Cognition 149 (2016) 84-94

Contents lists available at ScienceDirect

Cognition

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

Stimulation over primary motor cortex during action observation impairs effector recognition

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ARTICLE INFO

Article history: Received 1 June 2015 Revised 5 January 2016 Accepted 13 January 2016 Available online 22 January 2016

Keywords: Mirror system Motor resonance Motor simulation TMS Memory Recognition Motor cortex

ABSTRACT

Recent work suggests that motor cortical processing during action observation plays a role in later recognition of the object involved in the action. Here, we investigated whether recognition of the effector making an action is also impaired when transcranial magnetic stimulation (TMS) - thought to interfere with normal cortical activity – is applied over the primary motor cortex (M1) during action observation. In two experiments, single-pulse TMS was delivered over the hand area of M1 while participants watched short clips of hand actions. Participants were then asked whether an image (experiment 1) or a video (experiment 2) of a hand presented later in the trial was the same or different to the hand in the preceding video. In Experiment 1, we found that participants' ability to recognise static images of hands was significantly impaired when TMS was delivered over M1 during action observation, compared to when no TMS was delivered, or when stimulation was applied over the vertex. Conversely, stimulation over M1 did not affect recognition of dot configurations, or recognition of hands that were previously presented as static images (rather than action movie clips) with no object. In Experiment 2, we found that effector recognition was impaired when stimulation was applied part way through (300 ms) and at the end (500 ms) of the action observation period, indicating that 200 ms of action-viewing following stimulation was not long enough to form a new representation that could be used for later recognition. The findings of both experiments suggest that interfering with cortical motor activity during action observation impairs subsequent recognition of the effector involved in the action, which complements previous findings of motor system involvement in object memory. This work provides some of the first evidence that motor processing during action observation is involved in forming representations of the effector that are useful beyond the action observation period.

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1. Introduction

As we move through the world, we encounter numerous actions performed by other people in a range of contexts. How we perceive, interpret, and respond to these actions characterises social interaction. In the last two decades, the role of the motor system in how we recognise and understand observed action has received a lot of attention. Theories of the motor system's role in these functions followed the discovery of 'mirror neurons': cells in the premotor cortex of the macaque brain that respond both to the observation and the execution of actions (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). There appears to be a similar system in humans, with activity in the human motor system showing some modulation when a movement is passively observed (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Most theories and empirical studies have focused on how this motor modulation during action observation (referred to hereafter as 'MMAO') contributes to the perception of actions in real time, and there has been very little work on what happens after an action is observed. In this study, we investigated whether MMAO has a function beyond the real-time processing of actions. Specifically, we asked whether interfering with motor cortical processing during action observation affects the offline recognition of the effector executing the observed action.

A recent study by Decloe and Obhi (2013) suggested a causal role of motor processing during action observation in object recognition. Transcranial magnetic stimulation (TMS) was used to briefly disrupt motor processing during a recognition memory task. On a subset of trials, a single pulse of TMS was delivered over the thumb representation of the primary motor cortex (M1) while participants viewed a movie clip showing a hand typing (with the thumb) on a mobile phone. Subsequently, participants were required to judge whether a photograph of a mobile phone showed the same or a different phone to the one they had viewed









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previously in the trial. Accuracy was lower when TMS was delivered over M1 during action observation, compared to when TMS was delivered over the vertex, or when no stimulation occurred.

A role of motor processing in object memory is also implied by the results of studies by Downing-Doucet and Guérard (2014) and Guérard and Lagacé (2014), in which participants were required to recall lists of objects. Guérard and Lagacé (2014) found that objects were better retained when the manipulability of the object was different to the manipulability of other items in the list. Importantly, a motor suppression task (moving the fingers in sequence) performed by participants during the experiment abolished this effect of manipulability isolation. In a similar study, Downing-Doucet and Guérard (2014) found that lists were better recalled when there was variation within the list in the type of grasp afforded by the objects, compared to when all of the list items afforded the same grasp. Again, this effect was abolished when participants performed a motor suppression task. The fact that motor suppression abolished the effect of varying manipulability suggests that the motor system was involved in encoding, retaining, or recalling the manipulable objects. These studies (see also Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004) suggest that the motor system plays a causal role in recognition memory for objects associated with action, but exactly what is represented or retained by the motor system is unclear. In Decloe and Obhi's (2013) study, for example, it is not clear whether viewing the hand typing on the cell phone evoked a representation of the phone alone (the formation or maintenance of which was disrupted by stimulation of M1), or alternatively whether the representation of the object was embedded within a representation of the action.

