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56 The Eyes, the Hand, and the Mind: Behavioral and Neurophysiological Aspects of Social Cognition

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Nevertheless, the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind.
—Darwin (1871, p. 193)

What most clearly distinguishes primates from other mammal species in terms of cognition concerns the social domain. Although it is not deeply understood, many authors have proposed that the uniqueness of the intelligence of primates has to be sought in their complex social world (see Humphrey 1976). Primates are not the only mammals displaying complex social systems, but it seems that the quality and complexity of their relationships within their social groups, compared with other taxa, are different.

In the evolution of primate cognition, the relationships between group members have played a fundamental role. As Tomasello and Call (1997) pointed out, nonhuman primates understand the quality of the relationships within their social group, not only in terms of kin and hierarchies, but also in terms of coalitions, friendship, and alliances. Primate cognition can be considered very different from that of other mammalian species because primates can categorize and understand third-party social relationships.

In the past few decades, an ever-growing literature has raised questions about the possibility that social behaviors of nonhuman primates are driven by intentions and that these animals understand the behavior of others as intentional. Most scientists would agree on the fact that monkeys and apes behave as if they possessed objectives and goals, although, contrary to humans, their awareness of purpose is not assumed. The fact that nonhuman primates may understand the behavior of conspecifics as goal related can have considerable benefits in an individual's life because it allows the individual to predict the actions of others.

The problem of intentionality in primates was almost simultaneously and independently raised by Humphrey (1980) and Premack and Woodruff (1978). The capacity to attribute mental states such as intentions, beliefs, and desires to others has been described as a theory of mind (Premack and Woodruff 1978). So far there is no firm evidence that nonhuman primates possess a theory of mind. For most authors, a theory of mind constitutes the mental Rubicon between humans and nonhuman primates.

One of the most influential models of a theory of mind is that proposed by Baron-Cohen (1994, 1995). According to this author, separate brain modules constitute a mind-reading system that is layered on multiple modularized levels of increasing complexity. The importance of such a model for the study of social cognition is twofold. First, it enables researchers to investigate several aspects of mind-reading abilities at both the behavioral and the brain level. Second, it allows an empirical evaluation of the cognitive stage reached by a given species, thus paving the way for comparative investigations. Even if something like a theory of mind really underpins mind-reading abilities in humans, this cognitive feature of the human mind must have evolved from a nonhuman ancestor who shared with the present primates—humans included—several cognitive features. In this context, one of the major tasks of cognitive neuroscience should be to investigate the behavioral and neural basis of intentional behavior. The behavioral study of social cognition of nonhuman primates and the examination of the neural mechanisms supporting it are therefore necessary for a thorough understanding of how the human mind evolved and how it works.

In this essay we review a series of investigations of the social behavior of macaque monkeys conducted at a behavioral and a neurophysiological level. First we summarize some recent behavioral experiments carried out in our laboratory to investigate the presence of gaze-following behavior

in monkeys. Then we review neurophysiological data concerning the neural mechanisms that enable macaques to understand goal-directed actions performed by other individuals. We propose that such behavioral abilities and neural mechanisms corroborate the notion of cognitive continuity between human and nonhuman primates.

Gaze Following

A gaze-following response (GFR) is defined as the ability of one individual (X) to follow the direction of gaze of a second individual (Y) to a location in space (Emery et al. 1997). The ability to visually track the gaze direction of conspecifics to targets may have a considerable adaptive advantage because individuals can gain information about food sources, the social status of conspecifics, and the location of predators (Menzel and Halperin 1975; Whiten and Byrne 1988). It has been proposed that gaze perception plays a crucial role in social interactions (Whiten and Byrne 1988; Thomsen 1974; Tomasello et al. 1998).

