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Research report

Grasp-specific motor resonance is influenced by the visibility of the observed actor

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ABSTRACT

Motor resonance is the modulation of M1 corticospinal excitability induced by observation of others' actions. Recent brain imaging studies have revealed that viewing videos of grasping actions led to a differential activation of the ventral premotor cortex depending on whether the entire person is viewed versus only their disembodied hand. Here we used transcranial magnetic stimulation (TMS) to examine motor evoked potentials (MEPs) in the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) during observation of videos or static images in which a whole person or merely the hand was seen reaching and grasping a peanut (precision grip) or an apple (whole hand grasp). Participants were presented with six visual conditions in which visual stimuli (video *vs* static image), view (whole person *vs* hand) and grasp (precision grip *vs* whole hand grasp) were varied in a $2 \times 2 \times 2$ factorial design. Observing videos, but not static images, of a hand grasping different objects resulted in a grasp-specific interaction, such that FDI and ADM MEPs were differentially modulated depending on the type of grasp being observed (precision grip *vs* whole hand grasp). This interaction was present when observing the hand acting, but not when observing the whole person acting. Additional experiments revealed that these results were unlikely to be due to the relative size of the hand being observed. Our results suggest that observation of videos rather than static images is critical for motor resonance. Importantly, observing the whole person performing the action abolished the grasp-specific effect, which could be due to a variety of PMv inputs converging on M1.

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1. Introduction

When reaching to grasp an object, we have an exquisite ability to precisely shape our hand according to the object's three-dimensional structure. Such skilled hand movements require the brain to perform a complex transformation of the object's visual properties into a grasp-specific motor command acting on the hand muscles. Several lines of evidence implicate a cortical grasping circuit in this visuomotor transformation, including the anterior intraparietal area (AIP), ventral premotor cortex (PMv) and primary motor cortex (M1) (Davare, Kraskov, Rothwell, & Lemon, 2011; Davare, Rothwell, & Lemon, 2010; Janssen & Scherberger, 2015; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Nelissen & Vanduffel, 2011). Typically, when the object geometry requires either a precision grip (PG) or whole hand grasp (WHG), the excitability of cortical muscle representations increases in a grasp-specific fashion. This was first unveiled by probing excitability changes during grasping preparation and execution in intracortical circuits (late I-wave pathways) within M1 (Cattaneo et al., 2005), which probably reflected cortico–cortical interactions between PMv and M1 (Davare, Lemon, & Olivier, 2008; Davare, Montague, Olivier, Rothwell, & Lemon, 2009).

Selective activation of the motor system is not only critical for performing actions, but can also be detected when the individual passively looks at an action being performed by another. Indeed, action observation modulates motor evoked potentials (MEPs), elicited by transcranial magnetic stimulation (TMS) of M1, in muscles that human observers recruit during the actual performance of the same action (Alaerts, Senot, et al., 2010; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Mc Cabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2015; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006), a phenomenon known as motor resonance. This resonance has been proposed to result from the human mirror system, supposed to include homologues of areas F5 and AIP, housing mirror neurons in monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Maeda, Ishida, Nakajima, Inase, & Murata, 2015; Nelissen et al., 2011; Pani, Theys, Romero, & Janssen, 2014).

Since no direct recording has so far been obtained from these regions in humans for technical reasons (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010), the similarity between motor resonance and excitability changes in M1 during action preparation and execution have been cited as evidence in favour of the existence of mirror neurons in humans (Fadiga et al., 1995). While a number of reports have suggested similar changes in M1 excitability during both action observation and execution (Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Fadiga, Craighero, & Olivier, 2005; Senot et al., 2011), to date, only muscle-specific resonance has been reported (Catmur, Walsh, & Heyes, 2007; Cavallo, Becchio, Sartori, Bucchioni, & Castiello, 2012; Mc Cabe et al., 2015; Strafella & Paus, 2000; Urgesi et al., 2006).

Since motor resonance supposedly depends on premotor inputs to M1, an additional condition to be met by motor resonance is to reflect the properties of these inputs. It has been shown that static images of an action, because they may imply motion, increase M1 excitability (Urgesi et al., 2006). Yet, recently a study showed that the human homologues of F5 subsectors respond more to action videos than static images, even those taken close to the moment of contact (Ferri et al., 2015). Hence, one can predict that motor resonance should not only be grasp-specific but this pattern should be clearer for action videos rather than static frames taken from the video. Finally, the latter study (Ferri et al., 2015) has also shown that different parts of PMv [i.e., putative human area F5a (phF5a), phF5p and phF5c] react differentially to action videos depending on the visibility of the actor being observed. That is, phF5c was active when the actor was fully visible to the observer but not when only the hand was visible, leaving the other subsectors of PMv to transmit visuomotor information about the latter (hand only) condition. Hence, by manipulating visibility of the observer, we can effectively activate or deactivate the output of phF5c in order to test how phF5c contributes to motor resonance. Therefore, we manipulated four factors (3 visual and 1 muscle) in the first TMS experiment: muscle [first dorsal interosseous (FDI) and abductor digiti minimi (ADM)] and grasp (precision grip and whole hand grasp) to document the grasp specificity, type of visual stimulus (video *vs* static image) and view (with whole actor visible *vs* hand alone). We hypothesised that, similar to action execution, FDI MEPs would show greater modulation during observation of precision grip compared to ADM and ADM MEPs would show greater modulation during observation of whole hand grasp compared to precision grip. In addition we expected that if inputs to M1 from phF5c affect motor resonance, greater changes would be seen when observing an actor performing grasping actions compared with observation of the hand alone. Alternatively, if observation of the hand alone results in significant changes in motor resonance, inputs from other sub-regions of PMv might be more important. Observing a whole person in an image of equal size to that of the hand alone images and videos would invariably result in the hand being smaller in the whole person visual stimuli, thus the relative size of the hand is an uncontrolled variable that could contribute to results in the above experiment. We therefore carried out a second experiment investigating whether hand size was important in grasp-specific motor resonance.

2. Methods

2.1. Subjects

Thirty-two healthy subjects participated in the present study (mean age: 26.5 ± 5.0 years; 19 females). Twenty subjects participated in Experiment 1 and 15 subjects participated in Experiment 2, 3 subjects participated in both experiments. Experiment 1 and 2 were performed several weeks apart, therefore reducing any possible carry-over effects in the latter 3 subjects. All subjects were right-handed (self-reported via screening questionnaire), with normal, or corrected to normal vision and gave informed consent. None of the subjects had a history of neurological disease. Potential risks of adverse reactions to TMS were evaluated by the TMS Adult Safety Screen questionnaire (Keel, Smith, & Wassermann, 2001). The

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