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The mirror neuron system: New frontiers

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Since the discovery of mirror neurons, much effort has been invested into studying their location and properties in the human brain. Here we review these original findings and introduce the main topics of this special issue of *Social Neuroscience*. What does the mirror system code? How is the mirror system embedded into the mosaic of circuits that compose our brain? How does the mirror system contribute to communication, language and social interaction? Can the principle of mirror neurons be extended to emotions, sensations and thoughts? Papers using a wide range of methods, including single cell recordings, fMRI, TMS, EEG and psychophysics, collected in this special issue, start to give us some impressive answers.

INTRODUCTION

The discovery of mirror neurons in the premotor cortex of the monkey has been considered one of the most exciting recent breakthroughs in neuroscience. These neurons have been so named because they "mirror" actions of other individuals by re-enacting them on the observer's motor repertoire. Indeed, mirror neurons respond both when a monkey performs an action and when it observes (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), knows that (Umiltà et al., 2001) or hears (Keysers et al., 2003; Kohler et al., 2002) someone else performing a similar action. What has made these neurons so popular is that they opened a window into the neural clockwork that allows us to understand other individuals—a capacity that had fascinated philosophers and psychologists for centuries. With mirror neurons, it became clear that the brain could understand other people's actions by a process of "motor embodiment" or, in other words, by feeling what one would feel during the execution of a similar action.

Two techniques have been critical in studying this system in humans. On one hand, transcranial magnetic stimulation (TMS) has provided the first neurophysiological evidence that motor programs are facilitated by observing other people's actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Over the past decade, much effort has been expended in characterizing this observation-induced motor resonance (Borroni, Montagna, Cerri, & Baldissera, 2005; Gangitano, Mottaghy, & Pascual-Leone, 2004; Montagna, Cerri, Borroni, & Baldissera, 2005; Patuzzo, Fiaschi, & Manganotti, 2003; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Strafella & Paus, 2000; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006), leading to the observation that human motor facilitation is evoked also by

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intransitive hand gestures. This might explain the capability of our species to imitate also new (never seen/never executed) actions. Neuroimaging techniques, and fMRI in particular (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Buccino et al., 2001; Buccino, Lui et al., 2004a, 2004b; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006; Gazzola, Aziz-Zadeh, & Keysers, 2006; Gazzola, Rizzolatti, Wicker, & Keysers, 2007a; Gazzola et al., 2007b; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Armony, Rowe, & Passingham, 2003; Hamilton & Grafton, 2006; Iacoboni & Dapretto, 2006; Iacoboni et al., 1999, 2001, 2005; Lamm, Fischer, & Decety, 2007; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005; Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006; Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005), have allowed us to pinpoint the regions in which mirror neurons could be in humans. Experiments in which the same participants were scanned while they executed actions and while they viewed or heard other individuals perform similar actions have shown that voxels in the dorsal and ventral premotor, supplementary motor, posterior parietal, temporal and sometimes somatosensory cortices are indeed activated during both action execution and action perception, pinpointing the most likely location for the human mirror system (Buccino et al., 2004b; Gazzola et al., 2006; Gazzola et al., 2007a, 2007b). Interestingly, such activations are somatotopical: Dorsal premotor regions are more active both during the perception and the execution of hand actions as compared to mouth actions, while ventral regions are more active during the perception and the execution of mouth actions as compared to hand actions (Gazzola et al., 2006).

One additional area, almost constantly active during action observation and the sound of actions in particular (Gazzola et al., 2006) is Broca's region (BA44–BA45). The fact that Broca's region is classically considered the frontal area for speech suggests a possible evolutionary link between the implicit communication provided by the action-understanding mechanism based on monkey auditory and visual mirror neurons (Keysers et al., 2003; Kohler et al., 2002) and the explicit, verbal communication characterizing the human language (Fadiga et al., 2006; Fadiga, Roy, Fazio, & Craighero, 2007; Rizzolatti & Arbib, 1998). Recently, Roy Mukamel and his colleagues at UCLA have recorded the first single cells with motor mirror property in the supplementary motor cortex of humans, but these findings are still unpublished.

The confidence with which we can now claim that both monkeys and humans have a mirror system sets a solid foundation for investigating a much more complex set of questions: What does the mirror system code? How is the mirror system embedded into the mosaic of brain circuits that compose our brain? How does the mirror system contribute to communication, language and social interaction? Can the principle of mirror neurons be extended to emotions, sensations and thoughts? This special issue will try to tackle some of these questions.

WHAT DOES THE MIRROR SYSTEM CODE?

Although everyone seems to agree that mirror neurons transform the sight or sound of an action into a corresponding motor representation, what people mean by ''corresponding'' is often less clear: an action involving the same muscles or one with the same goal? Mirror neurons in the monkey vary in selectivity. Strictly congruent mirror neurons require the observed action to be extremely similar to the effective executed action for the neuron to respond. For these neurons—about 30% of mirror neurons—''corresponding'' seems to mean an action that achieves a similar goal and that involves the same motor details. Broadly congruent mirror neurons, making up about 60% of all mirror neurons, however, are less picky about the details of the observed action: It needs to achieve a similar goal (e.g., grasping an object) but can often involve another effector (e.g., grasping with the mouth or with the hand). For such neurons, ''corresponding'' thus means ''having the same goal.'' Together, strictly and broadly congruent mirror neurons could therefore represent both *what* another individual did, and *how* he did it (Thioux, Gazzola, & Keysers, 2008).

