buccino et al. 2001).

More recently, it has been shown that the mirror neuron system for actions in humans is directly involved in imitation (Iacoboni et al 1999; Buccino, Vogt, et al. 2004) and in the perception of communicative actions (Buccino, Lui, et al. 2004). Furthermore, the premotor cortex containing the mirror system for action is involved in processing action-related sentences (Hauk et al. 2004; Buccino et al. 2005; Tettamanti et al. 2005; see also Pulvermüller 2002).

Mirror Neurons and the Understanding of Intentions

What does the presence of mirror neurons in different species of primates such as macaques and humans tell us about the evolution of social cognition? Monkeys may exploit the mirror neuron system to optimize their social interactions. At least, the evidence collected so far seems to suggest that the mirror neuron system for actions is enough sophisticated to enable its exploitation for social purposes. This matching mechanism can support social facilitation in monkeys. It has been recently shown that the observation and hearing of noisy eating actions facilitates eating behavior in pigtailed macaque monkeys (Ferrari et al. 2005).

Another recently published study shows that pigtailed macaque monkeys recognize when they are imitated by a human experimenter (Paukner et al. 2005). Pigtailed macaques preferentially look at an experimenter imitating the monkeys' object-directed actions compared with an experimenter manipulating an identical object but not imitating their actions. Since both experimenters acted in synchrony with the monkeys, the monkeys based this preference not on temporal contingency, but took into account the structural components of the experimenters' actions.

It may well be the case, as repeatedly argued, that macaque monkeys are not capable of *motor* imitation—though recent evidence by Subiaul et al. (2004) shows that they are capable of *cognitive* imitation. The study by Paukner et al. (2005) nevertheless shows that macaque monkeys do entertain the capacity to discriminate between very similar goal-related actions on the basis of their degree of similarity with the goal-related actions the monkeys themselves have just executed. This capacity does not seem to be much less cognitively sophisticated than mere motor imitation, in that it implies a certain degree of self-related cognition in the domain of purposeful actions.

But monkeys do not entertain full-blown mentalization. So, what makes humans different?[1] At present we can only make hypotheses about the relevant neural mechanisms underpinning the still poorly understood mentalizing abilities of humans. In particular, we do not have a clear neuroscientific model of how humans understand the intentions promoting the actions of others they observe.

When an individual starts a movement aimed to attain a goal, such as picking up a pen, he or she has clear in mind what he or she is going to do, for example writing a note on a piece of paper. In this simple sequence of motor acts the final goal of the whole action is present in the agents' mind and is somehow reflected in each motor act of the sequence. The action *intention*, therefore, is set before the beginning of the movements. This also means that when we are going to execute a given action we can also predict its consequences.

However, in social contexts a given action can be originated by very different intentions. Suppose one sees someone else grasping a cup. Mirror neurons for grasping will most likely be activated in the observer's brain. A simple motor equivalence between the observed action and its motor representation in the observer's brain, though, can only tell us *what* the action is (it is a grasp) and not *why* the action occurred. This has led to argue against the relevance of mirror neurons for social cognition and, in particular, for determining the intentions of others (see Jacob and Jeannerod 2005).

We should ask ourselves: What does it mean to determine the intention of the action of someone else? We propose a deflationary answer. Determining *why* action A (e.g., grasping a cup) was executed can be equivalent to detecting the goal of the still not executed and impending subsequent action (e.g., drink from the cup).

In a recent fMRI study (Iacoboni et al. 2005) these issues were experimentally addressed. Subjects watched three kinds of stimuli: grasping hand actions without a context, context only (a scene containing objects), and grasping hand actions embedded in contexts. In the latter condition the context suggested the intention associated with the grasping action (either drinking or cleaning up). Actions embedded in contexts, compared with the other two conditions, yielded a significant signal increase in the posterior part of the inferior frontal gyrus and the adjacent sector of the ventral premotor cortex where hand actions are represented. Thus, premotor mirror areas—areas active during the execution and the observation of an action, previously thought to be involved only in action recognition—are actually also involved in understanding the "why" of the action, that is, the intention promoting it. For simple actions as those employed in this study, the ascription of intentions occurs by default and it is underpinned by the mandatory activation of an embodied simulation mechanism (Gallese in press 2006).

The neurophysiological mechanism at the basis of the relationship between intention detection and action prediction was recently unveiled. Fogassi et al. (2005) described a class of parietal mirror neurons whose discharge during the observation of an act (e.g., grasping an object) is conditioned by the

type of the not yet observed subsequent act (e.g., bringing the object to the mouth) specifying the overall action intention. This study shows that the inferior parietal lobe of the monkey contains mirror neurons discharging in association with the execution/observation of motor acts (grasping) only when they are embedded in a specific action aimed at different goals. It must be emphasized that the neurons discharge before the monkey observes the experimenter starting the second motor act (bringing the object to the mouth or placing it into the cup). Single motor acts are dependent on each other as they participate in the overarching distal goal of an action, thus forming prewired intentional chains, in which each next motor act is facilitated by the previously executed one.

