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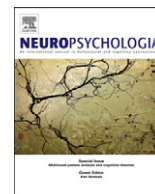
Motor cortex excitability is tightly coupled to observed movements

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A B S T R A C T

Although facilitation of the corticospinal (CS) system during action observation is a widely accepted phenomenon, it is still controversial if facilitation reflects the replica of observed movement kinematics or the tension to achieve a particular goal. In this study, transcranial magnetic stimulation (TMS)-induced motor evoked potentials (MEPs) were recorded from the abductor digiti minimi (ADM) and the first dorsal interosseus (FDI) muscles while participant–volunteers observed a model grasping a small target eliciting a precision grip or a large target eliciting a whole hand grasp directed toward an isolated object or flanked by different sized objects (i.e., distractor). A detailed movement analysis revealed that the model's kinematics were influenced by the distractor's size. Video clips filming the scene were edited in such a way that the distractor was removed from the scene. Participant–volunteers were asked to observe actions characterized by the same goal but performed using different kinematical patterns. Although the differences in movement kinematics were not noticed by the participant-volunteers, they nonetheless elicited distinct configurations of corticospinal activation. Detailed motor matching seems to recruit the same muscles in the onlooker as in the person actually carrying out the action during observation of grasping actions. These effects appear to be elicited by very subtle, imperceptible aspects of observed actions pointing to a finely tuned mechanism that specifically encodes body parts.

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1. Introduction

Observing another's action selectively facilitates the brain's motor circuits to carry out that same action (for review, see Heyes, 2011). In humans, the first demonstration of covert motor activation during action observation can be found in a work by Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) using transcranial magnetic stimulation (TMS). TMS was applied to the sector of the primary motor cortex (M1) that represents the hand, and motor evoked potentials (MEPs) were recorded from contralateral hand muscles during passive observation of hand movements. Observing hand actions elicited a MEP enhancement in the observer in the same muscular groups used to execute those actions, supporting the hypothesis that perceived actions are mapped onto the onlooker's motor system (for review see Fadiga, Craighero, & Olivier, 2005).

Motor facilitation during action observation has been replicated in numerous studies since then, and it is now well established that merely observing another's actions modulates the excitability of the observer's corticospinal (CS) circuitry

involved in executing those same movements (e.g., Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006).

Although CS facilitation during action observation is a widely accepted concept, the visual requirements necessary to elicit that facilitation are relatively unknown. Indeed action observation can be described and understood on at least two levels: its goal and kinematic ones (Grafton, 2009; Grafton & Hamilton, 2007). At what level of the hierarchy, then, does modulation in the onlooker's CS system occur? Or more precisely, is the muscle recruitment pattern during MEP testing linked to the movement kinematics or to the goal of an observed action?

Although the question appears simple enough, findings on this subject are contradictory. To examine the specific contributions of goals and/or movements to covert motor activation, Cattaneo, Caruana, Jezzini, & Rizzolatti (2009) designed a paradigm in which action goals were dissociated from the movements made to achieve them using two types of pliers: classic and reverse. Grasping was achieved by means of finger flexion when classic pliers were used and by means of finger extension when reverse pliers were used. Those investigators found that when there was no goal behind an observed behavior, MEPs recorded from the opponens pollicis (OP) reflected the movements performed by the agent. But when a goal was connected to the action, MEPs were

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enhanced while the goal was being achieved regardless of the type of pliers used or the finger movements observed (flexion versus extension). The Authors concluded on the basis of these findings that during observation of goal-directed actions the MEPs recorded from the OP were modulated by the action goal rather than by the hand movements observed.

This conclusion has recently been challenged by a similar experiment in which classic, reverse, and magnetic pliers were utilized. In the latter case, grasping was achieved by means of an *opening* movement of the hand and a corresponding *opening* movement of the pliers (Cavallo, Becchio, Sartori, Bucchioni, & Castiello, 2012). Essentially, if corticospinal excitability is connected to the the goal of an observed behavior (i.e., grasping an object), then a similar MEP amplitude modulation should be noted for all grasping actions regardless of the tool that is utilized (classic, reverse pliers or magnetic pliers). The main result of this experiment was, however, that only *minimal* OP muscle CS excitability was noted during observation of grasping actions performed using magnetic pliers requiring an opening hand/tool movement. This finding seems to sustain the hypothesis that motor cortex excitability strictly reflects observed hand/tool movements.

