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Grasping with Tools: Corticospinal Excitability Reflects Observed Hand Movements

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Although facilitation of the corticospinal system during action observation is widely accepted, it remains controversial whether this facilitation reflects a replica of the observed movements or the goal of the observed motor acts. In the present study, we asked whether, when an object is grasped by using a tool, corticospinal facilitation represents 1) the movements of the hand, 2) the movements of the tool, or 3) the distal goal of the action. To address this question, we recorded motor-evoked potentials (MEPs) to transcranial magnetic stimulation while participants observed a hand reaching and grasping a mothball by using 3 types of pliers, requiring different hand–tool movements to achieve the same goal (grasping the object). We found that MEPs recorded from the opponens pollicis and from the first dorsal interosseous reflected the observed hand movements rather than the movements of the tool or the distal goal of the action. These results suggest that during observation of tool actions, detailed motor matching recruits online the same muscles as those used in the observed action.

Keywords: action observation, goal, motor-evoked potentials, reach-to-grasp, transcranial magnetic stimulation

Introduction

Observation of other people's action selectively facilitates the brain's motor circuits for making the same action. In humans, the first demonstration of covert motor activation during action observation was provided by Fadiga et al. (1995) using transcranial magnetic stimulation (TMS). TMS was applied to the sector of M1 that represents the hand, and motor-evoked potentials (MEPs) were recorded from contralateral hand muscles during the passive observation of hand movements. Observing hand actions determined an enhancement of MEPs in the same muscular groups used in executing those actions, supporting the idea that the perceived actions were mapped onto the onlooker's motor system (for review, see Fadiga et al. 2005). Motor facilitation during action observation has since been replicated in numerous studies, and it is now well established that, in the absence of any detectable muscle activity, the mere observation of others' actions modulates the excitability of the observer's corticospinal circuitry (CS) involved in the execution of the same movements (e.g., Strafella and Paus 2000; Aziz-Zadeh et al. 2002; Maeda et al. 2002; Urgesi et al. 2006).

Although CS facilitation during action observation is widely accepted, it remains controversial how this facilitation relates to the observed behavior. The same behavior can be described and understood on at least 3 levels: goal level, kinematic level, and muscle level (Grafton and Hamilton 2007; Grafton 2009). Which level of the hierarchy does modulation in the observer's corticospinal system reflect? When a goal is present, is the MEP pattern of muscle recruitment linked to the observed movements or to the goal of the observed motor act?

To examine the specific contribution of goal and movements to covert motor activation, Cattaneo et al. (2009) designed a paradigm in which action goals were dissociated from the movements to achieve them by using 2 types of pliers: classic pliers and reverse pliers. With classic pliers, grasping was achieved by means of fingers' flexion, whereas with reverse pliers, it was achieved by means of fingers' extension. They found that when there was no goal in the observed behavior, MEPs recorded from the opponens pollicis (OP) reflected the movements performed by the agent. However, when a goal was present, MEPs increased during goal achievement, regardless of the pliers used and of the observed finger movements (flexion vs. extension). Based on these findings, the authors concluded that during observation of goal-directed actions, MEPs recorded from OP were modulated by the action goal rather than by the observed hand movements. In their words "observation of tool actions with a goal incorporates the distal part of the tool in the observer's body schema, resulting in a high order representation of the meaning of the motor act" (Cattaneo et al. 2009, p. 11134).

However, an alternative explanation for the findings reported by Cattaneo et al. (2009) is that corticospinal excitability during action observation reflected the movement of the tool and not the goal of the action. If the pliers were incorporated in the observer's body schema, as the authors suggest, then it might well be that OP muscle cortical excitability increased during the tool-closing phase. This is because with both classic and reverse pliers, grasping was achieved by means of a closing movement of the tool. This could indeed explain why the same modulation of OP muscle cortical excitability was observed for both classic and reverse pliers. It remains, therefore, an open question whether during observation of tool actions, CS facilitation represents 1) the movements of the hand, 2) the movements of the tool, or 3) the distal goal of the action.

