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How equivalent are the action execution, imagery, and observation of intransitive movements? Revisiting the concept of somatotopy during action simulation

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ABSTRACT

Jeannerod (2001) hypothesized that action execution, imagery, and observation are functionally equivalent. This led to the major prediction that these motor states are based on the same action-specific and even effector-specific motor representations. The present study examined whether hand and foot movements are represented in a somatotopic manner during action execution, imagery, and action observation.

The experiment contained ten conditions: three execution conditions, three imagery conditions, three observation conditions, and one baseline condition. In the nine experimental conditions, participants had to execute, observe, or imagine right-hand extension/flexion movements or right-foot extension/flexion movements. The fMRI results showed a somatotopic organization within the contralateral premotor and primary motor cortex during motor imagery and motor execution. However, there was no clear somatotopic organization of action observation in the given regions of interest within the contralateral hemisphere, although observation of these movements activated these areas significantly.

1. Introduction

A broad body of literature underpins the notion of a functional equivalence between the execution, imagery, verbalization, and observation of human actions (see, for reviews, Grèzes & Decety, 2001; Jeannerod, 2001). One comprehensive account of the underlying brain mechanisms assumes that the simulation of body movements is based on own motor representations in the brain (Grush, 2004; Jeannerod, 2001). Jeannerod has proposed an explanation for this in his mental simulation theory. It states that a movement possesses a covert action stage involving the goal, the means to achieve it, and its consequences (Jeannerod, 2001). Although these covert actions are also actions, they are, nonetheless, actions that have not yet been executed. Situations corresponding to such covert activity are, for example, the conscious, self-intended simulation of one's own actions (motor imagery) or the perception of actions by others (action observation). The main difference between these two cognitive motor states is that motor imagery is generated internally, whereas action observation is driven by external stimuli.

Many studies have delivered evidence that the neural representations for motor imagery and action observation are similar to those for motor execution (e.g., Filimon, Nelson, Hagler, & Sereno, 2007; Gazzola & Keysers, 2008; Lotze et al., 1999). They have shown that both motor imagery and action observation are related to activation within motor and motor-related areas, indicating that, to some degree, they use the same brain substrate as the human motor execution system. One central prediction based on these results is that a motor-based action simulation should be composed of action- and even effector-specific motor representations (Fernandino & Iacoboni, 2010). More precisely, simulation of movements with different effectors might engage different effector-specific motor representations, and simulation of different actions with different consequences might be associated with a map for actions leading to a comparable action consequence.

Ever since Penfield and Boldery's (1937) experiments, research has shown that the above – mentioned somatotopic or effector-specific mapping of motor representations within the human sensory and motor systems is a very prominent organization principle. This principle implies that actions relying on specific effectors are

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represented separately in the motor and somatosensory system. Somatotopic representations within different cortical and subcortical systems can be found in, for example, the primary motor and somatosensory cortex, the premotor cortex, the basal ganglia, the cerebellum, as well as the occipitotemporal cortex (Grafton, Woods, Mazziotta, & Phelps, 1991; Lotze et al., 2000; Orlov, Makin, & Zohary, 2010; Rintjes et al., 1999; Romanelli, Esposito, Schaal, & Heit, 2005; Schlerf, Verstynen, Ivry, & Spencer, 2010). The most prominent somatotopic representations are found in the precentral and postcentral gyrus of the contralateral hemisphere. Within these areas, the lower extremities are represented near the *margo superior cerebri* (dorsomedial); upper extremities such as the somatosensory hand area, on the lateral surface of the sensorimotor cortex (dorsolateral) (Grafton et al., 1991). In line with findings from studies investigating the neural basis of action simulation states (s-states), it has been suggested that motor imagery and action observation also possess a roughly somatotopic arrangement (Buccino et al., 2001; Ehrsson, Geyer, & Naito, 2003; Jarstorff, Begliomini, Fabbri-Destro, Rizzolatti, & Orban, 2010; Stippich, Ochmann, & Sartor, 2002; Szameitat, Shen, & Sterr, 2007; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). At first glance, these studies provide clear evidence for the notion that motor representations are involved not only in controlling movements of particular effectors, but also during the mere imagination or observation of the action performed by a specific effector. However, these data stem from studies focusing on only one cognitive motor state in one experiment. They compared either action execution with motor imagery or action execution with action observation. Furthermore, the different studies considered different types of movements and used different forms of data analysis and contrast calculation. Hence, until now, no study has systematically investigated somatotopic representations of the same movement for action execution, observation, and imagery. This means that it is still not known whether the execution, observation, and imagery of movements lead to a comparable somatotopic mapping within the primary motor and premotor cortex.

