

COGNITIVE NEUROSCIENCE

Kick with the finger: symbolic actions shape motor cortex excitability

Sonia Betti,¹ Umberto Castiello^{1,2,3} and Luisa Sartori^{1,2}¹Dipartimento di Psicologia Generale, Università di Padova, Via Venezia 8, 35131 Padova, Italy²Center for Cognitive Neuroscience, Università di Padova, Padova, Italy³Centro Linceo Interdisciplinare Beniamino Segre, Accademia dei Lincei, Roma, Italy**Keywords:** action observation, motor evoked potentials, motor resonance, transcranial magnetic stimulation

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Abstract

A large body of research indicates that observing actions made by others is associated with corresponding motor facilitation of the observer's corticospinal system. However, it is still controversial whether this matching mechanism strictly reflects the kinematics of the observed action or its meaning. To test this issue, motor evoked potentials induced by single-pulse transcranial magnetic stimulation were recorded from hand and leg muscles while participants observed a symbolic action carried out with the index finger, but classically performed with the leg (i.e., a soccer penalty kick). A control condition in which participants observed a similar (but not symbolic) hand movement was also included. Results showed that motor facilitation occurs both in the observer's hand (first dorsal interosseous) and leg (quadriceps femoris) muscles. The present study provides evidence that both the kinematics and the symbolic value of an observed action are able to modulate motor cortex excitability. The human motor system is thus not only involved in mirroring observed actions but is also finely tuned to their symbolic value.

Introduction

The human conceptual system contains knowledge that contributes to supporting all cognitive activities, such as perception and action (Barsalou *et al.*, 2003). Modality-specific theories (e.g., Embodiment Theory) claim that concepts are grounded in specific perceptual and motor representations (Kiefer & Pulvermüller, 2012). According to this approach, the motor system would play a role in the processing of action-related concepts (Pulvermüller *et al.*, 2001, 2005; Hauk *et al.*, 2004; Shtyrov *et al.*, 2004; Buccino *et al.*, 2005). By moving from a basic kinematic level up to a goal and an intention level, hierarchically organized motor representations would define how an action is performed, the aim of the motor act and the overall reason for executing it (Kilner, 2011).

A controversial issue in this research area is whether the motor system's output reflects the kinematics of the observed action or rather its abstract goal (Cattaneo *et al.*, 2009, 2013; Cavallo *et al.*, 2012, 2013; Mc Cabe *et al.*, 2014). Studies investigating corticospinal excitability facilitation induced by action observation seem to support both the low-level kinematic coding of the observed action (i.e., the muscular activation reflects the observed movements; Cavallo *et al.*, 2012, 2013) and the high-level goal coding (i.e., the muscular activation reflects the movements neces-

sary to reach the goal; Cattaneo *et al.*, 2009, 2013). Notably, other authors recently pointed out an integrated contribution of these two coding levels depending on the information provided to the observer about the action's goal (Mc Cabe *et al.*, 2014) on the different processing stage of the action (Cavallo *et al.*, 2013) or on the specific request addressed to the observer (Sartori *et al.*, 2015).

In the present study we aimed to extend these observations by exploring the reciprocal contribution of the kinematics of an observed action and its meaning in a symbolic action carried out with the index finger, but classically performed with the leg (i.e. a soccer penalty kick). By means of motor evoked potentials (MEPs) evoked by single-pulse (sp) transcranial magnetic stimulation (TMS; spTMS), we tested whether action observation induced, in the observer, a motor facilitation effect congruent with the effector performing the action (i.e. the finger) or related to the effector typically involved in the observed action (i.e. the leg). The stimuli were video clips showing an index finger kicking a ball into the goal, with or without wearing a miniaturized soccer shoe ('symbolic kick' and 'finger kick' conditions, respectively); a control condition ('biological movement') in which only finger movements were presented without the context was also included. We predicted that if participants merely resonate with the observed movements, only an index finger activation should be found throughout all the conditions. Conversely, if our manipulation is able to activate a symbolic representation of the action, the symbolic kick condition should trigger a

Correspondence: Luisa Sartori, ¹Dipartimento di Psicologia Generale, as above.
E-mail: luisa.sartori@unipd.it

muscular activation reflecting the muscle that is habitually used to reach the goal, namely the leg muscle. We also investigated whether a symbolic visual stimulus is able to activate a motor representation in the absence of direct motor practice.