To address this issue, in the present study, we recorded MEPs to TMS while participants observed a hand reaching and grasping a mothball by using 3 types of pliers: classic pliers, reverse pliers, and magnet pliers. With classic pliers, the object was grasped by means of a closing movement of the hand and a closing movement of the tool. With reverse pliers, the object was grasped by means of an opening movement of the hand and a closing movement of the tool. With magnetic pliers, the object was grasped by means of an opening movement of the hand and an opening movement of the pliers (see Fig. 1). MEPs were recorded simultaneously from the OP and from the first dorsal interosseous (FDI) muscles of the participants' right hand. We reasoned that if covert motor activation recruited during action observation reflects the observed hand

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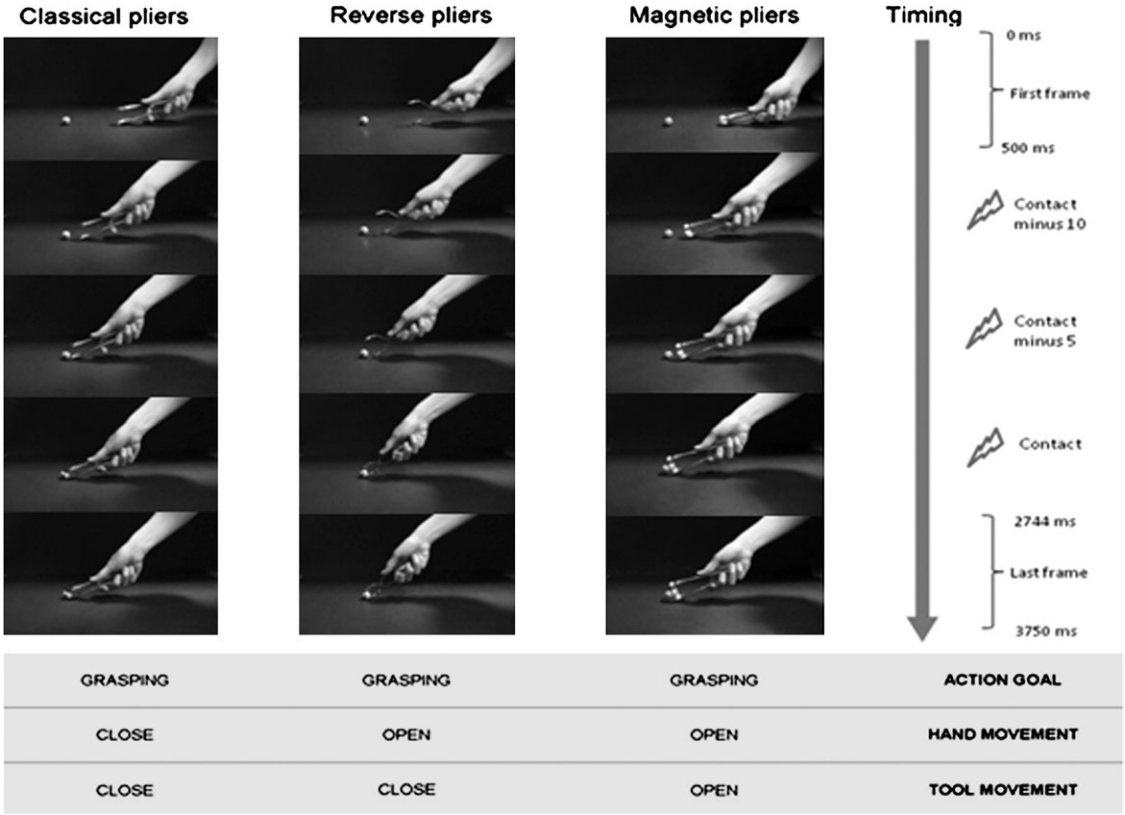

Figure 1. Schematic representation of event sequencing during a single trial for grasping with classic pliers, grasping with reverse pliers, and grasping with magnetic pliers. For each trial, the TMS pulse could be delivered at 1 of the 3 different delays: just before the frame showing the contact of the pliers with the mothball (contact 0); 5 frames before the contact of the pliers with the mothball (contact minus 5); and 10 frames before the contact of the pliers with the mothball (contact minus 10).

movements, then maximal CS excitability of OP and FDI muscles should be obtained during the observation of finger closure for tool actions performed using classic pliers. In contrast, if covert motor activation reflects the observed tool movements, then maximal CS excitability should be obtained during pliers closing for tool actions performed using classic or reverse pliers. Finally, if CS excitability represents the ultimate effect of the observed behavior, that is, grasping the object, a similar modulation of MEP amplitude should be obtained for tool actions using classic pliers, reverse pliers, and magnetic pliers, regardless of the observed hand–tool movements.