To further clarify the issues of functional equivalence and somatotopic organization, this study applied a design with nine experimental conditions in which participants had to execute, observe, or imagine either an intransitive hand movement, an intransitive foot movement, or a concurrent movement of both effectors. In line with the findings in the literature discussed above, the functional MRI measurements covered the brain from the *margo superior cerebri* to the temporal pole. If a motor-based action simulation is composed of action- and effector-specific motor representations, we expect an effector-specific mapping of motor representations within the primary and premotor area during the motor imagery, action observation, and execution of the single intransitive hand and foot movement in question performed with different effectors, because the movement differs with respect to the effectors used but not with respect to the action goals.

2. Materials and methods

2.1. Participants

Participants were 18 right-handed and right-footed college students (9 female, mean age = 26.33 years, *SD* = 4.2) with normal or corrected-to-normal vision. Imagery ability was assessed with the Movement Imagery Questionnaire (Hall & Martin, 1997). Average scores ranged from 1.44 to 2.60 (*M* = 1.99, *SD* = .09) on a scale from *very easy to imagine* (1) to *very difficult to imagine* (7), indicating that all participants showed good to very good imagery abilities. They reported no history of psychiatric or neurological disorders, and no history or current use of any psychoactive medication. The study was approved by the local ethics committee, and all participants gave their informed written consent in accordance with the Declaration of Helsinki.

2.2. Stimulus material and task

The experiment contained ten conditions: three execution conditions, three imagery conditions, three observation conditions, and one baseline condition. The same unilateral hand, unilateral foot, and a combination of unilateral hand and foot movements were used for execution, observation, and imagery. Before the fMRI experimental phase, participants learned to perform all conditions correctly in a training session that was also used to record EMG (see, for details, *Training Session*).

The stimulus material for the observation condition consisted of three 5-s video sequences of a hand, a foot, or a hand and foot movement performed by a human model. The hand sequence showed a human body from a first-person perspective performing an extension/flexion movement with the right hand (i.e., the fingers); the foot sequence, an extension/flexion movement with the right foot (i.e., the toes); and the third video sequence showed the same human body model performing both hand and foot movement at the same time (Fig. 1). This last condition was included to gain information on the neural correlates of the additivity of the two single movements during execution, observation, and imagery. The resulting data are available as a Supplement 1. The movements were paced at a frequency of 1 Hz.

All video stimuli were presented by a PC running Presentation software (Neurobehavioral Systems, Albany, USA) and projected onto a screen behind the scanner that could be viewed through a mirror attached to the head coil (visual field 188 mm in the horizontal and 168 mm in the vertical plane, rectangular aperture). For the execution and imagery conditions, participants either executed or imagined the same three movements.

Participants were scanned during the following nine target conditions and one rest condition: (a) motor imagery of a right-hand extension/flexion movement, (b) motor imagery of a right-foot extension/flexion movement, (c) motor imagery of the respective hand and foot movements at the same time, (d) observation of a right-hand extension/flexion movement from a first-person perspective, (e) observation of a right-foot extension/flexion movement from a first-person perspective, (f) observation of the respective movements at the same time from a first-person perspective, (g) execution of a right-hand extension/flexion movement, (h) execution of a right-foot extension/flexion movement, (i) execution of both movements at the same time, and (j) the baseline counting condition.

In conditions (a) through (i), 20 repetitions per trial of the respective movement were imagined, observed, or executed. Each participant was instructed to count the number of repetitions with a frequency of 1 Hz. This served as an internal timer and as a standardization instrument. Instructing participants to count their movements controlled whether they all performed the same number of repetitions, especially during imagery. To control for the neural activation resulting from counting, participants were instructed to also count with the same rhythm during the baseline condition.

All conditions were presented in a pseudo-randomized order counterbalanced across participants. Each trial started with the instruction (‘‘Imagine/Observe/Execute Hand/Foot/Hand & Foot’’ or ‘‘Count’’). Instruction presentation was followed by the respective imagery, observation, or execution phase. During imagery, execution, and baseline, participants kept their eyes closed, reopening them only when imagery, execution, or counting (during the baseline counting phase) was finished. Eye closure and opening were monitored with a video camera. After each imagery,