Materials and methods

Participants

Thirteen healthy female individuals aged 19–27 (mean \pm SD age 22.5 ± 2.9 years) took part in the experiment. All were right-handed according to the Standard Handedness Inventory (Briggs & Nebes, 1975). They had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Wassermann, 1998; Rossi *et al.*, 2009). None had any experience in playing finger and/or real soccer, as their motor experience could have biased the results (Calvo-Merino *et al.*, 2005; Molnar-Szakacs *et al.*, 2007; Abernethy *et al.*, 2008; Aglioti *et al.*, 2008; Makris & Urgesi, 2015). Furthermore, to be included in the study each participant was prescreened to check whether a reliable MEP could be elicited from the leg muscle in five out of ten consecutive trials. All participants were naïve as to the purpose of the study and gave written informed consent prior to their participation. At the end of the experimental session detailed information concerning the study was provided. Participants were financially compensated for their time (13 euros). The experimental procedures were approved by the Ethics Committee of the University of Padova and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. No discomfort or other adverse effects were reported during TMS.

Experimental stimuli

The stimuli were three digitally recorded video clips showing a right hand's index finger: (i) hitting a ball into a goal by means of a miniaturized soccer shoe (symbolic kick); (ii) hitting the ball into the goal without soccer shoe (finger kick); and (iii) performing a simple flex-and-stretch movement without ball, shoe or goal (biological movement; Fig.1). All the videos were captured from a lateral

point of view to guarantee a high degree of visibility from the onset to the end of the action. Each video lasted 2510 ms and the animation effect was obtained by presenting a series of single frames each lasting 30 ms (resolution 1920×1080 pixels, color depth 32 bits) following the first frame lasting 800 ms.

Procedure

Participants were tested individually in a sound-attenuated Faraday room during a single experimental session lasting ~ 90 min and consisting of two blocks ('hand' and 'leg' blocks). Each participant was directed to sit in a slightly raised armchair with the legs and the arms positioned on appropriate supports and the head sustained on a fixed head-rest. Each participant was instructed to remain as still and relaxed as possible and to watch the video clips that were presented on a 24" monitor (resolution 1920×1080 pixels, refresh frequency 120 Hz) set at eye level (the eye–screen distance was 80 cm). To ensure attention to the video-clips, participants were told that at the end of the experiments they would be questioned about the visual stimuli presented. During the 'hand block', TMS-induced MEPs were acquired from the participant's right first dorsal interosseous (FDI) muscle; while during the 'leg block' MEPs were acquired from the participant's right quadriceps femori (QF) muscle. The order of the two blocks was counterbalanced across the participants. A single TMS pulse was delivered during each video presentation at one of two moments: (T_1) at the time of maximum flexion of the index finger, before the contact with the ball (1640 ms); and (T_2) at the time of maximum extension of the index finger, just after the contact with the ball (1730 ms; Fig. 1). The order of the videos was randomized across participants within each of the two blocks. A total of 60 MEPs (two muscles \times three conditions \times 10 repetitions) was recorded for each participant. Prior to presenting the videos, each participant's baseline corticospinal excitability was assessed by acquiring 10 MEPs while they passively watched on the computer screen a white-colored fixation cross on a black background. Another series of 10 MEPs was recorded at the end of each block. Possible variations in corticospinal excitability related to TMS *per se* were assessed by comparing the MEP amplitudes recorded during the

