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Responses of the human motor system to observing actions across species: A transcranial magnetic stimulation study

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ABSTRACT

Ample evidence suggests that the role of the mirror neuron system (MNS) in monkeys is to represent the meaning of actions. The MNS becomes active in monkeys during execution, observation, and auditory experience of meaningful, object-oriented actions, suggesting that these cells represent the same action based on a variety of cues. The present study sought to determine whether the human motor system, part of the putative human MNS, similarly represents and reflects the meaning of actions rather than simply the mechanics of the actions. To this end, transcranial magnetic stimulation (TMS) of primary motor cortex was used to generate motor-evoked potentials (MEPs) from muscles involved in grasping while participants viewed object-oriented grasping actions performed by either a human, an elephant, a rat, or a body-less robotic arm. The analysis of MEP amplitudes suggested that activity in primary motor cortex during action observation was greatest during observation of the grasping actions of the rat and elephant, and smallest for the human and robotic arm. Based on these data, we conclude that the human action observation system can represent actions executed by non-human animals and shows sensitivity to species-specific differences in action mechanics.

1. Introduction

Over the past twenty years, a wealth of research has provided evidence for the involvement of a specific network of brain structures, referred to collectively as the mirror neuron system (MNS), in recognizing the actions of other individuals. Mirror neurons, first discovered in the brains of non-human primates, are cells in the premotor and posterior parietal cortices that become active during both the execution and observation of specific actions (see Rizzolatti & Craighero, 2004 for review). In the human brain, a similar system is purported to be activated during the observation and execution of actions. Although there is mounting evidence that the putative human MNS is sensitive to an action's end goal, the extent to which MNS responses to goal-directed action rely on the biomechanics and anatomy of the specific effectors involved in action execution has yet to be determined. That is, many goals can be achieved with different effectors. For example, a person may be capable of picking up small objects with their feet as well as their hands. While studies of non-human primates suggest the MNS is important in representing the *meaning* (e.g., di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) or *effect* (Umilta et al., 2001) of a given action, it is unclear whether such representations are reliant on the particular effectors involved in action execution.

There is currently some evidence to suggest that higher-order goals and the context-dependent nature of certain actions can be discerned during the observation of actions with different effectors. For example, Gergely, Bekkering, and Király (2002) have shown that preverbal infants can intuit goals from actions performed with different effectors, even when the effector used to execute an action is unusual. In these examples, the same goal is achieved—lifting an object or turning on a light—but the effector used to achieve the goal is different (e.g., turning on a light with the hand or the head). Preliminary evidence for effector-independent activation of brain regions involved in action observation is also provided by Sartori, Begliomini, and Castiello (2013). The authors used transcranial magnetic stimulation (TMS) to assess activity in the corticospinal tract related to covert motor imitation of observed actions (termed "motor resonance") in right- and left-handed participants observing a grasping action performed with either the right or left hand. The results showed that observers exhibited motor resonance in their dominant hand regardless of

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the hand with which the action was performed. Such findings indicate that motor resonance may not be a form of direct perceptual-motor matching, but a more complex encoding of the observed movement, involving spatial transformations of the observed action to match the observer's dominant hand. Although Sartori et al. (2013) demonstrated the possibility that the human action observation (i.e., MNS) system may respond during action observation independent from the effector used to execute a particular action, the authors were interested specifically in the effects of handedness, and used only stimuli involving hands as effectors. Further, the nature of higher-level goal representation was not explored. It is thus far unknown whether the human MNS, which becomes active during the observation hand actions, also becomes active when a different effector is used to execute a task with the same outcome goal.

To push this notion of the relationship between goal- and effector-dependency further, it is as of yet unclear how humans recognize, code, and interpret the meaning of other animals' actions when they are executed by effectors humans do not possess. There are many actions that can be performed similarly by both humans and non-human animals. Grasping actions are one such example; non-human animals may execute grasping actions by use of effectors similar to human hands (e.g., the paw of a monkey, raccoon, or rat), or by use of species-specific effectors (e.g., the tail of a monkey or the trunk of an elephant). Regardless of the effector used for action execution, humans are often able to understand the intended goals of non-human actions (Pinto & Shiffrar, 2009; see also Welsh, McDougall, & Paulson, 2014), but it is presently unclear whether the putative human MNS represents the goals of these actions rather than simply their (bio)mechanics. The present study examined the effector- and species-specific nature of action representations by investigating changes in corticospinal excitation in humans during observation of similar goal-oriented actions across species. Because primary motor cortex may be a component of the putative humans MNS (or at minimum reflect the activity of the human MNS, e.g., Rizzolatti & Craighero, 2004; see also Molenberghs, Cunnington, & Mattingley, 2012 for meta-analysis of fMRI data), this exploration of corticospinal activity will shed new light on the coding of action kinematics and action goals during action observation. Prior to outlining the specifics of the present investigation, a brief review of the relevant literature on human and monkey MNS will be provided.