Similar conclusions have been reached by other investigators studying participant–volunteers who were requested to observe video clips of reach-to-grasp actions that were either appropriate or inappropriate to interact with a target object (i.e., either a small or a large object) (Cavallo, Sartori, & Castiello, 2011). The results indicated that the CS facilitation induced by observing a reach-to-grasp movement was topographically attuned to the type of grasp being observed (i.e., precision vs. whole-hand grasp) regardless of any overlap between the action actually observed and the one the observer would have exhibited if he/she were acting under similar circumstances. This suggests that motor coding is based on the visual aspects characterizing an observed movement, regardless of the goal of the action or of what is considered appropriate in terms of hand/object interaction (Cavallo et al., 2011).

Another recent study (Sartori, Xompero, Bucchioni, & Castiello, 2012) went a step further and demonstrated that kinematic signatures are capable of automatically influencing an onlooker's CS activity by allowing motor functional strategies to be transferred. TMS-induced MEPs were thus analyzed while subjects were instructed to observe a model grasping a small object (target) eliciting a precision grip (PG; i.e., the opposition of the thumb with the index finger) or a large object eliciting a whole hand grasp (WHG; i.e., opposition of the thumb with all fingers) flanked by another object (i.e., distractor) implicitly requiring different types of grasping movements (i.e., a WHG or a PG, respectively). A detailed kinematic analysis of the model's action revealed that there were distractor effects. Reaching and grasping movements directed towards an object–target presented in conjunction with different sized distractors revealed, for example, that the model's kinematics were influenced by the distractor's size. While 'what' was being achieved was the same (e.g., grasping the target), 'how' it was achieved differed depending on whether or not there was a distractor. The parallel planning needed for both the object–target and the object-distractor stimuli evident in the model's hybrid kinematics seems to be reflected in an onlooker's cortical activity. Observing another person's hybrid kinematic pattern in the presence of a distractor leads an onlooker to covertly simulate the observed motor integration (Sartori et al., 2012). That motor resonance could be dictated by the object-distractor itself or by fine "reading" the kinematics of the observed action.

On the basis of the evidence outlined above, corticospinal excitability appears to be sensitive to both the goal of an action and how that goal is achieved. In order to shed further light on this question, an experiment was designed in which movement kinematics were *apparently* appropriate to the goal, but characterized by subtle differences imperceptible to the observer. The question the investigators intended to answer was: is the CS circuitry sensitive to the goal and its appropriate kinematics or does it merely duplicate an observed movement?

The paradigm outlined above (Sartori et al., 2012) was utilized once again but with a crucial variation. Specifically, there was an 'only target' condition in which participants were instructed to observe a model simply grasping a target (either small or large) and a 'distractor' condition in which there were also other, different sized objects (i.e., distractors) affecting the model's kinematics. A third, "hidden distractor" condition was created by editing the video clip so that the distractor was removed from the scene but leaving the model's kinematics untouched. The visual features of the scene were apparently the same as those for the 'only target' condition (i.e., target alone), but the movement kinematics were the same as those for the 'distractor' condition. If corticospinal facilitation is sensitive to the goal of an action, then we expected it to be similar across all these conditions. Conversely, if corticospinal facilitation is specific to the subtle, almost imperceptible differences characterizing the kinematics of an observed movement, we expected it to be similar in the 'distractor' and the 'hidden distractor' conditions, but not in the 'only target' condition and confirming that excitability of the motor cortex is tightly bound to observed, covertly simulated actions.

2. Methods

2.1. Participants

Thirty participant–volunteers (21 females and 9 males: age=24 ± 5 years), all right handed according to a Standard Handedness Inventory (Briggs & Nebes, 1975) and with normal or corrected-to-normal vision, took part in the experiment. None had any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998) or experienced discomfort during the experiment. The experimental procedures outlined here were granted ethical approval (Ethics Committee of the University of Padova) and were carried out in accordance with the principles of the 1964 Declaration of Helsinki, and all of the participants gave written informed consent. The participants were provided detailed information about the experimental design when the session was over.

2.2. Experimental stimuli

As the stimulus configuration had to evoke a kinematic interference pattern, sophisticated kinematic measurements were performed to select the experimental stimuli. A model performing reach-to-grasp actions was filmed in the following experimental conditions: (Fig. 1): (i) a precision grip action (PG; the opposition of the index finger with the thumb) towards a small, isolated object–target (2 cm in diameter); (ii) a whole hand grasp action (WHG; the opposition of all fingers with the thumb) towards a large, isolated object–target (11 cm in diameter); (iii) a reach-to-grasp action towards a small object–target flanked by a distractor its same size positioned to its right; (iv) a reach-to-grasp action towards a small object–target flanked by a distractor its same size positioned to its left; (v) a reach-to-grasp action towards a large target flanked by a distractor its same size positioned to its right; (vi) a reach-to-grasp action towards a large target flanked by a distractor its same size positioned to its left; (vii) a reach-to-grasp action towards a small target flanked by a larger distractor (11 cm in diameter) positioned to its right; (viii) a reach-to-grasp action towards a small target (2 cm in diameter) flanked by a larger distractor positioned to its left; (ix) a reach-to-grasp action towards a large target flanked by a smaller distractor (2 cm in diameter) positioned to its left; (x) a reach-to-grasp action towards a large target flanked by a smaller distractor positioned to its right.