To further explore the relation between corticospinal excitability and observed behavior, we investigated whether the amplitudes of MEPs were related to the phases of the shown hand–tool movement. In this respect, Gangitano et al. (2001) demonstrated that during observation of hand grasping actions, the amplitude of MEPs induced by TMS in FDI was modulated by the amount of the observed finger aperture. If covert motor activation during observation of tool actions reflects hand or tool movements, then a similar phase-specific modulation might be observed in relation to observed hand or tool movements, respectively.

Materials and Methods

Participants

Twenty-two healthy individuals (15 women and 7 men) aged 19–30 (mean 22.6 years) took part in the experiment. All were right handed according to the Standard Handedness Inventory (Briggs and Nebes 1975). They had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Wasserman 1998; Rossi et al. 2009). All participants gave their written informed consent prior to their inclusion on the study and were naive as to its purpose. They received credits for their participation in the study. Specific information concerning the study was provided after the experimental session was terminated. 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. Due to discomfort with TMS stimulation, 1 female participant withdrew from the experiment following the procedure implying the determination of the optimal scalp position (OSP). No discomfort or adverse effects during TMS were reported or noticed in any of the other participants.

Stimuli

The experimental stimuli consisted of 3 types of colored video clips showing the following: 1) a hand reaching and grasping a mothball by using a classic pliers that could be closed by the flexion of the thumb and the index finger. The grasping was achieved by means of a closing movement of the hand and a closing movement of the pliers (close–close; Fig. 1*a*); 2) a hand reaching and grasping a mothball by using a reverse pliers that could be closed by the extension of the thumb and the index finger. The grasping was achieved by means of an opening movement of the hand and a closing movement of the pliers (open–close; Fig. 1*b*); 3) a hand reaching and grasping a mothball by using a pliers that opened up by extending the thumb and the index finger. A magnet was attached to the pliers' extremities, and the mothball was covered with metal foil so that the mothball could be grasped by opening the pliers. Because we used a weak magnet, the attraction of the magnet did not determine per se any movement of the ball: To grasp the ball, participants had to open the pliers and bring them into contact with the object. The grasping was therefore achieved by means

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of an opening movement of the hand and an opening movement of the pliers (open–open; Fig. 1*c*). At the beginning of each video clip, the hand of the model was shown in a prone position resting on a table with the mothball placed in front of it. Following 500 ms, the model's hand reached for the mothball, grasped it, and lifted it. Each video clip lasted 3750 ms, and the animation effect was obtained by presenting series of single frames each lasting 33 ms except for the first and last frame, which lasted 500 and 1006 ms, respectively (Fig. 1*d*).