It is well established that apes (chimpanzees and orangutans) are able to follow the gaze direction of conspecifics (Tomasello et al. 1998) and humans (Itakura 1996; Povinelli and Eddy 1996) using a combination of head and eye stimuli. Chimpanzees are also able to follow the gaze direction of a human experimenter by observing the eye direction alone, independently of head movement (Itakura 1996; Povinelli and Eddy 1996; Tomasello et al. 1999). Physiological studies have shown that in monkeys (Perrett et al. 1985, 1992), as in humans (Puce et al. 1998; Hoffman and Haxby 2000), there are neural correlates for detection of eye direction. There is little evidence at the behavioral level, however, of the presence and development of such abilities in monkeys (see Lorincz et al. 1999).

The aim of our study (see Ferrari et al. 2000) was to assess in juvenile and adult pig-tailed macaques (*Macaca nemestrina*) the capacity to use only eye cues to follow the gaze of an exper-

imenter. An experimenter presented biological stimuli (head, eye, and trunk movements) that were oriented in each presentation to one of four spatial directions (up, down, left, or right; see figure 56.1A). The stimuli were presented randomly to 11 monkeys of different ages who were free to move in their home cages. A nonbiological stimulus served as control. In order to judge a monkey's response to the movements of the experimenter, we recorded the direction of the first gaze movement after a stimulus visual engagement (see figure 56.1B).

The results (see figure 56.1C and D) showed that macaques, like humans, are able to determine the direction of another's gaze by using eye cues alone. Furthermore, also as in humans, gaze-following responses in macaques dramatically improve with age. Juvenile monkeys showed a marked difference in gaze-following behavior compared with adults; they were unable to determine the direction of another's gaze using eye cues alone. These results cannot be explained on the basis of differences in attentional factors because adults and juveniles devoted the same amount of time to interacting with and visually exploring the experimenter. In juveniles, the movement of the head and eyes together is the first feature that triggers a shift in a visual attention response, suggesting that in young macaques the combined movement of head and eyes provides more salient signals for the direction of another's gaze than the eyes alone.