A digitising technique (Videotrack, Abacus srl, Italy) was used to extract the kinematics of the model from the videos. Paired *t*-tests were performed to compare the no-distractor and the distractor conditions. On the basis of previous literature (for review, see Castiello, 1999; Tipper, Howard, & Houghton, 1998) the dependent variables thought to be specifically relevant were: movement duration (MD), deceleration time (DT; the time from the moment of peak velocity to the end of the movement), and the maximum hand aperture calculated as the distance between the thumb and the index finger (AGAI) and the thumb with the little
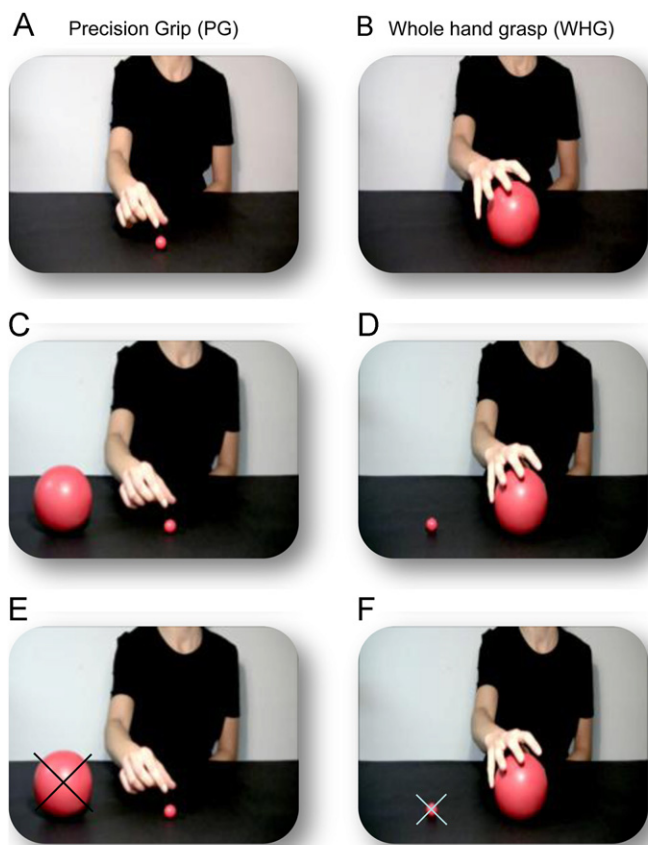
Fig. 1. Representation of the experimental conditions: (A) PG towards the small target object alone ('only target PG'); (B) WHG towards the large target object alone ('only target WHG'); (C) PG towards a small target object flanked by a large distractor evoking a WHG ("distractor present PG"); (D) WHG towards a large target object flanked by a small distractor evoking a PG ("distractor present WHG"); (E) PG towards the small target object apparently alone ("hidden distractor PG"); (F) WHG towards a large target object apparently alone ("hidden distractor WHG").

