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Research report

Motor facilitation during action observation: The role of M1 and PMv in grasp predictions

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ABSTRACT

Recent theories propose that movement observation is not a “passive mirror” of ongoing actions but might induce anticipatory activity when predictable movements are observed, e.g., because the action goal is known. Here we investigate this mechanism in a series of 3 experiments, by applying transcranial magnetic stimulation (TMS) to primary motor cortex (M1) while subjects observed either whole hand or precision grasping performed by an actor. We show that corticomotor excitability changes in a grip-specific manner but only once the grip can be decoded based on the observed kinematic cues (Exp. 1). By contrast, presenting informative contextual precues evokes anticipatory modulations in M1 already during the reach phase, i.e., well before the grip type could be observed, a finding in line with a predictive coding account (Exp. 2). Finally, we used paired-pulse (PP) TMS to show that ventral premotor cortex (PMv) facilitates grip-specific representations in M1 but only while grip formation is observed. These findings suggest that PMv and M1 interact temporarily and mainly when motor aspects of hand-object interactions are extracted from visual information. By contrast, no sustained input from PMv to M1 seems to be required to maintain action representations that are anticipated based on contextual information or once the grip is formed (Exp. 3).

1. Introduction

Movement observation activates the observer's motor cortex, a phenomenon mediated by so called ‘mirror neurons’. Mirror neurons were first discovered in the ventral premotor cortex (PMv) (area F5) of the macaque monkey and were shown to fire while the monkey executes a specific action, but also when the monkey merely observes the same action performed by others (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti,

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Abbreviations: WHG, whole hand grip; PG, precision grip; TMS, transcranial magnetic stimulation; M1, primary motor cortex; PMv, ventral premotor cortex; SMA, supplementary motor area; IPC, inferior parietal cortex; AIP, anterior intraparietal area.

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1992; Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Using a variety of neuroimaging and neurophysiological techniques, a similar 'mirror mechanism' has been demonstrated in the human brain, which includes, in addition to PMv, also the dorsal premotor cortex (PMd), supplementary motor area (SMA), primary motor cortex (M1) and the inferior parietal cortex (IPC) (Calmels et al., 2006; Fadiga et al., 1995; Hamzei et al., 2003; Hari et al., 1998; Kilner & Lemon, 2013; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Molenberghs, Cunnington, & Mattingley, 2012). In the past, studies using single-pulse transcranial magnetic stimulation (TMS) to measure changes in corticomotor excitability in M1 during movement observation have consistently demonstrated that observation-induced changes in excitability are highly specific to the actual muscles involved in the observed movement and occur time-locked to the observed kinematics while the movement unfolds (Alaerts, de Beukelaar, Swinnen, & Wenderoth, 2012; Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Alaerts, Swinnen, & Wenderoth, 2009; Fadiga et al., 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001; Koch et al., 2010). While most neurophysiological studies focused on M1, several lines of research have shown that PMv is a core area, upstream from M1, for mediating visual-to-motor transformations during both action execution and observation (e.g., Davare, Andres, Cosnard, Thonnard, & Olivier, 2006; Davare, Lemon, & Olivier, 2008; Davare, Rothwell, & Lemon, 2010; Lago et al., 2010). Both in primates and humans, PMv-M1 interactions are modulated during movement execution and action preparation, which is indicative of a strong influence from PMv over M1 during these processes (Binkofski et al., 1999; Davare et al., 2006, 2008, Davare, Montague, Olivier, Rothwell, & Lemon, 2009, Davare et al., 2010; Grèzes, Armony, Rowe, & Passingham, 2003; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Murata et al., 1997; Raos, Umilta, Murata, Fogassi, & Gallese, 2006; Umilta, Brochier, Spinks, & Lemon, 2007).

Human PMv-M1 interaction can be probed using paired-pulse (PP) TMS such that a sub-threshold conditioning stimulus (CS) is applied over PMv that is shortly followed by a supra-threshold test stimulus (TS) applied over M1. This PP paradigm measures effective connectivity, i.e., the influence that one neural system exerts over another (Friston, 2011). It probes changes in M1 excitability that originate from the modified input from PMv and therefore provide insights into the activation of these cortico-cortical pathways (Koch & Rothwell, 2009; Lago et al., 2010). Using this PP TMS technique, Davare et al., (2008, 2010) tested PMv-M1 connectivity and showed that PMv specifically facilitates M1 in a muscle-specific fashion during the preparation and execution of grasping movements but not during rest.

Similar PMv-M1 interactions have been demonstrated during action observation. Particularly, disrupting PMv activity by repetitive TMS (rTMS) was shown to abolish the typical observation-induced increase in M1 corticomotor excitability (Avenanti, Bolognini, Maravita, & Aglioti, 2007). Also PP TMS paradigms have demonstrated modulations in PMv-M1 connectivity during action observation. For example, a study by Lago et al. (2010) showed that the M1 excitability increases in parallel with PMv-M1 connectivity when observing a naturalistic grasping movement (e.g., human hand grasping a ball). Observing a noxious grasping movement (e.g., grasping a hot soldering iron) on the other hand, triggered a decrease in the strength of the PMv-M1 connectivity. Similarly, Koch et al. (2010) showed that PMv-M1 connectivity is specifically modulated when 'successful' goal directed reach-to-grasp actions are observed (i.e., actions in which the observed grasping posture is congruent with the goal of the action). No such change in PMv-M1 connectivity was shown for observing 'unsuccessful' actions, (i.e., actions in which the observed grasping posture is incongruent with the goal of the action).

Movement observation is not simply a passive perceptual process. Rather it fits within a predictive coding framework (Kilner, Friston, & Frith, 2007), suggesting that observed actions are encoded at different levels: the intention level, the goal level, the kinematic level and the muscle level. Therefore, in order to fully 'understand' or make a prediction about an observed action, information at these different levels needs to be compared and combined in order to minimize potential prediction errors. For example, if at the highest level, a prediction about the *intention* of a perceived action is formed, this information will be used to create a prediction at the *kinematic* level which will be compared to the actual kinematics once the observed action starts to unfold. This comparison will result in a prediction error which in turn will be used to revise and improve the proposed intention. By repeating this process at different levels of the cortical hierarchy, predictions about observed actions can be optimized.

In summary, it has been shown that goal-encoding of the to-be-performed action during movement execution occurs prior to actual movement initiation, as reflected in M1 excitability changes during movement preparation. Moreover, it has been shown that PMv facilitates M1 in a muscle-specific fashion while preparing and executing grasping movements (Davare et al., 2008, 2010). Here we investigated whether similar anticipatory motor activity can be demonstrated during mere movement observation, and whether this phenomenon is modulated by input from PMv. Exploring the dynamic interplay between PMv and M1 will further our understanding of how contextual cues versus observed kinematics influence muscle-specific encoding in the motor system.

To explore these processes, we performed a series of three experiments measuring corticomotor excitability of the index finger (first dorsal interosseous, FDI) and the little finger (abductor digiti minimi, ADM) during the observation of two types of grasping actions; a precision and a whole hand grip (WHG).

In the first experiment, we show that excitability changes in M1 are highly specific to the type of grasping action observed, allowing to decode whether a whole hand or precision grip (PG) is seen.

In the second experiment, we show that informative 'pre-cues' that are available prior to movement initiation and that provide information on the type of the upcoming grasp are sufficient to modulate M1 excitability in a way consistent with predictive coding of the upcoming movement, i.e., a grip-specific facilitation pattern is already present in M1 *before* actual grip-specific kinematic information is observed.

Finally, in the third experiment, PP TMS is used to test PMv-M1 interactions during anticipatory and online movement