This ontogenetic trend resembles that of humans; 3- to 6-month-old infants are able to follow the gaze of an adult by using a combination of head and eye cues, but it is not until 14–18 months that they are able to follow a gaze by using eye cues alone (Scaife and Bruner 1975; Butterworth and Jarret 1991; Moore and Corkum 1998). Thus, in humans this ability develops when children are still dependent on their parents. In monkeys, a gaze-following response based on head and eye cues develops between the second and the fourth year, a stage at which juveniles are weaned but still socially dependent on their mothers (Fa and Lindburg 1996; Smuts et al.
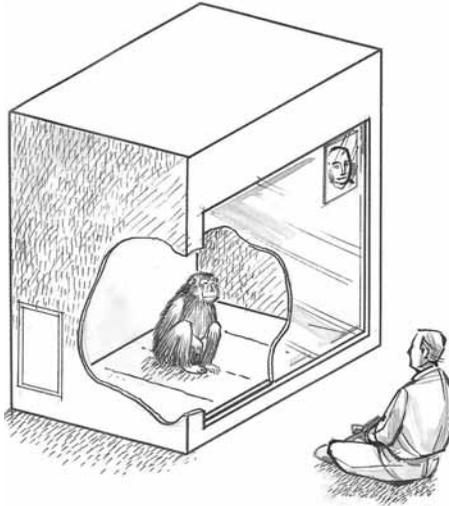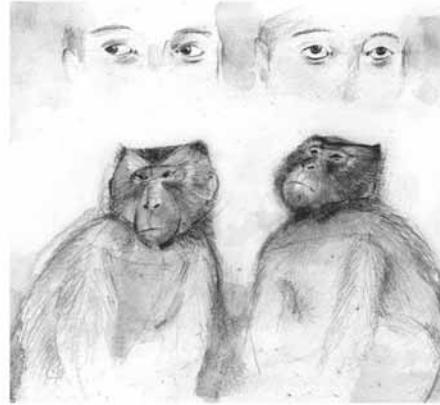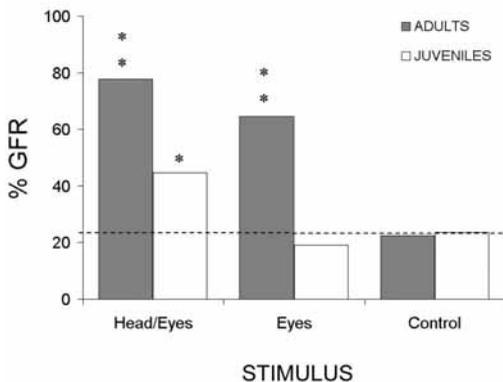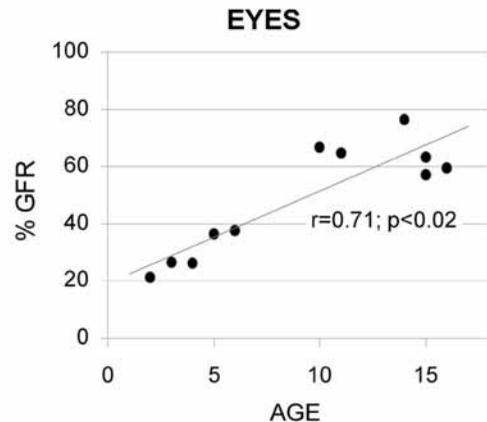
Figure 56.1
(A) Schematic illustration of the experimental setting. The experimenter was sitting facing the monkey at a 1.5-m distance. A camera placed behind the experimenter videotaped each session. A mirror placed on the front of the cage and facing the experimenter allowed the experimenter's gaze to be recorded. (B) Illustration of the results. The direction of the eyes as a stimulus presented by the experimenter (top) elicited a gaze-following response (GFR) in the adult macaque (bottom). (C) Percent of trials in which juvenile and adult monkeys showed a gaze-following response as a function of experimental condition. The data recorded for each monkey during two sessions are averaged and plotted together. Each bar represents the average of the percent of GFR in adults and juveniles. A single asterisk indicates the significance of the comparison between the experimental condition and the control ($p < 0.05$). A double asterisk indicates the significance of the comparison between the experimental condition and the control ($p < 0.05$) and between adults and juveniles ($p < 0.01$). The dashed line indicates the levels of expected probability by chance (25 percent; an animal's response could be oriented to one of the four possible spatial directions). (D) Percent of GFR to eyes alone as a function of age. (Modified from Ferrari et al. 2000.)

1987). However, according to our results, GFR based on eye cues alone seems to develop only at a later stage.

This finding makes it unlikely that the development of GFR is related to the maturation of visuomotor coordination and motor skills, which in monkeys are complete well before the end of the juvenile and adolescent period. It is possible therefore to hypothesize that the development of GFR could be related to the relatively long period preceding adulthood, during which young macaques have the opportunity to better explore the physical environment (Smuts et al. 1987; Janson and van Schaik 1993) and to learn the rules of their complex social world (Walters 1987). Indeed, it is well known that juveniles spend much of their nonfeeding time engaged in social play (for a thorough treatment of the relation between social play and cognition, see Allen and Bekoff 1997; Bekoff and Allen 1998). It has been proposed that through play, juveniles may establish dominance relationships and learn social and communication skills (Walters 1987).

Thus, it seems that in macaques the emergence of a gaze-following response based on head and eye cues could be linked to the processes of transition to adulthood, when individuals have to acquire social and cognitive skills that are crucial for their survival and reproduction. Juvenile monkeys are not able to orient their attention on the basis of eye cues alone. In general, gaze following is more frequent in adults than in juveniles. As in humans, however, in macaques such abilities dramatically improve with age, reinforcing the idea that the transition to a more complex social life is a key factor for the development of cognitive skills such as gaze-following behavior.

Understanding Action: The Role of Mirror Neurons

Observation of action appears to be important in order to build a meaningful account of conspecifics' behavior. How can individuals rec-

ognize, and possibly understand, the actions performed by other conspecifics?