finger (AGAL). Those fingers were the ones that were considered because they corresponded to those specifically targeted in the present study, and those variables were chosen because considerable findings in the context of the reach-to-grasp literature have shown that those movements are dependent upon the size of the stimuli. In particular, the MD and the DT are shorter, and the AGAI and the AGAL are greater for larger with respect to smaller stimuli (Jakobson & Goodale, 1991). The dependent measures were found to be significantly different in this respect. The MD and the DT were shorter for movements directed towards a smaller target in the presence of a large distractor than when it was presented alone (MD: 801 ± 78 vs. 848 ± 81 ms, $t_9 = 7.92$, $p < .001$; DT: 598 ± 65 vs. 646 ± 60 ms, $t_9 = 8.07$, $p < .002$). The AGAI and the AGAL for a small target were greater in the presence of a large distractor than when the target was isolated (AGAI: 48 ± 2 vs. 45 ± 3 mm; $t_9 = 9.01$, $p < .001$; AGAL: 74 vs. 70 mm; $t_9 = 11.03$, $p < .001$). On the contrary, the MD and the DT were longer for movements directed towards a larger target in the presence of a small distractor than when the target was isolated (MD: 837 ± 82 vs. 689 ± 74 ms, $t_9 = 9.88$, $p < .001$; DT: 602 ± 60 vs. 479 ± 52 ms, $t_9 = 8.83$, $p < .001$). The AGAI and the AGAL for a large target were smaller in the presence of a small distractor than when the target was isolated (AGAI: 126 ± 4 vs. 131 ± 3 mm, $t_9 = 12.21$, $p < .001$; AGAL: 140 ± 9 vs. 148 ± 12 mm, $t_9 = 7.77$, $p < .001$). On the whole, these data indicate that the presence of a distractor leads to an altered kinematical pattern. No differences were detected when the size of the distractor was similar to that of the target nor when the position of the distractor (to the left or right of the target) was diversified. The TMS paradigm did not, therefore, include conditions in which the distractor and target sizes were similar or distractor positions were changed.

Bearing this in mind, the action stimuli presented during the TMS experiment were the following:

(i) a PG towards a small, isolated target ("only target PG"; see Fig. 1A);
(ii) a WHG towards a large, isolated target ("only target WHG"; see Fig. 1B);
(iii) a PG towards a small target flanked by a large distractor evoking a WHG ("distractor present PG"; see Fig. 1C);

(iv) a WHG towards a large target object flanked by a small distractor evoking a PG ("distractor present WHG"; see Fig. 1D);
(v) a PG towards a small, *apparently* isolated target ("hidden distractor PG"; see Fig. 1E). In this case, the distractor was expressly deleted post-hoc from the video using video editing procedures. The final product was a video in which only a single target was visible, as in the 'small isolated target' condition, but in which the model's kinematics were the same as those in the 'small object alongside a large distractor' condition.
(vi) a WH towards a large, *apparently* isolated target ("hidden distractor WHG"; see Fig. 1H). The final product of the editing in this case was a video in which only a large target was visible, as in the 'large object alone' condition, but in which the model's kinematics were the same as those in the 'large object alongside a small distractor' condition.

In order to ascertain if differences in the stimuli belonging to the 'only target' and the 'hidden distractor' conditions were recognized, a preliminary test was carried out utilizing a sample group of participants ($N=10$) with characteristics similar to those participating in the real experiment. This forced-choice comparison test indicated that the stimuli for the two conditions were considered identical ($p_s > 0.05$).

The two 'hidden distractor' conditions also made it possible for us to assess potential confounding factors due to the presence of a distractor. According to the literature, objects' visual features of (e.g., size) could prime a corresponding motor representation (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Edwards, Humphreys, & Castiello, 2003; Tucker & Ellis, 1998). Deleting the distractor could, then, prevent parallel activation of motor representations associated with both the target and the distractor.

2.3. TMS stimulation and MEP recording

TMS was delivered using a 70-mm figure-of-eight coil connected to a Magstim BiStim^2 stimulator (Magstim, Whitlan, Dyfed, Wales, UK). Pulses were delivered over the left primary motor cortex corresponding to the hand region. The coil was angled 45° relative to the interhemispheric fissure and perpendicularly to the central sulcus with the handle pointing laterally and caudally (Brasil-Neto et al., 1992). This orientation induced a posterior-anterior current in the brain, which tends to activate corticospinal neurons indirectly via excitatory synaptic inputs (Di Lazzaro et al., 1998). The coil was placed in correspondence to the optimal scalp position (OSP), defined as the site at which stimuli of slightly suprathreshold intensity consistently produced the largest MEPs from both the abductor digiti minimi (ADM; the muscle serving little finger abduction) and the first dorsal interosseus (FDI; the muscle serving index finger flexion/extension) muscles. Held by a tripod, the coil was continually checked by the experimenters to maintain consistent positioning. Electromyography (EMG) recordings were performed using pairs of 9 mm diameter Ag–AgCl surface electrodes placed over the belly of the right ADM and FDI muscles and the reference electrodes over the ipsilateral proximal interphalangeal joint (belly-tendon technique). The electrodes were connected to an isolated portable ExG input box linked to the main EMG amplifier for signal transmission via twin fiber optic cable (Professional BrainAmp ExG MR, Brain Products, Munich, Germany). The ground electrode was placed over the participant's left wrist and connected to the common input of the ExG input box. The raw myographic signals were bandpass filtered (20 Hz–1 kHz), amplified prior to being digitized (5 kHz sampling rate), and stored on a computer for off-line analysis. The trials in which any EMG activity greater than 100 μV was present in the 100 ms window preceding the TMS pulse were discarded in order to prevent contamination of MEP measurements by background EMG activity. The EMG data were collected for 200 ms after the TMS pulse. The resting motor threshold (rMT) was determined for each participant as the minimum stimulation intensity producing reliable MEPs (≥ 50 μV peak-to-peak amplitude) in a relaxed muscle in five out of ten consecutive trials. The stimulation intensity during the recording session was 110% of the rMT and ranged between 33% and 67% (mean 49%) of the maximum stimulator output intensity. MEPs were recorded simultaneously from electrodes placed over the contralateral ADM and FDI muscles. Prior to watching the video, the participant's baseline corticospinal excitability was assessed by acquiring 10 MEPs while he/she passively watched a white-colored fixation cross on a black background in the center of the computer screen. Another series of 10 MEPs was recorded at the end of the experimental session. It was possible to check for corticospinal excitability variations related to TMS per se by comparing the MEP amplitudes of the two series. The average amplitude of the two series allowed us to set the individual baselines for data normalization procedures.