In the present paper we report two experiments conducted to further explore what aspects of an object-directed action are represented in M1 and retained beyond the action observation period. Specifically, we examined the effect of stimulation applied over motor cortex on subsequent recognition of the effector itself. If memory for objects relies on motor representations of the action associated with the object (rather than the object alone), then effector recognition should also be disrupted by TMS. Conversely, if the effects of stimulation over M1 (Decloe & Obhi, 2013) and object affordances (e.g., Guérard & Lagacé, 2014) are mediated by representations of the object alone, then recognition of the hand associated with the object should not be affected by TMS. In the experiments reported here, participants were required to judge whether a static image of a hand (Experiment 1) or video clip of a hand action (Experiment 2) showed the same or a different hand to that seen in a video clip presented previously in the trial. In Experiment 1, on a subset of trials, TMS was delivered over the hand area of M1 during the action observation period. Participants' recognition accuracy on these stimulation trials was compared to accuracy on trials on which no TMS was applied, and trials on which stimulation was delivered over the vertex. Experiment 1 also included two non-action recognition tasks - recognition of a still hand or of a dot configuration - to examine whether any effects were specific to stimulation delivered during action observation. It was predicted that, if MMAO plays a role in effector recognition (as it seems to in object recognition; Decloe & Obhi, 2013), then participants' recognition of the hand should be worse on trials in which stimulation was delivered over M1 than when no stimulation or stimulation over the vertex was delivered. If these effects are specific to recognition of an *acting effector*, then no impairment of recognition of still hands or dots should be found.

In Experiment 2, we made three adaptations to the design of Experiment 1, to clarify certain aspects of the effects of motor stimulation on effector recognition. First, as stimulation was delivered at action *offset* in Experiment 1, we examined whether further visual exposure to the action *after* M1 interference allows recognition to recover. To address this question, the action clips used in Experiment 2 were 500 ms in duration, and TMS was delivered at 300 or 500 ms on different trials. That is, stimulation time was no longer conflated with action offset. Second, we introduced a new control condition that showed the ball (from the action clips) being compressed, but without the presence of the hand. This condition was designed to be as visually similar as possible to the action stimuli with the exception of hand presence. A final difference between Experiments 1 and 2 was that the test stimulus used in Experiment 1 was a static photograph of the hand, whereas in Experiment 2 we used moving action video clips as the stimulus that participants had to judge as the same or different.

Crucially, as our experimental designs included both control tasks (dot configurations, still hand, moving shape) *and* a control TMS site (the vertex), we eliminate the possibility that recognition impairment was a result of cortical stimulation *per se* (i.e., not specific to M1) or that the stimulation affected processing of visual stimuli generally (rather than being specific to effector recognition in an action context).

2. Experiment 1

2.1. Method

2.1.1. Participants

This sample consisted of 16 participants (11 female, 5 male) between the ages of 18 and 21. All were right-handed by self-report, and had normal or corrected-to-normal vision. Participants were students at Wilfrid Laurier University, who took part in the study for partial course credit. Prior to participation, participants provided written informed consent, and were screened for con-traindications to TMS. Our screening questionnaire was based on the TMS adult safety screening questions proposed by Keel, Smith, and Wassermann (2001), with additional questions asking participants whether they experience claustrophobia, whether they had consumed alcohol in the previous 24 h, and whether they felt sleep deprived (as per the guidelines of Rossi, Hallett, Rossini, & Pascual-Leone, 2009). The study was approved by the local ethics committee, and conformed to the Declaration of Helsinki.

2.1.2. Design

The experiment used a 2×3 repeated-measures design, with the factors TMS site (M1, vertex) and stimulus type (action, still hand, dot configurations). The experimental session for each participant involved two blocks: one in which TMS was delivered over M1 and one in which it was delivered over the vertex. The order of these blocks was counterbalanced between participants. Each block contained a total of 240 trials, and TMS was delivered on 50% of these trials. For both TMS and non-TMS trials, all three types of stimuli were shown in equal numbers, such that participants saw a total of 80 action trials, 80 still hand trials, and 80 dot trials. Each individual trial showed two stimuli from the same category, with participants' task being to judge whether the second was the same or different to the first. Within every condition, half of trials were 'same' and half were 'different'. The order of trials within each block was randomised for each participant.

2.1.3. Apparatus and stimuli

The experiment was programmed using Superlab v.4.5 (Cedrus Corporation, San Pedro, CA, USA), and was run on a Dell desktop computer. Biphasic pulses of stimulation were delivered over either the hand region of M1 or the vertex (depending on the block) using a figure-of-eight coil attached to a Magstim Rapid² system. Electromyography (EMG) data was recorded using an MP150 data acquisition system (Biopac Systems). One ground

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