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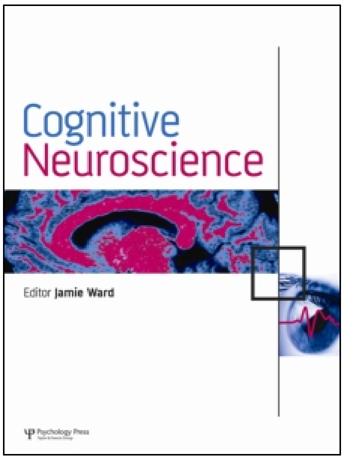

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Corticospinal excitability modulation to hand muscles during the observation of appropriate versus inappropriate actions

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Corticospinal excitability modulation to hand muscles during the observation of appropriate versus inappropriate actions

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Transcranial magnetic stimulation (TMS) studies have shown that the observation of an action causes subliminal activation within the motor system. However, the issue of whether such an effect is modulated by the match between the observed action and that the observer would have exhibited if acting under similar circumstances remains unclear. We address this issue by recording motor potentials evoked by single-pulse TMS from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles during the observation of video-clips representing prehensile actions towards small or large objects. In a separate behavioral study, participants were asked to evaluate which type of grasp would be the most appropriate for the tested objects. The TMS data revealed a selective motor facilitation during the observation of movements recruiting the targeted digits. We contend that, in action observation tasks, the human corticospinal system mediating action observation effects codes merely for the visual aspects of the observed action.

Keywords: Action observation; Transcranial magnetic stimulation; Motor-evoked potentials; Reach-to-grasp; Precision grip; Whole hand grasp.

INTRODUCTION

Previous transcranial magnetic stimulation (TMS) studies report that an observer's motor system is facilitated by the mere viewing of motor actions (for review, see Fadiga, Craighero, & Etienne, 2005). In a pioneering study, Fadiga, Fogassi, Pavesi, & Rizzolatti (1995) applied single-pulse TMS over the motor cortex of participants observing a model reaching and grasping for differently shaped objects. They demonstrated that observing an action induces an enhancement of the motor-evoked potentials (MEPs) recorded from participants' hand muscles corresponding to those involved in the observed action.

Since then, similar paradigms have been usefully applied to further investigate the nature of the corticospinal neural activity induced by peculiar visual characteristics of an observed action (Alaerts, Heremans, Swinnen, & Wenderoth, 2008; Gangitano, Mottaghy, & Pascual-Leone, 2001; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006a). For instance, it was demonstrated that the motor facilitation contingent upon action observation strictly reflects the temporal dynamics of the observed action kinematics (Gangitano et al., 2001), it is modulated by the laterality of the observed acting effector (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002), and it is not affected by the observer-model postural congruency (Urgesi, Moro, Candidi, & Aglioti, 2006b).

An issue that remains unresolved, however, is whether the reported facilitation reflects only the

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motor coding of the extrinsic visual aspects of the observed action or the meaning of what is observed. A crucial test to shed light on this issue might be to present actions of which the observer has previous experience, but which might be interpreted as inappropriate if performed. Does our motor system resonate merely to what we see or to what we would have actually done if acting under similar circumstances?

We test this by asking participants to observe video-clips representing reach-to-grasp actions in which the adopted type of grasp might be either appropriate or inappropriate for interacting with the target object (i.e., either a small or a large object). In this perspective the process of "action understanding," which might subtend the expected effects, is operationalized in terms of how the object is grasped rather than of complex action sequences (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005) or intentions (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005). We reasoned that if the motor coding of the seen action depends on its match with the action the observer would have performed, the facilitation effect on MEPs evoked by TMS should be only evident in those muscles that would have been involved in the most appropriate prehension pattern for that specific object, regardless of what is observed. By contrast, facilitation effects tuned to the observed type of grasp, independently of what is considered appropriate in terms of hand/object interactions, would be suggestive of a motor coding occurring on the basis of the visual aspects characterizing the observed action.

METHOD

Participants

Sixteen healthy individuals (3 men and 13 women) aged 19–28 (mean ± *SD*: age 23.3 ± 5.6 years) participated in the experiment. All participants were right-handed, as assessed via a condensed version of the Edinburgh Handedness Inventory (Oldfield, 1971) with normal or corrected-to-normal visual acuity. Participants were financially compensated and were naive as to the purpose of the study. Written, informed consent was obtained before the experiment started, and all participants were screened for potential risk of the adverse effects during TMS. The procedures were approved by the ethics committee of the University of Padova and conformed to the Declaration of Helsinki.