2.4. Procedure

Testing was carried out in a sound-attenuated Faraday room. The participant–volunteers were directed to sit in a comfortable armchair with their head positioned on a fixed head rest so that the eye–screen distance was 80 cm. They were asked to keep their hands in a prone position in a still and relaxed way and to watch the video-clips avoiding any movement. The right arm was positioned on a full-arm support, while the left arm was to be kept in a relaxed position with the

hand resting on the legs. During the first five seconds of each rest period, a message reminding the participants to keep their hands still and fully relaxed was presented. That message was replaced by a fixation cross for the remaining five seconds of the rest period. The participants were asked to watch the visual stimuli presented on a 19″ monitor (resolution 1280×1024 pixels, refresh frequency 75 Hz, background luminance of 0.5 cd/m^2) set at eye level. The animation effect was obtained by presenting a series of single frames each lasting 33 ms (resolution 720×576 pixels, color depth 24 bits, frame rate 30 fps) plus the first and last frames which lasted 500 and 1000 ms, respectively. The presentation of stimuli and the timing of TMS stimulation were managed by the E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC. To encourage the participants to maintain a good level of attention, they were advised that they would be questioned about what they had seen. Ten trials were presented for each of the six types of video clips, for a total of 60 trials. The order in which the trials were presented was randomized across the participants. TMS-induced MEPs from the right ADM and the right FDI muscles were acquired once during each video presentation, at the point in which the model reached the maximum grip aperture before contacting the object. Each video presentation was followed by a 10 s rest interval. Ten MEPs per muscle were acquired for each video, for a total of 120 MEPs per participant. Baseline CS excitability was assessed prior to and following the video presentations.

2.5. Data analysis

The peak-to-peak amplitudes of the MEPs from both the ADM and FDI muscles were measured and averaged for each condition. The MEP amplitudes deviating more than two standard deviations from the mean for each type of action and trials contaminated by muscular pre-activation were excluded as outliers ($< 2\%$). A paired sample t-test (2-tailed) was used to compare the amplitude of the MEPs from the ADM and FDI muscles in the two baseline trials at the beginning and at the end of the experimental session. Ratios were then computed using the individual means of the MEP amplitude recorded during the two fixation cross periods as baseline values (MEP ratio$=$MEP$_{obtained}$/MEP$_{baseline}$). A repeated measures analysis of variance (ANOVA) was conducted on the MEP ratios with 'distractor' (present, absent, hidden) and 'type of grasp' (PG, WHG) as within-subjects factors. 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 adjustment for multiple comparisons was applied.

