

Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions

Shannon Clark^a, François Tremblay^{b,*}, Diane Ste-Marie^a

^a School of Human Kinetics, Faculty of Health Sciences, University of Ottawa, Ottawa, Ont., Canada K1H 8M5

^b School of Rehabilitation Sciences, Faculty of Health Sciences, University of Ottawa, 451 Smyth Road, Ottawa, Ont., Canada K1H 8M5

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Abstract

In this study, we attempted to better delineate the changes in corticospinal excitability that accompany perceptual to motor transformations when people are asked to observe, image or imitate actions. Motor evoked potentials (MEP) from transcranial magnetic stimulation were recorded in the first dorsal interosseous (FDI) muscle of the dominant hand (15 right, 4 left) in five different conditions: (1) passive observation; (2) observation to imitate; (3) imagery; (4) imitation; and (5) counting backwards mentally. MEPs were also recorded at rest at the beginning and at the end of the session to establish baseline (BL) values. For the observation conditions, participants ($n = 19$, 18–38 years) watched video sequences (5 s) of hand actions performed by a model with the right arm (passive observation: scissors; observation to imitate: OK sign). Active imitation produced the greatest MEP facilitation compared to baseline, followed by the two observation conditions and the imagery conditions, which all produced similar levels of facilitation (post hoc comparisons). Mental counting produced some facilitation, but this effect was inconsistent. Baseline MEPs remained stable at the end of the session. A further comparison between right-handers ($n = 15$) and left-handers ($n = 4$) revealed no difference in the pattern of modulation across conditions. The similarity found between observation and imagery of hand actions in terms of corticospinal facilitation is interpreted in the light of the motor-simulation theory of Jeannerod [Neuroimage 14 (2001)], which proposes that perceiving actions involves neural simulation of the same action by the observer, thereby explaining the parallel between actions observed and actions imaged at the representational level.

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1. Introduction

Observing a model and mental imagery are commonly used methods to promote skill acquisition. Indeed, through observing demonstrations of skilled performances, one can derive cues that can be used subsequently to reproduce the intended action. Similarly, through mental rehearsal of previously learned actions, or parts of actions, one can prepare the sensorimotor apparatus for optimal performance in a subsequent execution. Such training strategies generally reflect traditional assumptions about the existence of links between the perceptual and motor systems. For instance, Meltzoff and Moore's (1977) active intermodal matching theory postulates that humans possess an innate capacity to imitate actions through a dedicated mechanism that transforms visual output of the model into motor output via supramodal representations. In another competing

theory, Heyes (2001) emphasizes the existence of a set of bi-directional excitatory links between sensory and motor representations that are formed largely from correlated experiences of observing and executing actions. Likewise, theories of motor imagery have been embedded within the same conceptual framework with regard to the transformation of perceived or learned actions into motor images and motor performance (Annett, 1996; Jeannerod & Frak, 1999).

From a neurobiological perspective, the perceptual–motor translation problem has been highlighted in recent years through brain imaging techniques (PET and fMRI) and electrophysiological methods. From converging evidence of neuroimaging studies in humans and neuronal recordings in non-humans primates, a picture has emerged indicating that the neural circuitry involved in action execution overlaps extensively with that activated when actions are imaged or observed (see Decety and Grèzes (1999); Grezes and Decety (2001) for recent reviews). The shared neural network includes the premotor cortex, supplementary motor area (SMA), the inferior parietal lobule, cingulated

* Corresponding author. Tel.: +1-613-562-5800; fax: +1-613-562-5428.
E-mail address: ftrembla@uottawa.ca (F. Tremblay).

gyrus, and the cerebellum (Decety & Grèzes, 1999). Activation of the primary motor cortex has also been reported during motor imagery tasks (Pfurtscheller & Neuper, 1997; Porro, Francescato, & Cettolo, 1996) and during action observation (Hari et al., 1998). Further evidence for the involvement of the primary motor cortex is derived from studies relying on the technique of transcranial magnetic stimulation (TMS). With this technique, dynamic modulations of corticospinal excitability have been described in hand muscles when participants observed (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000) or imaged (Abbruzzese, Trompetto, & Schieppati, 1996; Hashimoto & Rothwell, 1999; Kasai, Kawai, Kawanishi, & Yahagi, 1997) hand actions. Such results clearly established that the neural structures engaged in motor execution are also active when actions are observed or imaged.