Stimuli and procedure

The experimental stimuli consisted of video-clips in color representing a human right hand reaching towards and grasping a target object, which could be either small or large (Figure 1). The large objects were a mug, a can, a tennis ball, and a glass. The small objects were a chess pawn, a ping-pong ball, a bottle cap, and a spool of thread. In the video-clips, each object could be grasped by the model either by opposing the thumb with the index finger (i.e., precision grasp) or with all five fingers (i.e., whole-hand grasp) (Figure 1). Each video-clip lasted 2500 ms, and the animation effect was obtained by presenting a series of single frames, each lasting 33 ms except for the first and last frames, which lasted 500 and 383 ms, respectively. Experimentation was carried out in a dimly illuminated room. Participants sat on an armchair, 80 cm in front of a 19″ monitor (resolution 1280 × 1024 pixels; refresh frequency, 75 Hz) positioned at eye level, with their feet resting on the floor and relaxed forearms in prone position on the armchair rests. Participants were instructed to avoid any voluntary movement, and to simply observe the video-clip. The experimental session lasted approximately 60 min. Stimulus-presentation timing, electromyographic (EMG) recording, and TMS triggering were controlled by E-Prime V1.1 software (Psychology Software Tools, Inc., Pittsburgh, PA, USA) running on a PC. The experimental paradigm consisted of eliciting MEP responses with TMS facilitation, while participants observed video-clips representing four experimental conditions: (a) a hand reaching and grasping a large object with a whole-hand grasp (Figure 1a); (b) a hand reaching and grasping a large object with a precision grasp (Figure 1b); (c) a hand reaching and grasping a small object with a whole-hand grasp (Figure 1c); (d) a hand reaching and grasping a small object with a precision grasp (Figure 1d). Note that, in the video-clips for experimental conditions "a" and "d," the grasping actions performed by the model are those most appropriate to interact with the to-be-grasped object (see "Preliminary behavioral experimental session" below). By contrast, in the video-clips for experimental conditions "b" and "c," the grasps adopted by the model would not be appropriate to interact with the to-be-grasped object (see "Preliminary behavioral experimental session" below). At the beginning of each video-clip, the hand of the model was shown in a prone position resting on a table with the object placed at 35 cm (Figure 1a–d). After 500 ms, the model's hand reached for, grasped, and lifted the target object (Figure 1e). A total of 64 trials, with 16 trials for each of the four TMS conditions