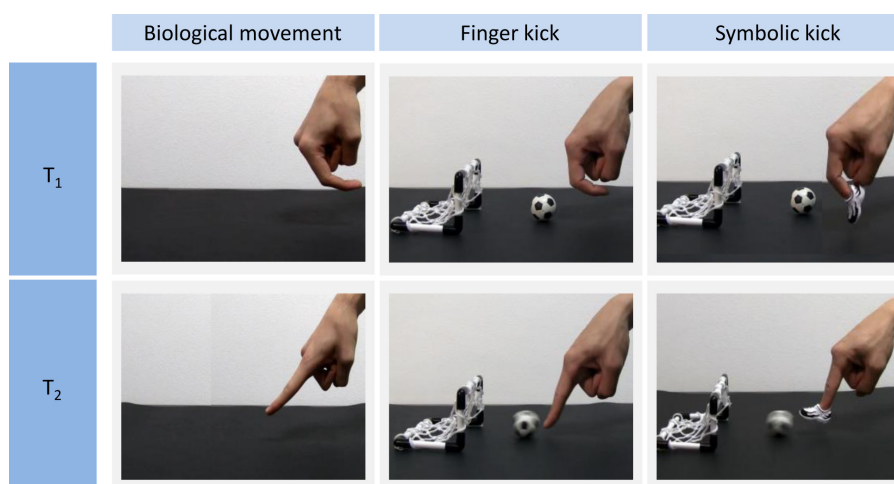


FIG. 1. Each column represents an experimental condition: biological movement, finger kick and symbolic kick, respectively. The rows denote the time points when single TMS pulses were delivered: at T_1 , during the maximum flexion of the index finger in the biological movement condition, and before the finger hit the ball in the symbolic kick and finger kick conditions; at T_2 , during the maximum extension of the index finger in the biological movement condition, and after the finger hit the ball in the symbolic kick and finger kick conditions.

two resting periods for each block. Their average amplitude was then utilized to set each participant's individual baseline for data normalization procedures. An inter-pulse interval lasting 10 s was presented between trials in order to minimize the potential risk of carryover effect of a TMS pulse on the subsequent one. During the rest period, a message reminding the participants to keep their arms and legs still and fully relaxed appeared on the screen for the first 5 s, and a fixation cross was presented for the remaining 5 s. Stimuli presentation, timing of TMS stimulation and electromyogram (EMG) recordings were managed by E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC.

Data recording

Transcranial magnetic stimulation

Single-pulse TMS was delivered using a 70 mm figure-of-eight coil connected to a Magstim Bistim² stimulator (Magstim Co., Whitland, UK). Pulses were delivered to the left primary motor cortex (M1) corresponding to either the hand or leg regions during the 'hand' and 'leg' blocks, respectively. The coil was placed tangentially on the scalp, with the handle pointing laterally and caudally (Brasil-Neto *et al.*, 1992; Mills *et al.*, 1992). The optimal scalp position (OSP) was determined by moving the intersection of the coil in ~ 0.5 -cm steps around the target area until a position was reached at which a maximal MEP amplitude was produced in the target muscle with a minimal stimulation intensity. This position was marked on a tight-fitting cap that each participant was asked to wear. During the experimental sessions the coil was held by a tripod and continuously checked by the experimenters to maintain a constant positioning with respect to the mark. The resting motor threshold (rMT), defined as the minimum stimulation intensity on the OSP that induced reliable MEPs (≥ 50 μ V peak-to-peak amplitude) in a relaxed muscle in five out of ten consecutive trials, was determined for each participant (Rossini *et al.*, 1994). rMTs ranged from 34 to 53% (mean \pm SD, $41.8 \pm 5.8\%$) of the maximum stimulator output in the hand block and from 51 to 63% ($55.5 \pm 3.0\%$) in the leg block. Stimulation intensity was set at 120% of the rMT to record a clear and stable EMG signal throughout the experiment.

