Review

Interpreting actions: The goal behind mirror neuron function

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A B S T R A C T

Crucial to our everyday social functioning is an ability to interpret the behaviors of others. This process involves a rapid understanding of what a given action is not only in a physical sense (e.g., a precision grip around the stem of a wine glass) but also in a semantic sense (e.g., an invitation to "cheers"). The functional properties of fronto-parietal mirror neurons (MNs), which respond to both observed and executed actions, have been a topic of much debate in the cognitive neuroscience literature. The controversy surrounds the role of the "mirror neuron system" in action understanding: do MNs allow us to comprehend others' actions by allowing us to internally represent their behaviors or do they simply activate a direct motor representation of the perceived act without recourse to its meaning? This review outlines evidence from both human and primate literatures, indicating the importance of end-goals in action representations within the motor system and their predominance in influencing action plans. We integrate this evidence with recent views regarding the complex and dynamic nature of the mirror neuron system and its ability to respond to broad motor outcomes.

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1. Introduction

Everyday social interactions require constant and accurate interpretations of others' behavior. It has been proposed that action comprehension is subserved by our ability to internally represent the actions of others within our own motor system. At the basis of this notion are frontoparietal cells collectively known as "mirror neurons" (MNs), which respond to both

action observation and execution (Gallese et al., 1996; Kohler et al., 2002; Rizzolatti et al., 1996; Umilta et al., 2001). The "mirror mechanism," as it has come to be known, decodes others' actions by transforming sensory information into a motor format similar to that required when observers perform the observed action themselves (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). By encoding the meaning or goal of an action, the mirror mechanism allows observers to bypass higher-order cognitive processes such as teleological reasoning and comprehend "from the inside" what other individuals are doing. An alternative view has recently been put forth by Hickok and Hauser (2010), who suggest that mirror neurons are simply "sensorimotor" cells whose primary role is response selection. That is, MNs map visual information directly onto corresponding motor representations, priming an observer to perform imitative responses. The main contention behind this view is that action-understanding accounts of mirror system function rely on evidence that non-human primates (in whom MNs were originally found) do not imitate. Given recent developments revealing that non-human primates are indeed capable of performing "mirror actions," Hickok and Hauser (2010) recommend an abandonment of the action understanding mirror system hypothesis.

However, based on evidence from both human and non-human primates, we believe that this view overlooks the nature of action organization within the motor system. A purely sensorimotor account is incompatible with how our own and others' actions are represented: according to the goal or meaning behind the motor act. Indeed, the notion that the mirror mechanism responds passively to observed actions by automatically preparing imitative reactions is largely unsupported by the literature. Within just over a decade, our knowledge of the function of MNs has altered: we are aware of the complexity and of the primacy of goals. We have also needed to modify original formulations, given recent evidence that MNs are indeed responsive to tools (e.g., Ferrari et al., 2005). Collectively, this indicates that imitatory accounts are not tenable. It also means that purely sensory accounts miss the broader context of meaning, goals, and interactions between agents in action observation.

In this review, we suggest that the complex nature of action organization within the motor system supports action understanding accounts of the mirror mechanism. Because our own actions are organized in terms of complex motor outcomes rather than simple physical properties, we can form interpretations of other's behaviors without the need to resort to mentalizing processes. To this end, we first outline the nature of action organization in the primate motor system. Then, we explore theories of action representations in humans, focusing on the role of motor mechanisms in intention understanding.

2. Evidence from non-human primates of goal-specificity in action organization

Prior to the discovery of mirror neurons, Rizzolatti et al. (1988) studied the functional properties of inferior area 6 (also referred to as premotor area F5) neurons in behaving macaque monkeys as they programmed reach-to-grasp actions. These neurons were dynamic in that they responded not only during the performance of a given action, such as a precision grip, but also to the observation of an object affording a similar grip-type (i.e., a small object). Furthermore, neurons in F5 responded specifically to the goal of an action. For example, some grasping neurons activated when the monkey flexed its fingers to grasp an object but not when the same flexion was made to push it away. Thus, our own actions are controlled by neurons that activate specifically to simple goals rather than kinematic parameters (Rizzolatti et al., 1988). This undermines the proposal that a subset of these very motor cells would discharge to observed actions only for the purpose of activating a direct motor representation (i.e., imitation) of those acts.

The first accounts of "mirror neurons" described a subset of F5 cells that fired not only when the monkey performed an action but also when it observed the experimenter perform a similar action (di Pellegrino et al., 1992). Some mirror neurons were characterized by a strict correspondence between the observed and executed actions for which they code. For example, a neuron which codes for the execution of a precision grip will only activate to the observation of a precision grip. Other F5 neurons, however, were found to be "broader" in nature. For example, observing the placement of an object on a table activated an F5 neuron coding for both bringing food to the mouth and grasping for an object. di Pellegrino et al. (1992) therefore concluded that the role of mirror neurons may be to retrieve actions in response to the meaning behind others' gestures. If MNs discharge to various motor acts that are semantically related to one concept, such as receiving food, then it is likely that these cells play a crucial role in action understanding.

Mirror neurons have two important characteristics, therefore. First, they are activated by the goal of an observed action regardless of how it is achieved. Second, they show selectivity for different motor outcomes. So, the same set of MNs will discharge when the monkey observes an immediate action (e.g., to reach-for-and grasp) performed with variable movement parameters (power or precision grips) (Gallese et al., 1996). The action's representation is broad and flexible enough to encapsulate all means of realizing the same motor outcome. This concept is crucial to an understanding-based account of MN functioning. For example, Bonini et al. (2010) recently recorded from neurons in F5 and inferior parietal cortex (PFG) as monkeys observed an experimenter perform reach-to-grasp actions. These actions were embedded in different motor outcomes (e.g., grasp-to-eat versus grasp-to-place). Neurons with mirror properties were equally responsive to the end-goal of the motor act (i.e., eat/place), irrespective of the type of grasp used to achieve it. Furthermore, most MNs were selective for the same grasping act (e.g., precision grip), only when aimed at achieving a specific end-goal. For example, they discharged to a precision grip used to grasp for and eat a piece of food, but they did not discharge when the same precision grip was used to grasp the food and place it elsewhere. Although some neurons activated equally during grasping for both actions, this evidence strongly supports the view that MNs encode an action's meaning to a greater extent than its specific motor characteristics and are thus likely to be involved in action understanding.

Single-cell recordings by Caggiano et al. (2009) also show that, while some MNs respond to actions regardless of their