3. Results

TMS per se did not induce any variations in CS excitability during our experiment. The mean raw MEP amplitudes during the two baseline trials administered at the beginning and the end of the experimental session were not significantly different for the ADM (487 vs. 415 μV, respectively; $t_{29}=1.06$, $p=0.30$) or the FDI (1090 vs. 927 μV, respectively; $t_{29}=1.35$, $p=0.19$) muscles. The MEP amplitude for the FDI muscle was higher for the PG than for
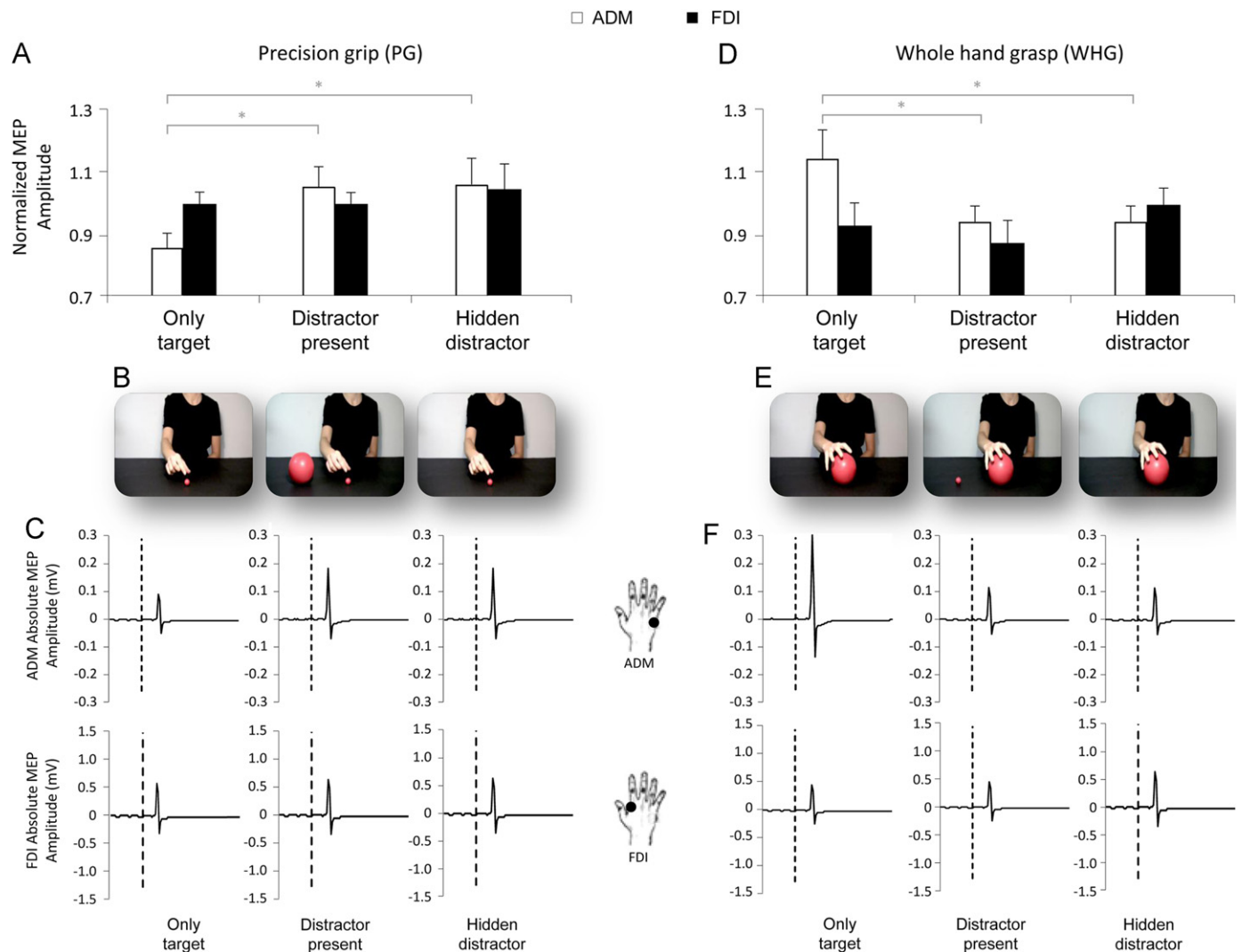
Fig. 2. (A) Normalized MEP amplitude for ADM (white bars) and FDI (black bars) for precision grip in the three conditions. (B) Snapshots representing the model in the considered experimental conditions. (C) Absolute MEP amplitudes of a representative participant (B.Z.) for both ADM and FDI muscles for the three conditions. (D) Normalized MEP amplitude for ADM (white bars) and FDI (black bars) for whole hand grasp for the three distractor conditions. (E) Snapshots representing the model in the considered experimental conditions. (F) Absolute MEP amplitude of a representative participant (B.Z.) for both ADM and FDI muscles for the three conditions. Asterisks indicate significant comparisons ($p < .05$). Bars represent the SEM.