Electromyography

MEPs were recorded from the FDI muscle of the right hand and from the QF of the right leg. EMG activity was recorded through pairs of surface Ag–AgCl surface electrodes (1 cm diameter) placed in a belly–tendon montage. The ground electrode was placed over the left wrist during the 'hand block' and over the patella of the left leg during the 'leg block'. The skin impedance condition, evaluated at rest prior to beginning the experimental session, was considered of good quality when below the threshold level (5 Ω). Electrodes were connected to an isolable portable ExG input box (Professional BrainAmp ExG MR, Munich, Germany) linked to the main EMG amplifier for signal transmission via a twin-fiber optic cable. The raw myographic signals were band-pass filtered (20 Hz–1 kHz), amplified prior to being digitalized (5 KHz sampling rate), and stored on a computer for off-line analysis. Trials in which any EMG activity > 50 μ V was present in the 100-ms window preceding the TMS pulse were discarded to prevent contamination of MEP measurements by background EMG activity.

Data analysis

Peak-to-peak amplitudes of the MEPs from the FDI and QF muscles were measured and averaged separately for each experimental condition. MEP amplitudes deviating by > 2 SD from the mean for each subject, and trials contaminated by muscular pre-activation, were excluded as outliers ($< 7\%$). A paired-sample *t*-test (two-tailed) was used to compare the amplitude of MEPs recorded during the two baseline trials carried out at the beginning and at the end of each block. Ratios were computed using the participant's individual mean MEP amplitude recorded during the pre- and post-testing periods as baseline values (MEP ratio = $\text{MEP}_{\text{obtained}}/\text{MEP}_{\text{baseline}}$). A repeated-measures ANOVA was conducted on the MEP ratios with type of action (symbolic kick, finger kick, biological movement) and timing (T_1 , T_2) as within-subjects factors and muscle (FDI, QF) as a between-subjects factor. In addition, we conducted one-sample *t*-tests to compare the normalized MEP values for each condition to 1, to assess directly modulation relative to baseline levels (Naish & Obhi, 2015). The sphericity of the data was verified prior to performing statistical analysis (Mauchly's test, $P > 0.05$). *Post hoc* pairwise comparisons were carried out using *t*-tests and the Bonferroni correction was applied for multiple comparisons (alpha level 0.05).

Results

The mean raw MEP amplitudes recorded for each participant during pre- and post-experimental sessions were not significantly different for either the FDI (1459.9 vs. 1395.3 μ V; $t_{12} = 0.335$, $P = 0.743$) or the QF (205.1 vs. 161.9 μ V; $t_{12} = 1.542$, $P = 0.149$) muscles. Therefore, TMS *per se* induced no changes in corticospinal excitability during the experiment and it can be thus concluded that modulation of EMG activity was linked exclusively to the different experimental conditions. The ANOVA on normalized MEP amplitudes showed a main effect of type of action ($F_{2,48} = 6.001$, $P = 0.016$, $\eta^2_p = 0.2$), timing ($F_{1,24} = 5.184$, $P = 0.025$, $\eta^2_p = 0.18$), and a three-way interaction of muscle \times type of action \times timing ($F_{2,48} = 3.461$, $P = 0.031$, $\eta^2_p = 0.13$). The results obtained from the *post hoc* contrasts exploring the significant three-way interaction are outlined as follows.

Motor resonance

When participants observed the index finger during maximum flexion before kicking (T_1), the FDI muscle was more activated than the baseline for the finger kick ($P = 0.036$), the biological movement ($P = 0.042$) and the symbolic kick conditions ($P = 0.038$; Fig. 2). This muscle-specific motor facilitation effect seems to reflect the activation of the muscle that is actually observed.