Electromyographic and TMS Recording

MEPs were recorded simultaneously from the OP and the FDI muscles of the right hand. It is worth noting that while both muscles are strongly involved in the execution of closing movements of the hand, they do not play a role in opening movements. Electromyographic (EMG) recording was performed through pairs of Ag–AgCl surface electrodes (9 mm diameter) placed over the muscle belly (active electrode) and over the associated joint or tendon (reference electrode) in a classical belly-tendon montage. 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 was placed over the participants' left wrist and connected to the common input of the ExG input box. Responses were sampled, amplified, band-pass filtered (20 Hz–2 kHz), and stored on a PC for off-line analysis. A prestimulus recording of 100 ms was used to check for the presence of EMG activity before the TMS pulse. In order to prevent contamination of MEP measurements by background EMG activity, trials with any background activity greater than 100 μV in the 100-ms window preceding the TMS pulse were excluded from the MEP analysis. EMG data were collected for 200 ms after the TMS pulse. TMS was performed using a 70-mm figure-of-eight coil connected to a Magstim BiStim^2 (Magstim, Whitland, Dyfed, UK) placed over the left primary motor cortex. The coil was held tangentially to the scalp with the handle pointing backward and laterally with a 45° angle to the midline. This orientation was chosen on the basis of the evidence that the lowest motor threshold is achieved when the induced electric current in the brain is flowing approximately perpendicular to the central sulcus (Brasil-Neto et al. 1992; Mills et al. 1992). During the recording session, the coil was positioned over the left motor cortex in correspondence with the OSP, defined as the position from which MEPs with maximal amplitude were recorded simultaneously from the FDI (the muscle involved in index finger flexion–extension) and the OP (the muscle that allows to oppose the thumb). To find individual OSP, the coil was moved in steps of 1 cm over the motor cortex and the OSP was marked on a bathing cap worn by the participants. Even if it has been demonstrated that holding the coil by hand or by a holder induces a comparable MEP variability (Ellaway et al. 1998), we choose to hold the coil by a tripod, and the coil position with respect to the mark was checked continuously. Once the OSP was found, the resting motor threshold (rMT) was defined as the lowest intensity of stimulation that produced 5 MEPs of 10 consecutive magnetic pulses with at least 50 μV of amplitude in both the targeted muscles (Rossini et al. 1994). Stimulation intensity during the recording session was 110% of the rMT and ranged from 40% to 59% (mean 48.2%) of the maximum stimulator output.

Procedure

Before starting the TMS session, participants were presented with classic pliers, reverse pliers, and magnetic pliers and asked to use them to grasp and place small objects. Then, they were informed that they were to be presented with video clips representing a ball grasped by using the experienced types of pliers. Each participant was tested in a single experimental session lasting ~60 min. Experimentation was carried out in a dimly illuminated room. Participants were seated on a comfortable armchair with a fixed headrest. They were instructed to keep their hands still and as relaxed as possible. The task was to pay attention to the visual stimuli presented on a 19-inch monitor (resolution 1280 × 1024 pixels, refresh frequency 75 Hz) positioned 80 cm in front of them, at eye level. As a control for attention, participants were told that they would be debriefed about what they had seen at the end of the experiment.

For each of the type of observed movement (close–close, open–close, and open–open), the magnetic pulse was randomly delivered at 3 different delays: 1) just before the frame showing the contact of the pliers with the mothball (contact-0 trials); 2) 5 frames before the contact of the pliers with the mothball (contact-minus-5 trials) and; 3) 10 frames before the contact of the pliers with the mothball (contact-minus-10 trials). The main scope for using different delays was to avoid any priming effects that might have affected MEP size and to evaluate whether MEPs changed their peak-to-peak amplitude as a function of the delay of the TMS pulse. Six trials were presented for each stimulation time (0, minus 5, minus 10) for each type of movement (close–close, open–close, open–open), for a total of 54 randomly presented trials (3 stimulation times × 3 types of movement × 6 repetitions). We also recorded 2 series of 5 MEPs while participants observed a white-colored fixation cross presented on a black background. One series was recorded at the beginning, whereas the other was recorded at the end of the experimental session. Comparisons of MEP amplitudes for the 2 series allowed us to check for any corticospinal excitability change related to TMS per se. Following each trial, a rest period of 10 000 ms was given. During the first 5000 ms of the rest period, a message informing 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. Therefore, the interpulse interval ranged from about 13 to 14 s. The choice of the interpulse interval was based on the research that showed that even 1 h of TMS at 0.1 Hz did not induce any change in corticospinal excitability (Chen et al. 1997). Stimulus-presentation timing, EMG recording and TMS triggering, as well as randomization of stimuli were controlled by using E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC.