A possible neural correlate of the mechanism allowing understanding of action could be represented by a class of neurons—mirror neurons—that our group discovered in area F5 of the ventral premotor cortex of the macaque monkey (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996a). In a series of single-neuron recording experiments, we discovered that in a sector of the monkey ventral premotor cortex, area F5 (see Matelli et al. 1985) (see figure 56.2A), a particular set of neurons that are activated during the execution of purposeful, goal-related hand movements, such as grasping or holding or manipulating objects, also discharged when the monkey observed similar hand actions performed by another individual (see figure 56.2B). We designated these neurons "mirror neurons" (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996a). In order to be activated by visual stimuli, mirror neurons require an interaction between the agent (human being or a monkey) and the object of its action. Figure 56.2C1–C3 shows an example of the response of an F5 mirror neuron. The visual presentation of objects such as food items or objects at hand in the lab did not evoke any response. Similarly ineffective or showing very little effect in driving the neuron response were actions that achieved the same goal and looked similar to those performed by the experimenter's hand, but were made with tools such as pliers or pincers. Actions having emotional content, such as threatening gestures, were also ineffective.

Frequently, a strict congruence was found between an observed action that was effective in triggering the neuron and the executed action. In one-third of the recorded neurons, the effective observed and executed actions corresponded both in terms of the general action (e.g., grasping) and in the way in which that action was executed (e.g., precision grip). In the other two-thirds, only a general congruence was found (e.g., any kind of observed and executed grasping elicited the

neurons' response). This latter class of mirror neurons is particularly interesting, because many of them appear to be used in generalizing across different ways of achieving the same goal, thus perhaps enabling a more abstract type of action coding.

Perrett and co-workers have described neurons buried within the superior temporal sulcus (STS) cortex that respond to the observation of complex actions, such as grasping or manipulating objects (for a review see Carey et al. 1997; Jellema and Perrett in press). These neurons, whose visual properties are in many respects similar to those of mirror neurons, could constitute the mirror neurons' source of visual information. The STS region, however, has no direct connection with area F5, but has links with the anterior part of the inferior parietal lobule (area PF or 7b, see figure 56.2A), which in turn is reciprocally connected with area F5 (Matelli et al. 1986; see also Rizzolatti et al. 1998). Area PF, or 7b, is located on the convexity of the inferior parietal lobule. Single-neuron studies showed that most of the PF neurons respond to passive somatosensory stimuli applied to the mouth, arm, leg, or chest (Leinonen and Nyman 1979; Leinonen et al. 1979; Hyvärinen 1981; Graziano and Gross 1995; Fogassi et al. 1998). A considerable number of neurons can be activated by both visual and somatosensory stimuli (bimodal neurons) (Leinonen et al. 1979; Graziano and Gross 1995). About one-third of PF neurons fire during mouth, arm, and hand goal-related movements (Leinonen et al. 1979).

Area PF, through its connections with the STS on one hand, and F5 on the other, could play the role of an intermediate step within a putative cortical network for understanding action, by feeding to the ventral premotor cortex visual information about an action received from the STS.

In a new series of experiments we decided therefore to better clarify the nature and the properties of such a cortical matching system in the monkey brain. The functional properties of area PF were studied by examining neuronal responses during monkeys' active movements and in response to somatosensory and visual stimuli. Visual stimuli included goal-related hand movements performed by the experimenter in front of the monkey. The results of this study showed that about one-third of the PF recorded neurons responded during both execution and observation of an action (Fogassi et al. 1998; Gallese et al. in press). Figure 56.2D1–D3 shows an example of a PF mirror neuron response. All PF mirror neurons responded to the observation of actions in which the experimenter's hand(s) interacted with objects. Similarly to the responses observed in F5, PF mirror neurons did not respond to presentation of an object or to actions performed using tools. Observed mimed actions evoked weaker responses, if any. What these experiments show is that the "mirror" system, matching observation of an action to its execution, is not a prerogative of the premotor cortex, but extends to the posterior parietal lobe as well.