This suggests that in addition to recognizing the goal of the observed motor act, mirror neurons allow the observing monkey to predict the agent's next action, henceforth its overall intention. It is possible to interpret this mechanism as the neural correlate of the dawning of more sophisticated intention understanding abilities, as those characterizing our species.

The mechanism of intention understanding just described appears to be rather simple: depending on which motor chain is activated, the observer is going to activate the motor schema of what, most likely, the agent is going to do. How can such a mechanism be formed? We hypothesize that the statistical frequency of action sequences, as they are habitually performed or observed in the social environment, can constrain preferential paths of inferences/predictions. This can be accomplished by chaining together different motor schemata. At the neural level this would be equivalent to the chaining of different populations of mirror neurons coding not only the observed motor act, but also those that in a given context would normally follow. Ascribing intentions would therefore consist in predicting a forthcoming new goal.

Cognitive Continuity in Primate Social Cognition

The main point we want to make is that social cognition is not only explicitly thinking about the contents of someone else's mind. The neuroscientific evidence presented here shows that our brains, as well as those of macaques, have developed a basic functional mechanism, embodied simulation, which can provide a direct access to the intentions of others. This evidence suggests that many aspects of social cognition are tractable at the neural level of description (Gallese in press 2006). We focused here on the issue of the ascription of intentions. According to us, and in contrast with what mainstream cognitive science would maintain, action prediction and the ascription of intentions—at least of simple intentions—do not appear to belong to different cognitive realms, but both pertain to embodied simulation mechanisms underpinned by the activation of chains of logically related mirror neurons.

If this is true, it follows that one important difference between humans and nonhuman primates could be the higher level of recursivity attained in our species—among many other neural systems—by the mirror neuron system for actions. A similar proposal has been recently put forward in relation to the faculty of language, by contrasting the human species, capable of mastering hierarchically complex "phrase structure grammars," with other nonhuman primate species, confined to the use of much simpler "finite state grammars" (Hauser et al. 2002; Hauser and Fitch 2004). The premotor system is likely one of the most important brain regions where this evolutionary process might have taken place.

The hypothesis we put forward is that the quantitative difference in computational power and degree of recursivity attained by the human brain with respect to the brains of nonhuman primates could produce a qualitative leap in social cognition. The appeal of this hypothesis consists in its parsimony. Embodied simulation and its neural underpinnings—the mirror neuron matching systems—may well fall short of providing a thorough account of what is implied in our sophisticated mentalizing skills. However, we believe that the evidence presented here indicates that embodied mechanisms involving the activation of the sensory-motor system seem to play a major role in social cognition.

The automatic translation of the folk psychology inspired "boxology"—endorsed by functionalism and by some quarters of cognitive science—into newly formed brain modules specifically dedicated to mind reading abilities should be carefully scrutinized. We suspect that language here may play some ontological tricks. Space can provide an illuminating example of how our language-based definitions do not necessarily translate into real entities in the brain. Space, although unitary when examined introspectively, is not represented in the brain as a single multipurpose map. On the contrary, in the brain there are numerous spatial maps (see Rizzolatti et al. 1997). The same might be true for the way we define through language what does it mean to mind read, namely the employment of cognitive tools such as intentions, beliefs, and desire.

Looking for the brain location of the neural correlates of intentions *as such* might not be the best epistemic strategy to disclose what social cognition really is. A more promising and potentially fruitful strategy in our opinion lies in the integration of multiple approaches (from genetics and molecular biology all the way up to neurophysiology, brain imaging, and cognitive psychology) to the study of the role played in social cognition by the sensory-motor systems of the primate brains.

Note

1   The easiest answer would be, of course, the presence of language. This answer, though, is in fact question begging, in that it only transposes the human cognitive endowment to be explained. Furthermore, it implies a perfect overlap between language and our mentalizing abilities. A discussion of these debated issues is beyond the scope and space limits of this short article.

References

Allen C, Bekoff M (1997) Species of Mind. New York: MIT Press.

Arbib MA (2005) From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. Behavioral and Brain Sciences 28: 105–167.

Barrett L, Henzi P (2005) The social nature of primate cognition. Proceedings of the Royal Society of London B 272: 1865–1875.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund H-J (2001) Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. European Journal of Neuroscience 13: 400–404.

Buccino G, Lui F, Canessa N, Patteri I, Lagravinese G, Benuzzi F, Porro CA, Rizzolatti G (2004) Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. Journal of Cognitive Neuroscience 16: 114–126.

Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G (2005) Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. Cognitive Brain Research 24: 355–363.

Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G (2004) Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. Neuron 42: 323–334.

Byrne RW (1995) The Thinking Ape: Evolutionary Origins of Intelligence. Oxford: Oxford University Press.

Byrne RW, Whiten A (1988) Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Oxford: Oxford University Press.

de Waal F (2001) The Ape and the Sushi Master: Cultural Reflections of a Primatologist. New York: Basic Books.