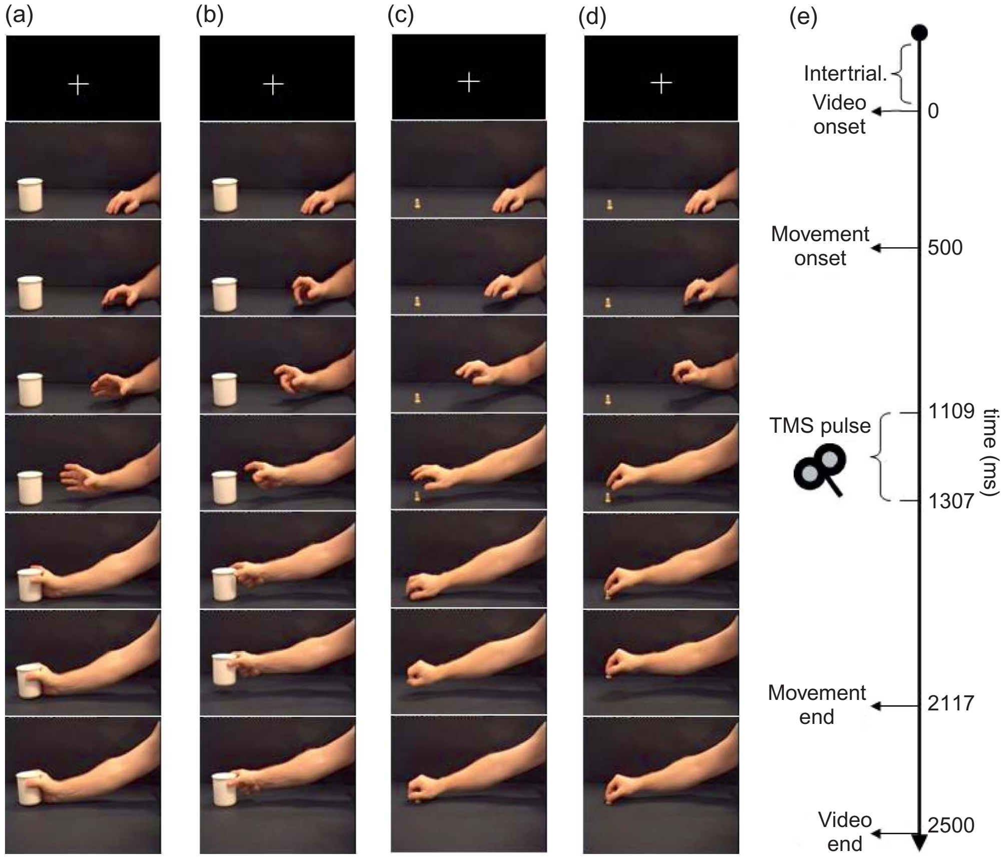

Figure 1. **(a, b, c, and d)**. Schematic representation of events sequence during a single experimental trial for reach-to-grasp movements performed towards either a large (i.e., a mug) or a small target (i.e., a chess pawn) by either a whole-hand (i.e., five fingers) or a precision grasp (i.e., thumb and index finger), respectively. At the beginning of each trial, participants were presented with a centrally displayed fixation cross. **(e)**. Schematic of experimental timing for the TMS experiment. The TMS pulse was applied 609–807 ms after movement onset just before the hand being observed in the video-clip made contact with the target object.

(i.e., a combination of four trials for the small target object and four trials for the large target object), were administered. Trial order was randomized within and between participants.

Preliminary behavioral experimental session

In order to obtain an objective reference for the type of grasps naturally afforded by the objects shown in the video-clips, a preliminary experimental session was administered. In this session, participants were sitting in front of a monitor upon which 20 photographs of objects normally used for daily activities were displayed. Among these 20 photographs, 8 photographs depicted the same objects as those used for the TMS experiment (i.e., 4 small, 4 large), whereas the remaining 12 photographs were considered as filler items. These items depicted 6 small and 6 large objects. After stimulus presentation, participants were presented with two photographs depicting a precision and whole-hand grasp in the absence of the object. Participants were requested to indicate which type of grasp they would have adopted if they had to grasp the objects depicted in the photographs. The experimenter recorded the participants' responses. In order to avoid a series effect, the order of presentation for the photographs was randomized across participants. The data obtained for the filler items were not analyzed.

TMS

Focal TMS was performed by means of a 70-mm, figure-eight stimulation coil (Magstim polyurethane-coated coil) connected to a Magstim 200 Rapid stimulator (Magstim, Whitlan, Dyfed, UK). The coil was placed over the left primary motor cortex (M1), tangentially to the scalp with the handle pointing backward and laterally at 45° away from the midline, such that the induced current flow was approximately perpendicular to the line of the central sulcus. This orientation was chosen on the basis of the evidence that under these circumstances the lowest motor threshold is achieved (Brasil-Neto, Cohen, Panizza, Nilsson, Roth, & Hallett, 1992). The optimal scalp position (OSP) was defined as the position from which MEPs with maximal amplitude were recorded simultaneously from the first dorsal interosseous (FDI; the muscle serving index finger flexion/extension) and the abductor digiti minimi (ADM; the muscle serving little finger abduction) muscles. In order to detect OSP, the participants wore a tight-fitting bathing cap on which the scalp positions for stimulation were marked. The OSP was identified by moving the intersection of the coil in steps of 1 cm around the hand-motor area and delivering pulses of constant intensity so as to obtain a stable signal from both muscles in all participants. The OSP was marked on the bathing cap to provide a reference point for the experimental session. The coil was held by a tripod and its position with respect to marks was checked continuously. The resting motor threshold (rMT) was defined as the minimal TMS intensity needed to evoke MEPs with an amplitude of at least 50 μV in both the targeted muscles in 5 out of 10 consecutive stimuli (Rossini et al., 1994). During the recording session, the stimulation intensity was 110% of the rMT and ranged from 55% to 72% (mean 64.4%) of the maximum stimulator output. To avoid any priming effects that could affect MEP size, in each trial, the magnetic pulse was delivered between 1109 and 1307 ms before the end of the video (Figure 1e). After each trial, a rest period of 8000 ms was given. During the first 3000 ms of the rest period, a message advising the participants to keep their hand still and fully relaxed was presented. Such a message was replaced by a fixation cross for the remaining 5000 ms.