the WHG ($F_{1,29} = 7.03$, $p < 0.05$), but there was no 'distractor' effect ($F_{2,58} = 2.00$, $p > 0.05$) or interaction effect between 'type of grasp' and 'distractor' ($F_{2,58} = 1.48$, $p > 0.05$). A repeated measures ANOVA performed on normalized MEP amplitudes for the ADM muscle revealed a statistically significant interaction of 'distractor' with 'type of grasp' ($F_{2,58} = 14.46$, $p < 0.001$). Post hoc contrasts revealed that the MEP amplitude for the ADM muscle was higher for the large target requiring a WHG than for the small target requiring a PG ($p < 0.05$), but only in the 'only target' condition. When a small target eliciting a PG was presented along with a *large* distractor evoking a WHG, the MEP amplitude was *higher* than when that target was alone ($p < 0.001$; see Fig. 2). More importantly, the MEP amplitude was likewise higher even when the large distractor was hidden ($p < 0.001$; see Fig. 2) and despite the fact that only a small target was visible in both conditions. The same effect was evident when a large target was presented. In particular, when a large target evoking a WHG was presented along with a *small* distractor potentially evoking a PG, the MEP amplitude was *lower* with respect to when a large target was presented alone ($p < 0.05$; see Fig. 2). More importantly, the MEP amplitude was likewise lower when the distractor was hidden ($p < 0.05$; see Fig. 2) and despite the fact that only a large target was visible in both cases. Accordingly, no statistically significant difference was found when conditions in which movement kinematics were identical were compared. The MEP amplitude did not differ when the participants observed the model grasping a small target in the presence of a large distractor or when a large distractor was hidden ($p = 0.92$). Similarly, MEP amplitude did not differ when the participants observed the model grasping a large target in the presence of a small distractor or when a small distractor was hidden ($p = 0.96$).

4. Discussion

The aim of this study was to identify what aspect of an observed action – the goal or the kinematics – modulates CS activity. An experiment was designed whereby participant observed actions characterized by the same goal but slightly different kinematical patterns. Although the differences in movement kinematics went unnoticed by the participants, they nonetheless elicited distinct configurations of corticospinal activation. The experiment showed that, in the absence of contextual cues, motor cortex excitability appears to be modulated by the hand movements observed and that, regardless of the goal, the object–target, or their corresponding motor representations, MEPs are closely linked to the kinematics characterizing observed actions.

When an object–target was presented in an isolated context, CS activity reflected the muscular activity characterizing the type of grasp observed. When the action observed was a whole hand grasp, both the FDI and the ADM muscles were activated. Conversely, only the FDI but not the ADM muscle was activated when the action observed was a precision grip. In those conditions in which the target was not alone, parallel planning for both the target and the distractor stimuli embedded in the model's kinematics was reflected in the onlooker's cortical activity. When the target was small and the distractor was large, ADM activation was increased compared to the 'only target' condition. But when the target was large and the distractor was small, ADM activation was decreased compared to the 'only target' condition. Unexpectedly, these same effects were also noted even when the distractor itself was hidden. There were, in fact, statistically significant differences in ADM activation when the 'only target' and the 'hidden distractor' conditions were compared even though the participants claimed they were visibly identical. In contrast to the hypothesis that CS facilitation reflects an action goal regardless of

the movements necessary to achieve it, the findings presented here strongly suggest that CS facilitation reflects a tight coupling with observed hand movements.

The data outlined here also support the hypothesis of an observation–execution matching system by which visual information concerning an observed action is integrated within the observer's motor system (Fadiga et al., 1995). Corticospinal facilitation based on passive action observation seems to reflect then a direct link between sensory representations of topographic features of an action and motor representations of the same or "corresponding" topographic features of that action, even if what is viewed does not necessarily coincide with what an observer would actually do to carry out that task. In the event of a conflict between the kinematics and the goal of an action, the muscles corresponding to the former rather than to the latter are facilitated.

The present study aimed to investigate what level of the hierarchy – observed movements or action goals – is reflected in CS excitability. It is important to remember that TMS experiments typically fail to show goal-related modulation in an observer's motor cortex and succeed in demonstrating that observed movements are processed in a strictly time-locked, muscle specific fashion (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Baldissera, Cavallari, Craighero, & Fadiga, 2001; Borroni & Baldissera, 2008; Borroni, Montagna, Cerri, & Baldissera, 2005; Candidi, Urgesi, Ionta, & Aglioti, 2008; Cavallo et al., 2011; Gangitano, Mottaghy, & Pasqual-Leone, 2001; Montagna, Cerri, Borroni, & Baldissera, 2005). The results outlined in this article complement and take these findings a step further by demonstrating that when different levels of representation are dissociated, modulation of M1 excitability reflects observed movements rather than action goals. They also indicate that these effects can be elicited by very subtle, unrecognizable aspects of observed actions, thus pointing to a finely tuned mechanism encoding body parts.