But what about the human mirror system? A number of TMS studies have shown how precise the matching of observed and executed action seems to be in humans as well (Borroni et al., 2005; Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Gangitano et al., 2004; Montagna et al., 2005; Urgesi et al., 2006). A number of fMRI studies, on the other hand, evidence a combination of "what" and "how" similar to that found at the level of single cells in monkeys. Repetition suppression experiments show that certain parts of the mirror system are sensitive to the precise kinematics of observed movements, while others seem to represent the goal of an action (Hamilton & Grafton, 2006). Other fMRI experiments show an important consequence of goal matching: The human mirror system can resonate with actions even if the observer lacks the body parts that would directly match those with which the agent performed the action (Gazzola et al., 2007a, 2007b). In this issue, these questions are addressed further. Is the mirror system, for instance, involved in the representation of biologically impossible or intransitive gestures (Borroni & Baldissera, 2008 this issue; Candidi, Urgesi, Ionta, & Aglioti, 2008 this issue; Lui et al., 2008 this issue)? Does the mirror system resonate for actions different from hand or mouth ones (Saarela & Hari, 2008 this issue)? How quickly does the mirror-neuron system respond (van Schie et al., 2008 this issue)? Does it respond to non-biological stimuli (Engel et al., 2008 this issue)? What do these properties tell us about what the mirror system represents (de Vignemont & Haggard, 2008 this issue)? When, during ontogenesis, do mirror neurons start responding to others' actions (Nyström, 2008 this issue)?

EMBEDDING THE MIRROR SYSTEM

The more we understand the mirror neuron system, the more we have to ask ourselves how this circuitry interacts with other brain systems. How, for instance, can regions involved in spatial attention interact with the mirror neuron system to help us distinguish our own actions from those we observe while they are performed by other people? What brain circuits are responsible for inhibiting motor output while we observe the actions of others? Gangitano, Mottaghy, and Pascual-Leone (2008 this issue) and Jeannerod and Anquetil (2008 this issue) provide new insights into these important questions.

THE MIRROR SYSTEM AND COMMUNICATION

The capacity of the mirror system to activate action representations in the observer links it to communication, an issue that Gallese (2008 this issue) explores in detail. The mirror system has shown us how social cognition is at least partially based on our own bodily representations. Aziz-Zadeh (2008 this issue) and her coworkers show us that the understanding of words that refer to bodyparts may also be embodied. Oberman and Ramachandran (2008 this issue) give data that suggests that linking vocal sounds to shapes is abnormal in autism, and interpret these results within the framework of mirror neurons, and Pratt and Kelly (2008 this issue) show that our own emotional state colors our processing of emotional words.

THE MIRROR SYSTEM AND SOCIAL INTERACTIONS

By influencing the observer's actions, the mirror neuron system creates a bond between the behaviors of social partners. This bond is reciprocal: During most social interactions there is not a single agent and a single observer: both partners are both observer and agent, both the source and the target of the social contagion the mirror neuron system conveys. It is therefore essential to start exploring the reciprocal nature of social influences within the framework of the mirror system. Fujii and his team (2008 this issue) pave the way to such investigations. They record the brain activity simultaneously from two interacting monkeys, and show how this allows novel analysis methods to capture how mirror neurons participate in such unconstrained social interactions. Whenever humans collaborate to achieve a goal together (e.g., sending a rocket onto the moon), an important element of the social interaction goes beyond the actions themselves: Both partners need to keep the goals and rules of the interaction in mind. Atmaca and colleagues show that this process of goal-sharing is a strong and spontaneous property of the human mind. Finally, Paus et al. (2008 this issue) investigate the functioning of the mirror-neuron system in adolescents with different degrees of resistance to peer influence.

GOING BEYOND ACTIONS

One of the most fundamental breakthroughs in the study of the mirror neuron system has been the observation that the concept of mirror neurons extends beyond actions: Not only does the sight of an action activate regions involved in motor execution, but the sight of touch also activates somatosensory regions (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004) and the perception of other people's emotions such as pain, happiness and disgust activates regions involved in experiencing similar emotions (Jabbi, Swart, & Keysers, 2007; Singer et al., 2004; Wicker et al., 2003) and producing similar facial expressions (van der Gaag, Minderaa, & Keysers, 2007). We will see that the sight of emotional body movements leads to similar activations (Pichon, de Gelder, & Grèzes, 2008 this issue). Most recently, Michael Platt and colleagues have possibly extended the concept of mirror neurons to eye movements: Certain neurons in the lateral intraparietal region, thought to control eye movements, respond to the sight of another monkey's eye movements as if they were mirror neurons for gaze (Shepherd, Deaner, Klein, & Platt, 2007). This discovery may help elucidate the neural basis of gaze-following, and Ferrari and coworkers (2008 this issue) explore the development of gaze-following in the macaque.

CONCLUSION

Now that we know that both humans and monkeys have a mirror neuron system, we need to focus on understanding the architecture and the functional properties of this system. It is hoped that this special issue will inspire this research.

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