EMG recording and data analysis

MEPs were recorded simultaneously from the FDI and the ADM muscles of the right hand. EMG recordings were performed with surface Ag/AgCl cup electrodes (diameter = 1 cm; Micromed, Treviso, Italy) placed in a belly tendon montage with active electrodes over the motor point and the reference electrodes over the interphalangeal joint of the index and the little finger, respectively. Responses were sampled at 8 kHz, amplified, band-pass filtered (20–1000 Hz), and stored on a PC for off-line analysis. In order to prevent contamination of MEP measurements by background EMG activity, trials with EMG activity greater than 100 μV in the 50-ms window preceding the TMS pulse were excluded from the MEP analysis. EMG data were collected for 200 ms. Raw amplitudes of MEPs recorded from FDI and ADM muscles, respectively, were *z*-normalized within participants. Such values have been used to control for interindividual variability of the absolute level of MEP amplitudes. The individual *z*-scores, calculated for each condition and muscle separately, were entered into repeated-measures ANOVAs with target size (small, large) and type of grasp (precision grasp, whole-hand grasp) as within-subjects variables. The data from the preliminary behavioral experimental session were analyzed by performing a chi-square test on the percentage proportion of "precision grasp" and "whole-hand grasp" responses obtained for each item from each participant.

RESULTS

Behavioral data

The chi-square test performed on the data obtained from the preliminary behavioral experimental session revealed that participants consistently selected the type of grasp appropriate for the size of the to-be-grasped object, $\chi^2(3) = 99.13$, $p < .0001$. Data indicated that when participants were requested to choose which type of grasp (i.e., whole-hand or precision grasp) they would adopt for grasping the small objects (i.e., chess pawn, ping-pong ball, bottle cap, and spool of thread), the majority of them significantly oriented their response to "precision grasp" ("precision grasp" response proportion = 90%). Similarly, when presented with photographs of large objects (i.e., mug, can, tennis ball, and glass), the majority of respondents reported that they would adopt a "whole-hand" grasp rather than a "precision grasp" ("whole-hand" response proportion = 98%).

TMS data

The aim of the present study was to test whether the compatibility between the observed movement kinematics and those afforded by the to-be-grasped object modulates the facilitation effect contingent upon action observation. The raw mean amplitudes of MEPs from FDI and ADM muscles are reported in Table 1. As shown in Figure 2, the absolute amplitudes of MEPs evoked by TMS delivered during the observation of reach-to-grasp movements were modulated depending on the observed type of grasp. In particular, a greater MEP amplitude for ADM was visible when the observed reach-to-grasp movement ended

TABLE 1

Potential amplitudes from the FDI and the ADM muscles during the observation of reach-to-grasp movements for large and small objects performed by either a whole-hand or a precision grasp

	Potential amplitude (μV)			
	Large object		*Small object*	
	Whole-hand	*Precision grasp*	*Whole-hand*	*Precision grasp*
FDI	392.98 ± 97.81	459.14 ± 129.14	442.05 ± 120.49	444.44 ± 112.12
ADM	254.66 ± 40.89	209.97 ± 50.09	245.28 ± 53.71	226.44 ± 51.51

Notes: Values are given as means ± *SEM*. FDI: first dorsal interosseous; ADM: abductor digiti minimi muscle.