Data Analysis

Data were analyzed off-line. Background EMG level prior to TMS was calculated for each trial. Individual mean peak-to-peak amplitudes of MEPs recorded from the OP and the FDI muscles were calculated separately for each baseline condition, type of movement (close–close, open–close, and open–open), and trigger delay (0, minus 5, and minus 10). MEP amplitudes deviating more than 2 standard deviations from the mean of each experimental condition and single trials contaminated by muscular preactivation were excluded as outliers (1%) and precontracted trials (<1%). The individual mean amplitude of MEPs recorded in the 2 fixation-cross conditions served as baseline. A paired-sample *t*-test (two tailed) was used to compare the amplitude of MEPs recorded from the OP and the FDI muscles in the 2 series of baseline trials presented at the beginning and at the end of the experimental session. For each participant, MEP amplitudes were converted into a proportion of the baseline value. For each muscle, the mean MEP size was then normalized using log transformation to address nonnormality resulting from positive skew. In accordance with recommendations by Osborne (2002), a $\log_{10}$ and constant value of 1 were selected to resolve the issue while maintaining as closely as possible the order and spacing of the original distribution. For each muscle, normalized data were submitted to 2 separate repeated-measures analyses of variance (ANOVAs) with type of movement (close–close, open–close, and open–open) as a within-subjects factor. Moreover, for each type of movement, MEP amplitudes for the 2 considered muscles were entered into separate repeated-measures ANOVAs with trigger delay (0, minus 5, and minus 10) as a within-subjects factor. Post hoc pairwise comparisons were carried out by using *t*-tests, and Bonferroni corrections were applied. A significance threshold of $P < 0.05$ was set for all statistical tests.

Results

The raw mean amplitudes of MEPs from the OP and the FDI muscles recorded for different types of movement (close–close, open–close, and open–open) and baseline blocks are reported in Table 1. Mean raw MEP amplitudes during the 2 baseline

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Table 1
Amplitudes of MEPs recorded during baseline and experimental conditions

	Baseline		Classic pliers: close–close			Reverse pliers: open–close			Magnetic pliers: open–open		
	B1	B2	C 0	C-5	C-10	C 0	C-5	C-10	C 0	C-5	C-10
OP raw (μV)	507	543	551	516	558	465	459	552	430	475	479
Proportion			1.08	1.04	1.01	0.90	0.92	1.02	0.88	0.91	0.84
FDI raw (μV)	925	961	881	948	900	744	797	909	692	805	866
Proportion			1.01	1.22	1.06	0.82	0.86	0.97	0.77	0.81	0.95

Note: Mean peak-to-peak amplitudes of MEPs (raw and expressed as proportion of baseline values) recorded from the OP and the FDI muscles during the 2 baseline conditions run at the beginning (B1) and at the end (B2) of the experimental session and during the observation of grasping movements performed by using classic pliers (close–close movement), reverse pliers (open–close movement), and magnetic pliers (open–open movement). For each participant, MEP amplitudes were converted into a proportion of the baseline value. For each muscle, the mean MEP size was then normalized using log transformation to address nonnormality resulting from positive skew. C 0, contact-0 trials; C-5, contact-minus-5 trials; C-10, contact-minus-10 trials.

blocks administered at the beginning and at the end of the experimental session were not significantly different for either the OP (t_{21} = –0.587, P = 0.563) or the FDI muscle (t_{21} = –0.275, P = 0.786). This suggests that TMS per se did not induce any changes in corticospinal excitability in our experimental procedure. For both the OP and the FDI muscle, MEP amplitudes recorded for the different types of movements were not significantly different from baseline (P's ranging from 0.089 to 0.649). This nonsignificant effect has probably to be ascribed to the small number of MEPs recorded as to establish baseline values. Because facilitation compared with baseline was not the focus of the present work, only 5 MEPs were recorded during the fixation-cross trials administered at the start and at the end of the experimental session.

The repeated-measures ANOVA on normalized MEP amplitudes yielded a statistically significant main effect of type of movement for both the OP ($F_{2,42}$ = 6.810, P < 0.01) and the FDI ($F_{2,42}$ = 7.577, P < 0.01] muscle. Polynomial contrast revealed a significant linear effect for both the OP ($F_{1,21}$ = 15.545, P < 0.01) and the FDI ($F_{1,21}$ = 9.161, P < 0.01) muscle. For the OP muscle, post hoc comparisons revealed that MEP peak-to-peak amplitudes were greater for the "close–close" movement than for the "open–open" movement (P = 0.002) (Fig. 2*a*). Similarly, for the FDI muscle, post hoc comparisons revealed that MEPs were greater for the close–close movement than for the open–open movement (P = 0.019) and the "open–close" movement (P = 0.01) (Fig. 2*b*).