On the basis of these findings, it appears that the sensorimotor integration process supported by the F5-PF fronto-parietal cortical network creates an internal copy of actions that is used to generate and control goal-related behaviors and to provide, at a preconceptual and prelinguistic level, a meaningful account of behaviors performed by other individuals.

Several studies that used different methodologies have demonstrated the existence of a similar matching system in humans (see Fadiga et al. 1995; Grafton et al. 1996; Rizzolatti et al. 1996b; Cochin et al. 1998; Decety et al. 1997; Hari et al. 1998; Iacoboni et al. 1999; Buccino et al. 2001). In particular, it is interesting to note that brain-imaging experiments in humans have shown that during observation of hand action, a cortical network composed of sectors of Broca's region, the STS region, and the posterior parietal cortex is activated (Grafton et al. 1996; Rizzolatti et al. 1996b; Decety et al. 1997; Decety and Grèzes 1999; Iacoboni et al. 1999; Buccino et al. 2001). Given the homology between monkey's area F5 and Broca's region in humans (for discussion see Matelli and Luppino 1997; Rizzolatti and Arbib 1998; Gallese 1999), it appears that a

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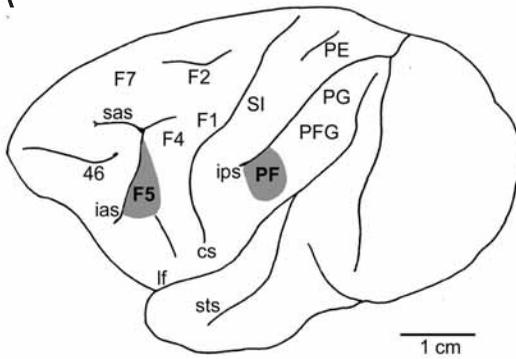
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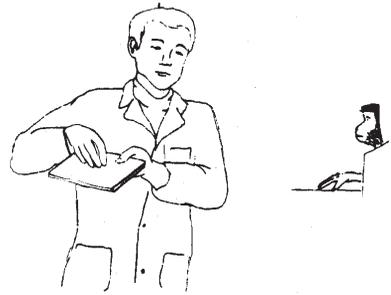
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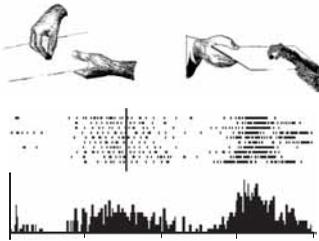
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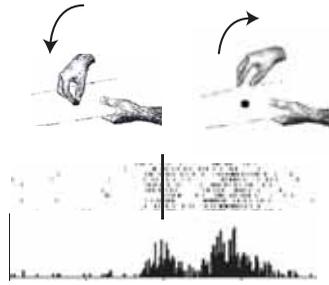
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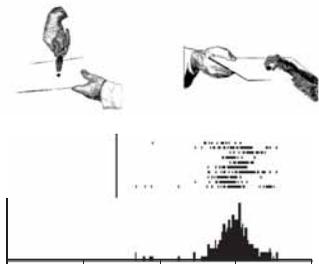
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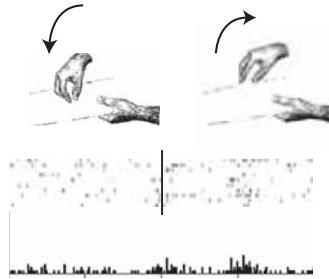
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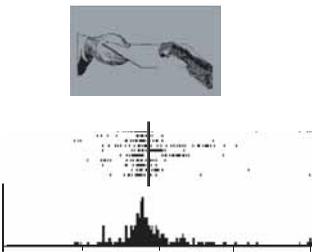
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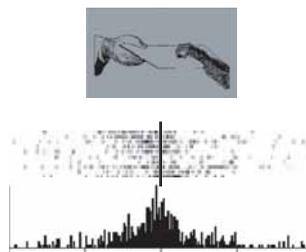
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part of the human brain traditionally considered to be unique to our species nevertheless shares a similar functional mechanism with its nonhuman precursor area. In other words, Broca's region appears to be involved not only in speech control, but also, similarly to monkey's area F5, in a prelinguistic analysis of others' behavior. [For a discussion of the possible link between mirror neurons and the origin of language, see Fadiga and Gallese (1997), Rizzolatti and Arbib (1998), Gallese (1999).]