Symbolic coding

Post hoc comparisons for the QF muscle at T_1 showed that normalized MEPs were significantly enhanced when participants watched the symbolic kick compared to the finger kick ($P = 0.028$; Fig. 2) and to the biological movement ($P = 0.023$; Fig. 2) conditions. This suggests that only when the symbolic value of the observed action is manipulated (i.e. the finger is inserted into a miniaturized soccer shoe), the effector that is usually involved in performing the action (namely, the leg) is significantly activated. Notably, the QF muscle was less activated than the FDI muscle for both the finger kick ($P = 0.039$) and the biological movement ($P = 0.035$; Fig. 2) condi-

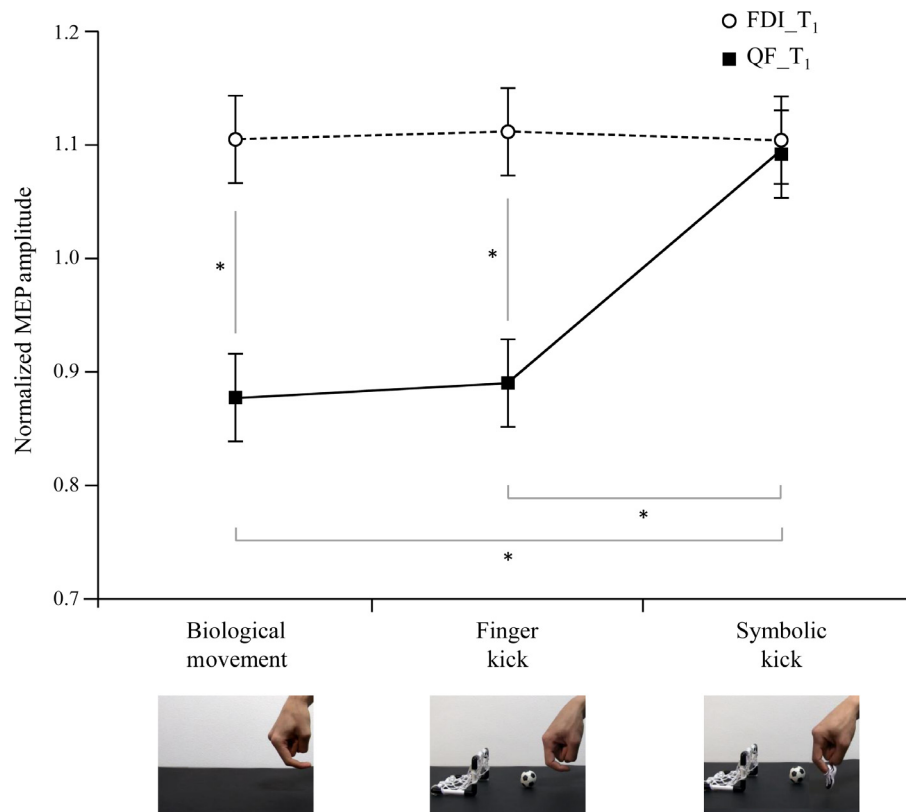


FIG. 2. Corticospinal activation during the observation of biological movement, finger kick and symbolic kick, respectively. The graph represents the means of the normalized MEP amplitudes recorded from the FDI and QF muscles at T₁. Error bars indicate SEM. Asterisks indicate statistically significant comparisons (* $P < 0.05$). Bottom panel shows frame extracted from the video clips at T₁ (i.e., during the maximum flexion of the index finger in the biological movement condition, and before the finger hit the ball in the symbolic kick and finger kick conditions).

tions, but not for the symbolic kick ($P = 0.845$) condition, suggesting that the symbolic action is able to simultaneously activate both the muscle that is observed and the one that is associated with the context.

Predictive coding

Post hoc contrasts for the FDI muscle showed an increased muscular activation before the contact with the ball (T₁) compared to just after the contact with the ball (T₂) for both the finger kick (1.099 vs. 0.894, respectively; $P = 0.025$) and the biological movement (1.095 vs. 0.916, respectively; $P < 0.001$) conditions, in line with the Predictive Coding account (Gangitano *et al.*, 2001; Urgesi *et al.*, 2010). This decrease in the FDI muscle at T₂ with respect to T₁ was not shown for the symbolic kick condition (1.077 vs. 1.073, respectively; $P = 0.83$).