For the open–open movement, the repeated-measures ANOVA on MEP amplitudes yielded a statistically significant main effect of trigger delay for the FDI muscle ($F_{2,42}$ = 3.412, P < 0.05). The linear contrast was statistically significant ($F_{1,21}$ = 8.186, P < 0.01), suggesting that MEP amplitudes became smaller during hand opening (see Fig. 3*a*). A similar trend, although not statistically significant, was observed for the open–close movement (see Fig. 3*b,c*). Note that if CS excitability reflected the observed tool movements, then an opposite trend should have been observed for the open–close movement (MEPs smaller for "contact-minus-10" trials, larger for "contact-minus-5" trials, and largest for "contact-0" trials).

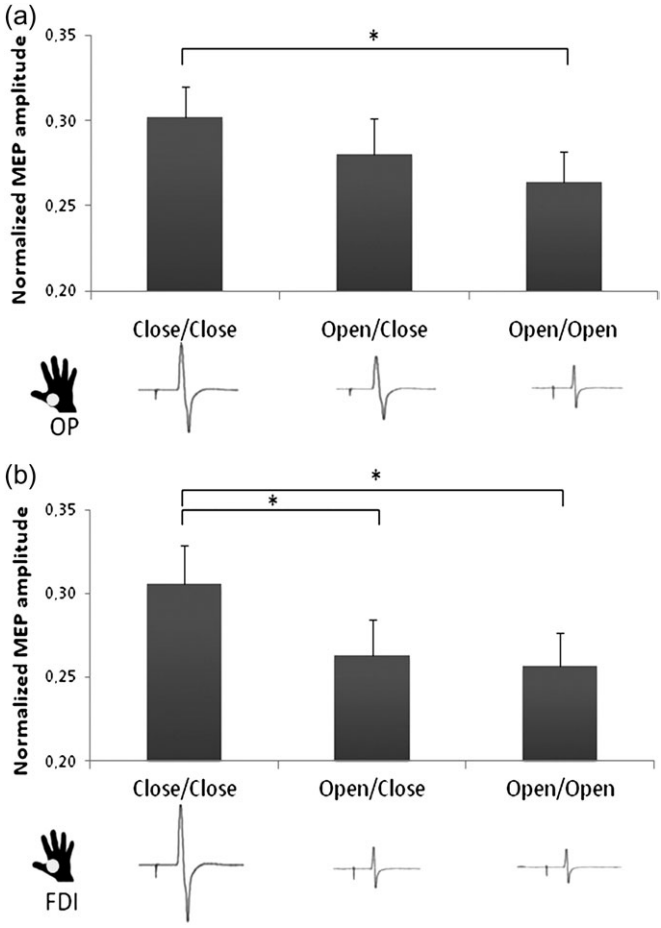

Figure 2. Normalized peak-to-peak amplitude scores recorded during the observation of different types of movement from the OP muscle (*a*) and the FDI muscle (*b*). Gray dots indicate to which muscle MEP scores refer to. Waveforms beneath the bars show representative examples of OP and FDI MEPs for different types of movement. Vertical bars denote ±standard errors. Asterisks indicate significant post hoc comparisons (P < 0.05).

Discussion

When an object is grasped by using a tool, which aspect of the motor behavior does CS facilitation reflect: the movements of the hand, the movements of the tool, or the distal goal of the action? The first main result of our experiment was the demonstration that maximal corticospinal excitability for OP and FDI muscles is obtained during the observation of tool actions performed using classic pliers. Because classic pliers imply a closing movement of the hand—whereas reverse pliers and magnetic pliers imply an opening movement of the hand—this finding provides direct evidence to show that motor cortex excitability reflects the observed hand movements. This conclusion was further supported by a phase-specific modulation of MEP amplitude in relation to observed hand movements during grasping with reverse and magnetic pliers. Amplitudes of MEPs for the FDI muscle were larger