A recent brain-imaging study (Buccino et al. 2001) showed that when we observe goal-related behaviors executed with effectors as different as the mouth, the hand, or the foot, different specific sectors of our premotor cortex become active. These cortical sectors are the same sectors that are active when we perform the same actions. Whenever we look at someone performing an action, in addition to the activation of various

visual areas, there is a concurrent activation of the motor circuits that are recruited when we ourselves perform that action. Although we do not overtly reproduce the observed action, nevertheless our motor system acts as if we were executing the same action that we are observing.

When a given action is planned, its expected motor consequences are forecast. This means that when we are going to execute a given action, we can also predict its consequences. Through a process of "equivalence" between what is acted and what is perceived, this information can also be used to predict the consequences of actions performed by others. According to this perspective, perceiving an action is equivalent to internally simulating it. This implicit, automatic, and unconscious process of motor simulation enables the observer to use his or her own resources to penetrate the world of the other without the need to explicitly theorize about it. The process of

Figure 56.2
(A) Lateral view of macaque monkey cerebral cortex showing frontal and parietal areas. Frontal agranular cortical areas (F_1, F_2, F_4, F_5, F_7) are classified according to Matelli et al. (1985; 1991). The posterior parietal areas (PE, PF, PFG, PG) are classified according to Von Bonin and Bailey (1947). Shaded areas indicate the cortical sectors where mirror neurons were recorded. Abbreviations: cs, central sulcus; ias, inferior arcuate sulcus; ips, intraparietal sulcus; lf, lateral fissure; SI, primary somatosensory area; sas, superior arcuate sulcus; sts, superior temporal sulcus. (B) Illustration of the experimental situation for testing the visual properties of mirror neurons. (Modified from di Pellegrino et al. 1992.) (C) Example of the visual and motor responses of an F5 mirror neuron. The behavioral situation during which the neural activity was recorded is illustrated schematically in the upper part of each panel. In the lower part, rasters and the relative peristimulus response histograms are shown. (C1) A tray with a piece of food placed on it was presented to the monkey; the experimenter grasped the food and then moved the tray with the food toward the monkey, which grasped it. A strong activation was present during observation of the experimenter's grasping movements and while the same action was performed by the monkey. Note that the neural discharge was absent when the food was only presented and moved toward the monkey. (C2) The same as C1, except that the experimenter grasped the food with pliers. Note the absence of response when the observed action was performed with a tool. (C3) The monkey grasped the food in the dark. Rasters and histograms are aligned (vertical bar) with the moment in which the experimenter (C1 and C2) or the monkey (C3) touched the food. Abscissae: time; ordinate: spikes/second; bin width: 20 ms. (Modified from Rizzolatti et al. 1996.) (D) Example of the visual and motor responses of a PF mirror neuron. (D1) A tray with a piece of food placed on it was presented to the monkey; the experimenter grasped the food and then released it, moving the hand away from the food. Note the strong response during the observation of the experimenter's grasping and releasing actions. The neuron did not respond during the presentation of the food on the tray. (D2) The same action as in D1 was mimed. Note that in this condition the neural response was virtually absent. (D3) The monkey grasped the food in the dark. Rasters and histograms are aligned (vertical bar) with the moment in which the monkey (D3) or the experimenter touched the food (D1) or the tray (D2). All other conventions are as in part C. (Modified from Gallese et al. 2002.)

simulating action automatically establishes a direct implicit link between agent and observer (see Gallese and Goldman 1998).