Discussion

Modulation of motor outputs following observation of an action is specific to the motor representation involved in the observed action. As human beings, however, we respond not only to visual percepts but also to symbolic actions (i.e., actions able to activate an abstract representation of the action; e.g., Fecteau *et al.*, 2010). In the present experiment we investigated whether a symbolic action activates in the onlooker the specific muscle involved in the observed action, or is also able to cross-refer to an abstract representation of the action, thereby activating the effector that is typi-

cally used to perform that action. We thus presented to participants video clips showing an index finger kicking a ball with a miniaturized shoe, an action classically performed with the leg, and we measured corticospinal excitability before and after interaction with the ball.

The crucial finding was a motor facilitation both in the observed muscle and in the effector typically engaged when performing that action (i.e., the leg). To better investigate this effect, a control condition was included showing the same index finger performing the kick but without the miniaturized shoe. This was sufficient to restore the classic motor resonance effect (i.e., a muscle-specific activation in the corresponding index finger).

The time course of motor activations

According to Lago & Fernandez-del-Olmo (2011), the level of the motor coding (i.e., goal or kinematics) depends on the phase of the observed movement (i.e., before or after interaction with an object). When a static image of an effector in front of an object is shown, participants' corticospinal excitability would be generally enhanced in muscles that are able to achieve the goal of the observed action (Lago & Fernandez-del-Olmo, 2011). However, when the effector-object interaction is shown, the motor activation becomes muscle-specific, referring to the movement actually observed (Lago & Fernandez-del-Olmo, 2011). Here, we used two timings of TMS stimulation, namely before and after the index finger hit the ball, in order to test whether goal-related and muscle-specific activations were present. Crucially, according

to the amount of contextual information provided to the observer (i.e., only for the symbolic condition), we found a temporal coupling of symbolic and muscle-specific activations throughout the entire course of action, before and after contact with the ball. This seems to indicate that motor resonance was running until completion of the action sequence, in line with our hypothesis of a working memory process tailored for action, able to maintain salient information available for further processing (Sartori *et al.*, 2013a). This process would be in fact particularly functional when new or unusual motor plans are observed and assimilated in the onlooker's motor repertoire. In the control conditions (i.e., biological movement and finger kick), in contrast, we found a decreased activation of the index finger after contact with the ball. This is consistent with the fact that the motor system is preferentially activated by ongoing but not yet completed actions (Gangitano *et al.*, 2001; Urgesi *et al.*, 2010). The tendency of the motor system to predict the outcome of an action could be at the basis of the effect that we found in our study. In order to successfully interact with the environment, the human motor system seems to adopt a predictive coding by means of a reciprocal influence of lower and higher level representations (Kilner *et al.*, 2007). The discrepancy with the study by Lago & Fernandez-del-Olmo (2011) could be simply due to the fact that although we had stimulated before the effector-object interaction took place, here the action was already started and no static image was shown.

The role of symbolic significance

Many studies report that action observation results in a muscle-specific activation in the observer's corticospinal system, reflecting the muscles actually recruited to perform the action (e.g., Fadiga *et al.*, 1995; Borroni *et al.*, 2005; Romani *et al.*, 2005; Cavallo *et al.*, 2012). However, more general aspects of the action have been shown to modulate this matching response. The goal of the action plays a crucial role in influencing how actions are coded in the observer's motor system (e.g., Cattaneo *et al.*, 2013). Furthermore, it is known that the observer's motor expertise is able to activate effectors that are not directly involved in the action but would be recruited to achieve the same goal (Buccino *et al.*, 2004; Gazzola *et al.*, 2007; Senna *et al.*, 2014). Crucially, Fecteau *et al.* (2010) found that observation of a neutral stimulus mimicking a hand (i.e., dots) did not significantly enhance motor cortical output excitability. However, when hand stimuli were used as primes the neutral stimuli elicited a specific motor facilitation, thus suggesting that the prime endowed the dot stimuli with symbolic significance. Our results also support previous findings suggesting that a facilitation effect can be found even upon observation of a dot motion, depending on what the participants believe the motion represents (i.e., a human- or a computer-generated movement; Stanley *et al.*, 2007). In our case, the mere presence of a football shoe endowed the finger movement with a symbolic significance, therefore activating a motor representation of the kicking action.