TMS explorations have further indicated that changes of corticospinal excitability during action observation and motor imagery are largely specific to the muscles involved in the observed (Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000) or imaged (Fadiga et al., 1999; Rossini, Rossi, Pasqualetti, & Tecchio, 1999) action. To our knowledge, however, no TMS studies to date have actually compared the changes in corticospinal excitability that occur when participants are required to observe actions versus observe in order to subsequently image or imitate the previously seen actions. There is evidence both from behavioural and neuroimaging studies that participant's intentions do influence attentional processes (Mataric & Pomplun, 1998) and patterns of cortical activation (Decety, Grezes, & Costes, 1997; Grezes, Costes, & Decety, 1999), during action observation. The importance of cognitive factors in the transformation of perceptions into actions has been further emphasized recently in the theoretical framework developed by Jeannerod (2001) on motor simulation. According to this theory, attending to another person's actions involves the neural simulation of the same perceived action, thus explaining the equivalence between action imaged and action observed in terms of neural processing.

In the present study, our goal was to better delineate the changes in corticospinal excitability in hand muscles that accompany perceptual to motor transformations when participants are asked to observe, image and imitate specific hand actions.

2. Method

2.1. Participants

The participants consisted of 19 healthy individuals, 6 males and 13 females, between the ages of 18 and 38 years (mean, 24.8 ± 8.9 years). Four participants were left-handed and 15 were right-handed. Prior to the experimental session, all participants completed a medical questionnaire to ensure that they did not have any contraindications for transcranial

magnetic stimulation. The local Institutional Ethics Committee approved the study's procedures and each participant provided informed consent before participation.

2.2. TMS and recording of motor evoked potentials

For magnetic stimulation, the participants were seated comfortably in a recording chair, with their arms and hands resting on armrests and their feet supported by a stool. A U-shaped cushion was placed around the neck to ensure participants' comfort and also to limit head movements during the experiment. Magnetic stimulation was delivered with a MagStim 200 (The MagStim Co., Dyfed, UK) connected to a figure-of-eight coil (70 mm loops). To record motor evoked potentials (MEP), small auto-adhesive surface electrodes (1 cm^2) were placed in a belly-tendon bipolar montage over the first dorsal interosseous (FDI) muscle of the dominant hand (i.e. hand for writings). The electromyographic (EMG) signals were amplified ($100 \mu\text{V}/\text{div}$) and filtered (bandwidth, 10 Hz to 5 kHz) with a polygraph amplifier (RMP-6004, Nihon-Kohden Corp.). For each trial, 100 ms epochs were recorded with a 5 ms delay preceding stimulus onset. EMG signals were digitized at a 2 kHz sampling rate using custom software on a PC running under Microsoft® Windows®98 equipped with a digital/analog acquisition card (BNC-2090, National Instrument Corp.).

2.3. Determination of the relaxed motor threshold and baseline MEPs

The first step in the TMS session consisted of localizing the optimal site on the scalp to evoke responses in the contralateral FDI muscle. To this end, the coil (intersection site) was placed over the approximate location of the hand motor area on the left ($n = 15$) or right ($n = 4$) hemi-scalp (i.e. $\sim 4\text{--}5$ cm laterally from the vertex on the inter-aural line (Mills & Nithi, 1997; Weber & Eisen, 2002). With the handle oriented $\sim 45^\circ$ in the mid-sagittal plane and the stimulator set at 60% of its maximal output, the target area was systematically explored by displacing the coil in small steps until large responses could be evoked in the contralateral FDI. Once the optimal spot was localized, the site was marked with a red dot to ensure consistent coil positioning. In all sessions, the same experimenter (F.T.) was responsible for holding the coil in place for the duration of the experiment, which lasted $\sim 20\text{--}25$ min. When the coil had to be moved in some rare occasions, for instance to accommodate participants (e.g. for coughing), the experimenter used the red dot and other marks on the scalp and/or the ear to reposition the coil over the same site.

The second step consisted of determining the relaxed motor threshold using the method outlined by Mills and Nithi (1997). Starting from supra-threshold intensity, the stimulator's output was gradually decreased in 1% steps until no MEPs could be evoked for 10/10 consecutive stim-

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