Ferrari PF, Gallese V, Rizzolatti G, Fogassi L (2003) Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. European Journal of Neuroscience 17: 1703–1714.

Ferrari PF, Maiolini C, Addessi E, Fogassi L, Visalberghi E (2005) The observation and hearing of eating actions activates motor programs related to eating in macaque monkeys. Behavioural Brain Research 161: 95–101.

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G (2005) Parietal lobe: From action organization to intention understanding. Science 302: 662–667.

Gallese V (2001) The "shared manifold" hypothesis: From mirror neurons to empathy. Journal of Consciousness Studies 8(5–7): 33–50.

Gallese V (2003a) The manifold nature of interpersonal relations: The quest for a common mechanism. Philosophical Transactions of the Royal Society of London B 358: 517–528.

Gallese V (2003b) A neuroscientific grasp of concepts: From control to representation. Philosophical Transactions of the Royal Society of London B 358: 1231–1240.

Gallese V (2005a) Being like me: Self-other identity, mirror neurons and empathy. In: Perspectives on Imitation: From Cognitive Neuroscience to Social Science, Vol. 1 (Hurley S, Chater N, eds), 101–118. Cambridge, MA: MIT Press.

Gallese V (2005b) Embodied simulation: From neurons to phenomenal experience. Phenomenology and the Cognitive Sciences 4: 23–48.

Gallese V (in press 2006) Intentional attunement: A neurophysiological perspective on social cognition. Cognitive Brain Research.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. Brain 119: 593–609.

Gallese V, Fogassi L, Fadiga L, Rizzolatti G (2002) Action representation and the inferior parietal lobule. In: Attention and Performance XIX (Prinz W, Hommel B, eds), 247–266. Oxford: Oxford University Press.

Gallese V, Goldman A (1998) Mirror neurons and the simulation theory of mind-reading. Trends in Cognitive Sciences 12: 493–501.

Gallese V, Keysers C, Rizzolatti G (2004) A unifying view of the basis of social cognition. Trends in Cognitive Sciences 8: 396–403.

Gallese V, Lakoff G (2005) The brain's concepts: The role of the sensory-motor system in reason and language. Cognitive Neuropsychology 22: 455–479.

Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. Animal Behaviour 59: 771–785.

Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic representation of action words in human motor premotor cortex. Neuron 41: 301–307.

Hauser MD (2005) Our chimpanzee mind. Nature 437: 60–63.

Hauser MD, Chomsky N, Fitch WT (2002) The faculty of language: What is it, Who has it, and how did it evolve? Science 298: 1569–1579.

Hauser MD, Fitch WT (2004) Computational constraints on syntactic processing in a nonhuman primate. Science 303: 377–380.

Heyes CM (1998) Theory of mind in nonhuman primates. Behavioral and Brain Sciences 21: 101–148.

Humphrey NK (1978) Nature's psychologists. The New Scientist (29 June).

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G (2005) Grasping the intentions of others with one's own mirror neuron system. Public Library of Science Biology 3: 529–535.

Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. Science 286: 2526–2528.

Jacob P, Jeannerod M (2005) The motor theory of social cognition: A critique. Trends in Cognitive Neuroscience 9: 21–25.

Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: Action representation in mirror neurons. Science 297: 846–848.

Paukner A, Anderson JR, Borelli E, Visalberghi E, Ferrari PF (2005) Macaques (*Macaca nemestrina*) recognize when they are being imitated. Biology Letters 1: 219–222.

Povinelli DJ, Bering JM, Giambrone S (2000) Toward a science of other minds: Escaping the argument by analogy. Cognitive Science 24: 509–541.

Povinelli DJ, Eddy TJ (1996) What young chimpanzees know about seeing. Monographs of the Society for Research in Child Development 247: 1–147.

Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? Behavioral and Brain Sciences 1: 515–526.

Pulvermüller F (2002) The Neuroscience of Language. Cambridge: Cambridge University Press.

Rizzolatti G, Arbib MA (1998) Language within our grasp. Trends in Neurosciences 21: 188–194.

Rizzolatti G, Craighero L (2004) The mirror neuron system. Annual Review of Neuroscience 27: 169–192.

Rizzolatti G, Fadiga L, Fogassi L, Gallese V (1997) The space around us. Science 277: 190–191.

Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. Cognitive Brain Research 3: 131–141.

Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nature Neuroscience Reviews 2: 661–670.

Subiaul F, Cantlon JF, Holloway RL, Terrace HS (2004) Cognitive imitation in rhesus macaque. Science 305: 407–410.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D (2005) Listening to action-related sentences activates fronto-parietal motor circuits. Journal of Cognitive Neuroscience 17: 273–281.

Tomasello M, Call J (1997) Primate Cognition. Oxford: Oxford University Press.

Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G (2001) "I know what you are doing": A neurophysiological study. Neuron 32: 91–101.

Whiten A, Byrne RW (1997) Machiavellian Intelligence II: Evaluations and Extensions. Cambridge: Cambridge University Press.