It has been proposed that motor practice is needed to associate a visual stimulus to a motor representation (e.g., Reithler *et al.*, 2007), but if the ability to link perception to action depends on motor practice, then the lack of an experience-based skill should lead to a corresponding decrease in the ability to activate the appropriate motor representation following action observation (see for example Casile & Giese, 2006; Cross *et al.*, 2009). Here, however, we demonstrate that female participants lacking any visual and motor experience with the observed action were nonetheless able to activate the

abstract motor representation of a soccer kick, as indicated by the significant activation in the leg muscles. A symbolic action seems therefore able to elicit motor facilitation effects even in the absence of specific motor practice.

Our results seem to suggest that when observing an action performed with an atypical effector, such as a symbolic action, our abstract representation of the action goal activates a motor representation corresponding to the motor pattern usually adopted to carry out the action. Notably, manipulating critical components of the symbolic action (e.g., removing the miniaturized shoe from the finger) is sufficient to re-establish the classic motor resonance output. These results highlight the role of contextual information during the motor resonance effect contingent upon action observation (e.g., Sartori *et al.*, 2012, 2015). It seems that it is not only the phase or the kinematics of the observed action that modulates the level of motor coding, but an interplay of low- and high-level factors (e.g., the context; Iacoboni *et al.*, 2005). In this vein, a modulation of corticospinal excitability violating the classic motor facilitation effect has been shown when participants are instructed to perform incongruent actions (Newman-Norlund *et al.*, 2007; Ocampo & Kritikos, 2010), when the observed action itself calls for a gesture involving different hand muscles with respect to the observed ones (Sartori *et al.*, 2013a-c), and when participants involved in face-to-face interactions mutually adjust their movements in time and space in the absence of instructions to either imitate or perform a complementary response (Sacheli *et al.*, 2012, 2013). In a recent study, observers' upper and lower limb muscles were both found activated while observing a soccer player kicking a ball straight in their direction (Sartori *et al.*, 2015), thus suggesting that motor coding might reflect different processes (providing literal copies of the observed action, predictive and non-congruent muscular activations) in a non-mutually exclusive way. Here, we add to this evidence showing that variations of corticospinal output can also reflect an abstract coding level, depending on the interplay between real and symbolic movements. In particular, we hypothesize that corticospinal activation during action observation in symbolic contexts might reveal the occurrence of a functional strategy. Activating an index finger when the context simply shows an index finger is the classical output of motor resonance (e.g., Gangitano *et al.*, 2001). On the other hand, when the miniature shoe links the actual context to a specific symbolic context (i.e., a real kick) the optimal solution is the activation of the leg muscle (i.e., the most appropriate effector to perform that action).

Clinical implications

The definition of the conditions and the modalities through which observation of a symbolic action can activate the motor representation of the muscle typically used to perform the action will have specific translational implications for patients with localized lesions to cortical motor areas (e.g., ischemic stroke) leading to motor impairment. Observation of symbolic actions performed with an atypical effector could provide, for instance, a useful method of rehabilitation when the traditionally used effector is damaged or injured, by virtue of activating its motor representation. Recent studies on Action Observation Therapy have indeed confirmed the potential use of action observation as a strategy to enhance motor rehabilitation (Pomeroy *et al.*, 2005; Buccino *et al.*, 2006; Ertelt *et al.*, 2007; Mulder, 2007). In line with this, the present study opens the possibility of exploring new frontiers.

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Abbreviations

EMG, electromyogram; FDI, first dorsal interosseous; MEP, motor evoked potential; QF, quadriceps femori; spTMS, single-pulse transcranial magnetic stimulation; TMS, transcranial magnetic stimulation.

Conflict of interest

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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