Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Object visibility alters the relative contribution of ventral visual stream and mirror neuron system to goal anticipation during action observation

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ARTICLE INFO

Article history: Accepted 13 October 2014 Available online 25 October 2014

Keywords: Action perception Dynamic causal modeling Embodied cognition fMRI Forward models Repetition suppression

ABSTRACT

We used fMRI to study the effect of hiding the target of a grasping action on the cerebral activity of an observer whose task was to anticipate the size of the object being grasped. Activity in the putative mirror neuron system (pMNS) was higher when the target was concealed from the view of the observer and anticipating the size of the object being grasped requested paying attention to the hand kinematics. In contrast, activity in ventral visual areas outside the pMNS increased when the target was fully visible, and the performance improved in this condition. A repetition suppression analysis demonstrated that in full view, the size of the object being grasped by the actor was encoded in the ventral visual stream. Dynamic causal modeling showed that monitoring a grasping action increased the coupling between the parietal and ventral premotor nodes of the pMNS. The modulation of the functional connectivity between these nodes was correlated with the subject's capability to detect the size of hidden objects. In full view, synaptic activity increased within the ventral visual stream, and the connectivity with the pMNS was diminished. The re-enactment of observed actions in the pMNS is crucial when interpreting others' actions requires paying attention to the body kinematics. However, when the context permits, visual-spatial information processing may complement pMNS computations for improved action anticipation accuracy.

Introduction

Mirror neurons in the ventral premotor cortex and inferior parietal lobe of the monkey fire when it performs an action, and when it sees or hears similar actions performed by others (di Pellegrino et al., 1992; Fogassi et al., 2005; Fujii et al., 2008; Gallese et al., 1996; Keysers et al., 2003; Kohler et al., 2002; Kraskov et al., 2009; Rozzi et al., 2008; Umiltà et al., 2001). In humans, the presence of cells with mirroring properties has been confirmed with intra-cranial recording (Mukamel et al., 2010). The existence of a human mirror neuron system is further supported by the finding that the increases in BOLD signal recorded during action observation and execution overlap in a variety of brain regions, including in particular the ventral premotor cortex (areas BA6 and BA44), and several parietal regions along the postcentral and intraparietal sulci (areas BA2, PF/PFt, hIP1-3, BA7) (Gazzola and Keysers, 2009; Iacoboni et al., 1999; Shmuelof and Zohary, 2006). Moreover, it was found that the neuronal activity in these parietal and premotor regions is attenuated when observing an action that was recently executed relative to one that was not (Chong et al., 2008; Kilner et al., 2009), which suggests that the same neuronal ensembles are

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recruited during both action observation and execution (but see Lingnau et al., 2009). Collectively, these regions have thus been termed the putative mirror neuron system (pMNS), where putative refers to the fact that, in humans, mirror neurons have not been recorded from all of these regions (Keysers, 2009). The mirror neuron discovery has offered a biological explanation for many findings suggesting that action perception and execution share a common coding system (Hommel et al., 2001), like for instance the fact that action execution is perturbed by the simultaneous perception of an incongruent movement (Kilner et al., 2003).

The functional role of parietal and premotor activations during action perception is however still hotly debated (Dinstein et al., 2008; Goodale, 2005; Hickok, 2009; Keysers, 2009; Mahon and Caramazza, 2005; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2008; Turella et al., 2009a), and very little is known about the exchanges of information between the pMNS and other brain regions contributing to action perception, like the extrastriate body area and the posterior superior temporal sulcus involved in the perception of body shape and biological motion (Beauchamp et al., 2002, 2003; Bonda et al., 1996; Downing et al., 2001, 2006; Grossman and Blake, 2002; Grossman et al., 2000; Jastorff and Orban, 2009; Peelen et al., 2006; Pelphrey et al., 2003), or other visual areas carrying information about the environment in which the action is taking place. The notion that the reactivation of parietal and premotor cortices necessary for action execution contributes to the perception of some aspects of the actions of