1.1. Coding of goals and effectors in non-human primate MNS

Mirror neurons were first characterized via single-cell recording studies in the monkey brain. Di Pellegrino et al. (1992) first reported that area F5 in the monkey inferior premotor cortex contains cells that became active when the monkey executed a grasping action, and when the monkey observed an experimenter performing the same action. Gallese et al. (1996) subsequently showed that mirror neurons are activated by meaningful actions only. The authors showed monkeys videos of a human performing a hand or mouth action, either on a specific object (e.g., a piece of food) or as a pantomime (non-object-oriented actions). Activity in mirror neurons only increased when the monkey observed a meaningful interaction between the agent and the object; the cells did not become active at the sight of the agent pantomiming or of the object alone. Importantly, a subset of mirror neurons was equally active for hand and mouth movements when the goal of the actions was the same (e.g., to eat). These findings suggest that mirror neurons may be important for representing the meaning of actions based on the agent's intentions, and their activity does not depend on a specific pattern of visual input.

Umilta et al. (2001) provided further evidence for the representation of meaning and/or intentions in mirror neurons by showing that some mirror neurons in the monkey brain become equally active during observation of object-oriented grasping actions, even when the end phase of the action (i.e., the actual grasping of an object) is occluded from view. In other words, when the monkey knew an object was present but hidden from direct view by a screen, mirror neurons became active during grasp observation, even when the grasping of the object had to be inferred. When no object was present, mirror neurons did not respond to grasping actions whether in full view or not. Kohler et al. (2002) further showed that some mirror neurons respond to multimodal action cues and do not require visual input at all. The authors found a population of mirror neurons in monkey premotor cortex that were equally responsive when the monkey executed a specific action and when the monkey heard the sound associated with the same action (e.g., ripping a piece of paper). Many of these neurons were also activated when the monkey observed an experimenter performing the same action. Together, these findings provide compelling support that at least some mirror neurons respond to multimodal cues signaling a specific action and thus seem to represent an action's meaning. Studies of the monkey MNS also provide initial evidence for cross-species action representation, as in most research to date, stimuli have comprised human actors.

1.2. The coding of action goals in the human action observation system

Due to the limitations in implementing single-cell recordings in human subjects, research to date on the existence and functional role of the MNS in humans is less conclusive (e.g., Turella, Pierno, Tubaldi, & Castiello, 2009). Nonetheless there is mounting evidence in favor of a system of brain areas whose collective function is largely homologous to that of monkey MNS (see Rizzolatti & Craighero, 2004 for review). The most compelling evidence to date is provided by Mukamel et al. (2010), who recorded extracellular activity in the brains of patients with intractable epilepsy. The authors found that a significant proportion of the 1177 cells observed demonstrated mirror properties, as indexed by modulation of the cells' firing rate during both action-observation and action-execution.

Of particular relevance to the present study, evidence for the goal-directed nature of the coding in the human action observation system has been garnered from studies in which TMS was used to assess the modulation of the corticospinal tract during the observation of actions. Irrespective of whether or not primary motor cortex is part of the putative human MNS, it seems that the modulation of the activity in the corticospinal tract reflects the coding of observed actions in the central nervous system of the observer. Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) were the first to report that the human primary motor cortex is similarly active during execution and observation of actions. Specifically, they found that motor-evoked potentials (MEPs) in hand muscles were facilitated while subjects either performed or observed grasping actions (compared to a non-motor perceptual task), indicating sub-threshold activation of the motor cortex in both cases. These changes in the corticospinal excitability during action observation are thought to occur because either primary motor cortex is part of the putative human MNS, or because the coding of the response in this action observation system affects the excitability of primary motor cortex.

Regardless of the origins of these changes in corticospinal excitability, it is important to note that there are similarities between the conditions under which these modulations of corticospinal excitability occur in the human primary motor cortex and monkey mirror neurons. For example, Villiger, Chandrasekharan, and Welsh (2011) recently reported that the MEP amplitudes were modulated during the observation of a grasping action on an object both when