Action is therefore the most suitable a priori candidate principle that enables social bonds to be initially established. By an implicit process of simulating action when we observe other individuals acting, we can immediately recognize them as goal-directed agents like us, because a similar neural substrate is activated when we ourselves attempt to achieve the same goal by acting. In sum, we propose that observed behaviors acquire their full meaning only to the extent that they constitute one of the poles of the dynamic sensorimotor relation between agent and observer. Mirror neurons are the neural correlate of such a relation.

Mirror neurons are found in cortical regions endowed with motor properties because premotor neurons are able to establish relationships between expectancies and results. Thus, understanding action can be viewed as a subpersonally mediated function, that is, it relies on neural circuits involved in action control. In this respect, we can hypothesize a continuous path leading from action control to action representation (see Gallese 2000 a,b, 2001).

Conclusions

The results briefly summarized here suggest two things. First, humans share with nonhuman primates, not only particular types of social behavior (i.e., gaze following), but also similar developmental patterns leading to the full-blown acquisition of those same behaviors. Second, both humans and monkeys, when engaged in observing the actions of other individuals, display a similar pattern of covert action simulation, which is underpinned by the activation of a similar cortical network.

A link between gaze following and a theory of mind has been theorized by Baron-Cohen[1] (1995). According to this author, the perception of eye gaze is a crucial step to the development of a mind-reading system that allows individuals to understand not only what another individual is attending to but also what it is thinking about. Thus, the eyes can be considered as "windows" to the mind of others. Our results do not allow us to conclude that a theory of mind exists in monkeys. However, the fact that macaques, together with humans and great apes, display the ability to follow the gaze of others by using eye cues, suggests that essential mechanisms for the development of mind reading are shared by all these primate species.

The discovery that both monkeys and humans share a similar mechanism that matches the observation of an action with its execution is in our opinion an even stronger argument against the theses positing a sharp discontinuity between the cognitive toolkit employed by humans and by nonhuman primates in their social transactions. Most of the emphasis so far has been on clarifying the extent to which our species differs from other primates with respect to the use of propositional attitudes such as beliefs, intentions, and desires. According to this influential view, humans have a theory of mind, nonhuman primates do not, period. However, as pointed out by Allen and Bekoff (1997), this all-or-nothing approach to higher-order intentionality is strongly debatable.

When trying to account for our cognitive abilities, we tend to forget that these abilities are the result of a long evolutionary process. It is reasonable to hypothesize that this evolutionary process proceeded along a line of continuity (see Gallese and Goldman 1998; Gallese 2001). We think that it is worth taking a different heuristic approach; namely, establishing to what extent apparently different cognitive strategies may be underpinned by similar functional mechanisms. The empirical data briefly reviewed here represent, we think, a justification of this investigative approach. The data on mirror neurons and their human homolog seem to suggest that the ease with which we are capable of "mirroring" our-

selves in the behavior of others and recognizing them as similar to us—in other words, our capacity to empathize with others—may rely on a series of matching mechanisms that we have just started to uncover.

Acknowledgments

Note

1. Two cognitive components of Baron-Cohen's model of a theory of mind—the eye direction detector (EDD) and the shared attention mechanism (SAM) modules—are related to social gaze behavior. The EDD module supposedly detects the presence of eyes, computes the direction of gaze, and finally establishes the equivalence between the act of looking and the mental state of seeing. The SAM module would use information from the EDD to establish a link between the agent's and the observer's gaze behavior, thus enabling individuals to share the same mental state on a given object, action, or state of affairs. Both EDD and SAM components are characterized by behavioral and mental features. It could be argued that all behavioral aspects of both components could be underpinned by a matching system that enables the observer to map the agent's gaze behavior to his or her own gaze behavior. In other words, a putative gaze behavior mirror matching system could parsimoniously account for aspects of both the EDD and SAM modules.

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