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others is supported by studies showing impairments in action perception following neurological conditions that affect regions of the pMNS (Fazio et al., 2009; Kalénine et al., 2010; Pazzaglia et al., 2008a, 2008b). It is also supported by the results of a transcranial magnetic stimulation study in which participants had to judge the weight of a box lifted by an actor (Pobric and Hamilton, 2006). Virtual lesions to the vPM impaired weight estimation in this condition but did not influence the participants' capacity to estimate the weight of a bouncing ball, suggesting that the pMNS participate to perception most, when the source of information is the kinematics of a human body. This notion is consistent with recent findings showing that humans can successfully derive the intentions of others from an analysis of their arm movement, even if only the initial part of the action is shown (Becchio et al., 2012; Sartori et al., 2011). Undoubtedly however, the pMNS is not the only process contributing to action perception, and a great deal of it can be accomplished satisfactorily without re-enacting other's actions within the pMNS. As a matter of fact, patients with apraxia show severe problems in motor planning (Rumiati et al., 2001) or motor execution (Rapcsak et al., 1995), but although some apraxic patients show deficits in the perception of the actions of others (Pazzaglia et al., 2008a, 2008b) others do not (Rapcsak et al., 1995; Rumiati et al., 2001; for a review Mahon and Caramazza, 2005). Furthermore, the reverse dissociation has been documented as well, with patients being able to execute the actions that they could not recognize when seeing them done by someone else (Cubelli et al., 2000; Rothi et al., 1986). In the tasks used with these neurological patients, action perception is typically measured by requiring the patients to arrange sets of pictures depicting everyday actions (like preparing tea) in the correct sequence, to discriminate between correctly and incorrectly executed actions, or to view an action and choose the word that best describes the action (e.g. hammering) or the image of the tool most associated with the action (e.g. a hammer). In the light of these findings, the most balanced account of the existing literature is that the pMNS provides just a part of the information that constitutes the multifaceted perception of others' actions. The challenge is therefore to determine (i) to what facets of perception the pMNS contribute to, (ii) how that compares to the contribution of other regions, and (iii) how these regions communicate with each other to solve particular tasks. Accordingly, here we explore the hypothesis, fuelled by the general properties of the regions composing the pMNS (Keysers, 2011) and the abovementioned TMS and lesion studies (Fazio et al., 2009; Kalénine et al., 2010; Pazzaglia et al., 2008a, 2008b; Pobric and Hamilton, 2006; Rapcsak et al., 1995; Rumiati et al., 2001), that pMNS computations are most important when the kinematics of the human agent are the only source of information to determine the goal of the action. In contrast, pMNS computations become less important when other, non-biological cues are also informative.

To test this hypothesis, we harness the observation that in monkeys passively watching reach-to-grasp actions, about half of the mirror neurons also respond to the sight of reaching to grasp when the final part of the action, the grasp itself, is concealed from view (Kraskov et al., 2009; Umiltà et al., 2001). This opens the possibility to show only the first part of a reach-to-grasp action and yet preserve activations in at least some mirror neurons. We can then test the effect of hiding the target object on the parietal and pre-motor activations of participants requested to anticipate the size of the object being grasped by the actor. Specifically, we asked participants to watch blocks of 6 videos of an actor reaching to grasp one of two balls and to report how often the actor reached for the larger ball (Fig. 1A). In one condition, the two balls were visible in each movie (Full-View), in the other they were both concealed inside a box (Occlusion, Fig. 1B). In both cases, the movies were stopped 120-200 ms before the hand contacted the object (Fig. 1B, rightmost frame of each movie), and this is in order to keep the visual information regarding the kinematics of the actor similar across conditions, while manipulating how much non-kinematic information was present: only in the Full-View condition, analyzing the shape of the ball closest to the





Fig. 1. Experimental design and movie stimuli. (A) Design of an observation block including a warning sign, an instruction screen, a 12-s movie composed of 6 videos, a response screen with 2 possible answers, and a resting period. There were 12 such blocks per observation session, and 3 consecutive sessions for a total number of 72 volumes per condition (1 volume per TR = 2.0 s). (B) Illustration of the movie stimuli. The 6 videos composing a movie were of variable length (between 0.8 and 2.9 s). The length of the 6 videos was pairmatched across the 3 conditions for every actor. In the Full-View and the Occlusion conditions, the videos stopped 3–5 frames (120–200 ms) before the hand touched the ball. The outcome of the action had therefore to be anticipated in both conditions, and the main difference was whether the target of the grasping action was visible or not.

hand would help solve the task. To explore the effect of attending to a grasping action on connectivity, we included a visual control condition in which an object was sometimes touched but no grasping ever occurred. To constrain whether brain activations could be considered as belonging to the pMNS, we also included an action execution condition in which participants had to grasp balls in the scanner to approximate the actions of the actor. Hence, if our hypothesis is true and pMNS computations are most important when the only available information to interpret the action is in the body kinematics, pMNS activations should be stronger in the Occlusion than the Full-View condition, since in this condition there is no other source of information available to infer what ball is being grasped by the actor. In contrast, activity in brain regions of the ventral temporal cortex involved in processing object shape should be stronger in the Full-View condition and the performance should improve in this condition, if the participants actually take advantage of the additional information provided by the sight of the target object on the table.

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