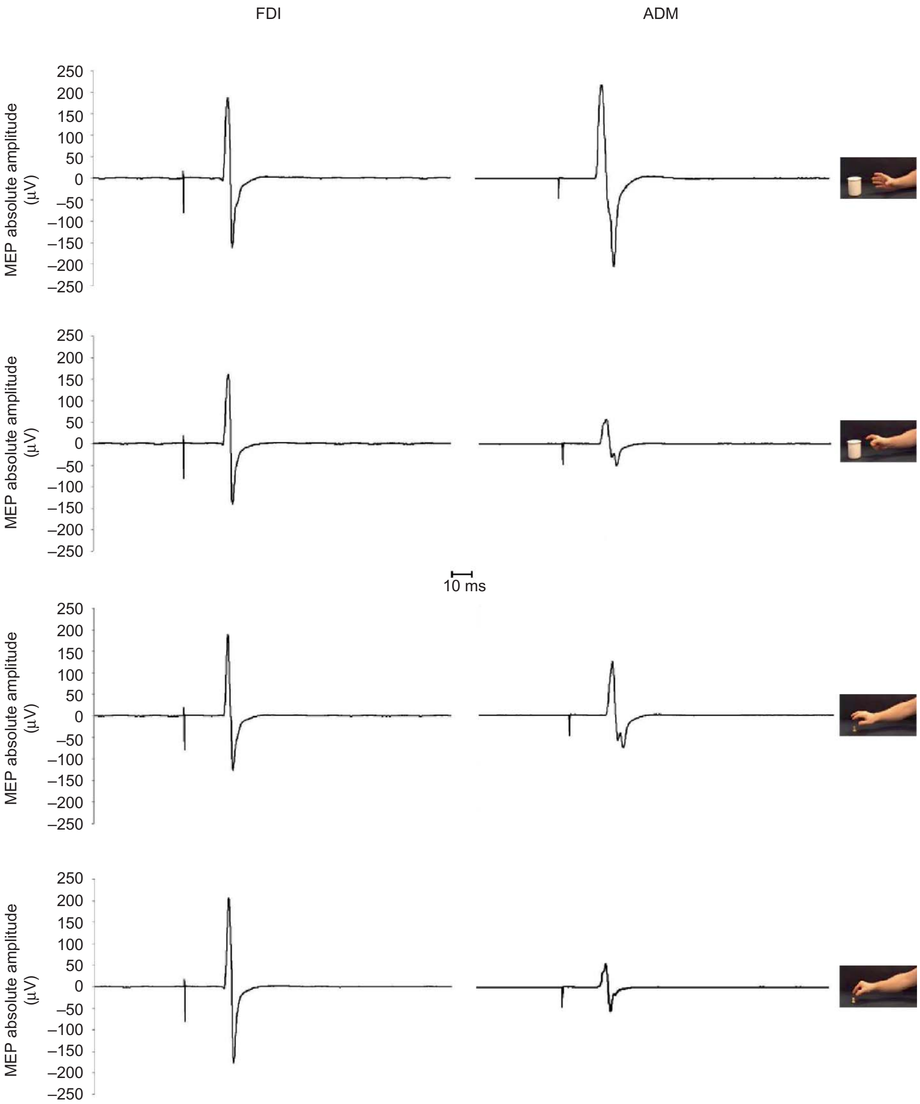

Figure 2. Example of MEPs absolute amplitude evoked by TMS during the four experimental conditions from the first dorsal interosseous (FDI) and the abductor digiti minimi (ADM) muscles (left and right columns, respectively). The photographs shown on the right of the figure refer to the type of experimental condition. Traces are aligned with and shown from the pre-stimulus record. Averaged data from one representative participant that portrays the trend of the entire sample are reported (participant no. 4).