Corticospinal excitability during passive action observation seems then to simply reflect what is seen and not the suitability of an observed action, a theory that might also explain why facilitation emerges during observation of intransitive, meaningless movements (Alaerts et al., 2009; Catmur, Walsh, & Heyes, 2007; Fadiga et al., 1995; Urgesi et al., 2006).

The finding that motor resonance is very precise could appear to be at odds with the notion of a more abstract action representation which codes an observed action in terms of its goals but is neutral in terms of the executor (i.e., across different people). According to a recent hypothesis (Lepage, Tremblay, & Theoret, 2010; Lago & Fernandez-del-Olmo, 2011), there may be two different mechanisms simultaneously governing motor resonance: the first, which is neutral as far as the agent is concerned, maps an observed action in terms of the goal and the second specifies the muscles involved in the action. Lago and Fernandez-del-Olmo (2011) recently demonstrated that the specificity of a motor program activated via action observation depends on the temporal phase of the movement observed. During the observation of action preparation, both the action goal and the motor program are coded. Subsequently, when the actual hand–object interaction takes place, the specific muscles involved in the action are coded. The data outlined in this article are consistent with that hypothesis in view of the fact that MEPs acquired at the contact phase indicated that motor resonance effects were indeed muscle specific. It cannot be excluded that a more abstract representation that is neutral as far as the agent is concerned is activated during observation of action preparation.

Connected to this line of thought, Buccino and colleagues (2001) demonstrated that when humans observe an action, an internal replica of the action goal is automatically generated in their premotor cortex. This motor resonance reaches the motor neurons

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from the ventral premotor cortex through the primary motor cortex in which a muscle specific coding is activated (Borroni & Baldissera, 2008; Montagna, Cerri, Borroni, & Baldissera, 2005).

The results of the experiment outlined here also clarified another aspect with regard to action observation. In past studies, environments in which experiments were carried out were typically sparse, usually containing only one object to be acted upon. The ambiances in which humans live and move about in and interact with, are, instead, far more complex containing numerous objects towards which actions could be directed. In the face of the complex, dynamic environments in which humans move about in, highly efficient systems are needed to link perception and action (Allport, 1987). Those systems must, by necessity, process not only information about the object–target itself, but also about the motor features of all the objects which might become potential targets. The findings of the present study point to a simulation mechanism reflecting a model's action strategies. The MEP activity pattern analyzed by our experiment showed that during action observation the motor cortex recruits the same hybrid muscular activity in the onlooker as in the person actually performing the action, indicating that the motor system resonates with the extrinsic visual aspects of what the brain sees (Candidi et al., 2008; Cavallo et al., 2011; Gangitano, Mottaghy, & Pasqual-Leone 2001; Urgesi et al., 2006; see also Noy, Rumiati, & Flash, 2009). While our understanding of the activity in the human motor system during action observation has until now been limited to actions directed towards single objects, we have recently shown that this system can and does take into account an array of potential actions (Sartori et al., 2012). Just as individuals need to prepare for the possibility of changing their minds by integrating parallel motor plans, onlookers can also mirror motor integration finely conveyed in the kinematics of an observed action in order to predict possible outcomes. Inferring an underlying second goal rather than merely reading the kinematics of an observed action could lead to an alternative explanation for these results: that the cortical excitability pattern might be goal-directed to some extent.

Recent evidence suggests that covert imitation in the brain contributes to the perception of the behavior of conspecifics (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002; Loula, Prasad, Harber, & Shiffrar, 2005; Wilson & Knoblich, 2005). In particular, if actions are represented in terms of their perceptual consequences (Hommel, 2009; Hommel & Elsner, 2009), translating perceived human movement into corresponding motor programs would function as an emulator, tracking the behavior of conspecifics in real time to generate predictions of an unfolding action (Wilson & Knoblich, 2005). This internal modeling would allow the perceiver to rapidly interpret the perceptual signal, to quickly react, and to disambiguate uncertain situations such as those characterizing the present experimental paradigm. Although our data do not directly support a predictive coding hypothesis, they might be consistent with that hypothesis. Observing others' behaviors activates imitative motor plans in an observer even when the task does not explicitly require the motor simulation of the observed movements.

In conclusion, the experiment outlined here can be seen as an empirical contribution towards the emerging notion that motor cortex excitability is particularly sensitive to the topographic aspects of observed actions. Although the goal of an action is certainly an important element which modulates corticospinal excitability, our findings indicate that it is probably not the only factor to do so. These data seem to be directly relevant to theories concerning action observation and action prediction as they suggest that CS excitability is highly sensitive to the visual properties of observed movements.

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