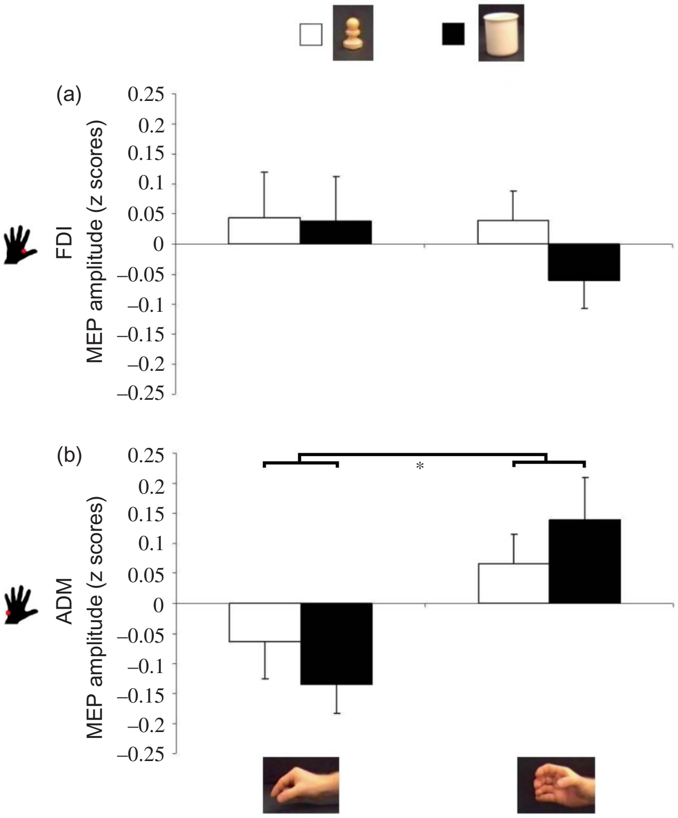

Figure 3. **(a and b).** Normalized peak-to-peak amplitude scores recorded during the observation of a precision and a whole-hand grasp for small and large objects from the first dorsal interosseous (FDI) and the abductor digiti minimi (ADM) muscles, respectively. The mean values for the entire experimental sample are reported. The red dots indicate to which muscle MEP *z*-scores refer. White and black bars indicate MEPs obtained during the observation of reach-to-grasp movements performed towards small and large objects, respectively. The photographs of the hand shown at the bottom of the figure are extracted from the video-clips used in the experiment, and they illustrate the type of grasp being observed by the participants (i.e., precision and whole-hand grasp at the left and the right of the x-axis, respectively). Asterisk indicates significant comparison ($p < .05$). Vertical bars denote ±*SE*.

with a whole-hand grasp that implied the use of the ADM muscle to be performed (see Figure 2). Likewise, a similar MEP amplitude was evident for the FDI muscle, a muscle recruited during the execution of both whole-hand and precision grasps (Figure 2). These qualitative observations were confirmed by the ANOVA performed on the normalized MEP amplitudes recorded from the FDI and the ADM muscles. Specifically, for the FDI muscle, the main effects of target size, $F(1, 15) = 0.383$, and type of grasp, $F(1, 15) = 0.599$, as well as the target size by type of grasp interaction, $F(1, 15) = 0.560$, were not significant (see Figure 3a). By contrast, the normalized MEP amplitude recorded from ADM revealed a significant main effect of type of grasp, $F(1, 15) = 6.708$, $p = .021$ (see Figure 3b). The MEP amplitude from the ADM was higher when participants observed a reach-to-grasp movement performed by using a whole-hand grasp rather than a precision grasp (0.103 vs. –0.099, respectively; Figure 3b). Surprisingly, the main effect of target size, $F(1, 15) = 0.000$, as well as the interaction type of grasp by target size, $F(1, 15) = 1.356$, was not significant. This suggests that the somatotopic mapping of the targeted muscle was not influenced by the type of action indicated as the most appropriate for grasping the presented object, as emerged from behavioral data (i.e., precision grasp for a small object and whole-hand grasp for a large object).

GENERAL DISCUSSION

The present results indicate that the corticospinal facilitation induced by the observation of a reach-to-grasp movement is topographically attuned to the type of grasp being observed (i.e., precision vs. whole-hand grasp) regardless of the overlap between the observed action and the action the observer would have exhibited if acting under similar circumstances.

Previous studies have applied TMS during action observation tasks in order to disclose neural facilitation induced by action observation within the observer's motor system (for a review, see Fadiga et al., 2005). However, the possible role played by the observer's previous motor experience in determining/modulating such a facilitation has been poorly investigated. So far, only one study has addressed this issue (Catmur, Walsh, & Heyes, 2007). Here one group of participants was first trained to observe either little- or index-finger movements and then to perform a movement congruent with that observed (e.g., observation: little-finger movement; execution: little-finger movement), whereas another group was first trained to observe either little- or index-finger movements and then to perform a movement incongruent with that observed (e.g., observation: little-finger movement; execution: index-finger movement). Then, in a second phase in which MEPs were recorded, participants belonging to both groups were asked only to observe either little- or index-finger movements. Results indicate that, independently of the observed movement, MEPs were always higher for the trained finger (Catmur et al., 2007). This was taken as evidence that motor experience affects how the motor cortex resonates during action observation. In this connection, the current study extends this research to the domain of transitive actions by asking whether the congruence between what is observed and what an observer would have actually done under similar circumstances is a *conditio sine qua non* for corticospinal facilitation to emerge.

This issue becomes particularly relevant in light of the notion classically advanced for interpreting the results from TMS action observation tasks; that is, the existence of an observing–execution matching system. In these terms, the corticospinal facilitation stemming from the passive observation of others' action would reflect a direct mapping of this action onto the observer's own motor system. However, in some circumstances what is viewed does not necessarily coincide with what an observer would actually do as to fulfill the same task. Here we provide compelling evidence that, in the event of a conflict between the observation and the execution dimensions, the muscles corresponding to the former rather than to the latter dimension are facilitated. This result might seem at odds with a previous study by Gangitano and colleagues (2004). They found that the observation of either an uncommon or an unpredictable reach-to-grasp movement does not modulate or evoke any matching activity to that obtained during the observation of a natural movement. This result was taken as a demonstration that when the visual properties of the observed movement cease to match those of the observer's resonant plan, action observation facilitation does not occur (Gangitano et al., 2004). Nevertheless, as the authors themselves indicate, the kinematics of the observed movements were novel and, in turn, their representation within the observer's motor repertoire might have been weaker or absent with respect to those representations corresponding to common, frequently experienced actions. By contrast, here the observed kinematics were not novel to participants; indeed, they were familiar with both the observed types of grasp, i.e., precision and whole-hand grasp. Therefore, the very fact that motor facilitation via action observation occurs demonstrates that facilitation contingent upon action observation is not modulated according to the appropriateness of the observed action, but purely by its visual aspect. This finding is in line with previous evidence reporting that motor facilitation was present during the observation of finger adduction/abduction movements which were beyond normal biomechanical joint mobility (Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005). An implication of these findings is that we cannot fully exclude that sensorial rather than motor effect might have accounted for the reported facilitation (e.g., joint stretch feeling when observing impossible hand movements). The transitive nature of the actions observed in the present study, as well as the fact that these actions fall within the participants' motor range, permits us to reject such an interpretation. Thus, we can conclude with a certain degree of confidence that the excitation of the human corticospinal system during passive action observation simply reflects what is seen. But, the human corticospinal system is not sensitive to properties which go beyond the physical aspect of what is seen, such as the suitability of the observed action. This might also explain why facilitation emerges during the observation of intransitive, meaningless actions (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Catmur et al., 2007; Fadiga et al., 1995; Urgesi et al., 2006a).

Regarding the possible neural substrates mediating the reported effect, the use of TMS does not allow us to make inferences regarding their exact origin. However, on the basis of functional magnetic resonance imaging (fMRI) studies of action observation, some considerations might be advanced. First, it has been demonstrated that the observation of impossible or erroneous hand movements leads to a level of activation within premotor areas similar to that found for the observation of possible and appropriate movements (Costantini et al., 2005). If these neural structures code observed actions independently of their feasibility, then our neurophysiological results might reflect the anatomic and functional link between premotor and motor cortices during action observation. Support for this contention comes from the demonstration that corticocortical projections from the premotor cortex to M1 play a major role in mediating the influence of visually perceived action on M1 excitability (Strafella & Paus, 2000). It must be said, however, that the present results do not allow us to exclude that other structures responsible for action execution might "map" the analysis of observed action suitability. In this respect, previous fMRI studies report that the supramarginal gyrus (Brodmann area 40) is selectively activated by the observation of actions outside the observer's motor repertoire (Costantini et al., 2005; Manthey et al., 2003). Further investigation is needed to clarify the role played by parietal areas in the determination of whether what is observed matches what is eventually executed.

In conclusion, our findings indicate that observed actions are directly matched to the observer's motor system at a low motoric level rather than at a level that includes concepts such as goal and intention. They suggest that motor facilitation via action observation occurs even when the observed action does not match the stored motor commands suitable for acting under the observed circumstances. In this view, the "direct match" concept would be the consequence of a "passive" rather than an "interpretative" simulating process.

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