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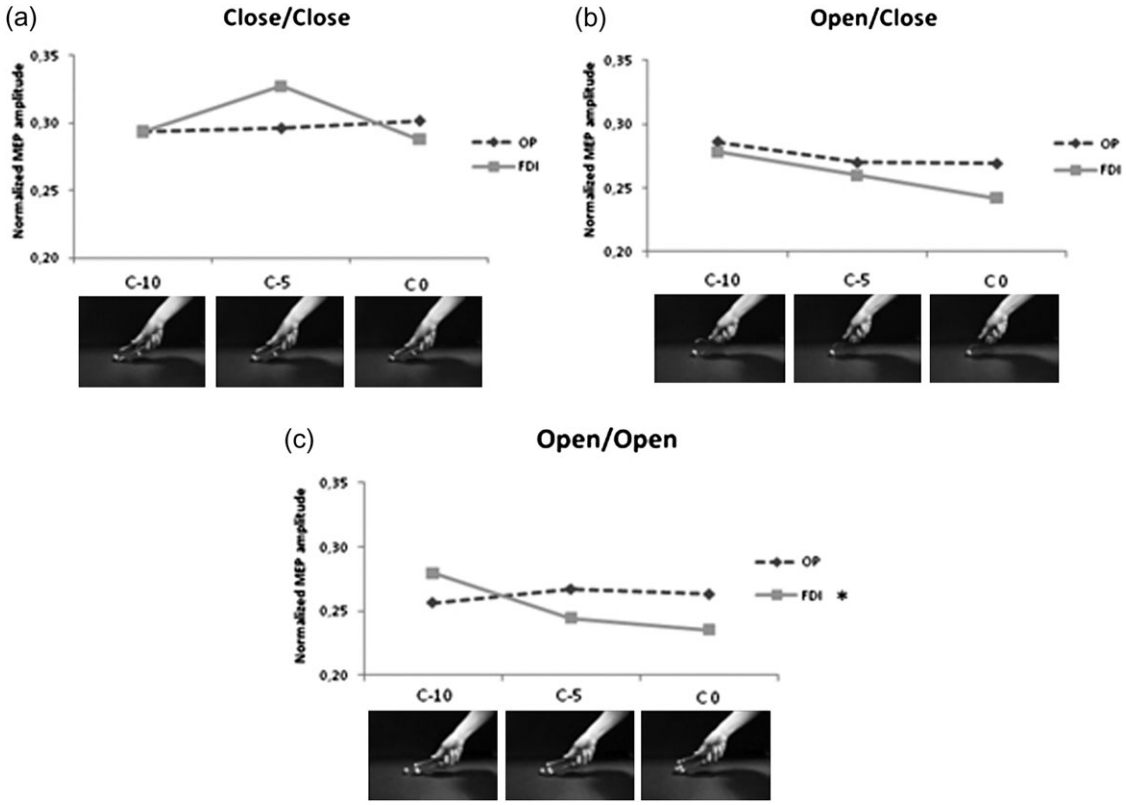

Figure 3. Representation of trigger-delay effect for the close–close (*a*), the open–close (*b*), and the open–open (*c*) movement. MEPs collected from the OP and the FDI were modulated by the degree of the shown finger aperture–closure. C-10, contact-minus-10 trials; C-5, contact-minus-5; C 0, contact-0 trials. Asterisk indicates a statistically significant effect of trigger delay ($P < 0.01$).

during hand closing and became smaller during hand opening. This suggests that CS excitability matched the dynamics of the observed hand movement (Gangitano et al. 2001, 2004). The finding that for the OP muscle no significant effect of trigger delay was observed is in line with previous evidence showing phase-specific modulation of MEP amplitude for index muscles but not for thumb muscles (Gangitano et al. 2001). Gangitano et al. (2001) interpreted this finding in terms of reduced thumb displacement: When grip closure is developed on a plane parallel to the observer point of view and the thumb appears almost statically transported on the target, no significant facilitation is observed for thumb muscles. A similar explanation might account for the lack of a phase-specific OP modulation in the present study: Because hand aperture and closure was mainly determined by the displacement of the index finger, whereas the movement of the thumb was minimal (see Fig. 1), phase-specific modulation of activity was observed in the FDI muscle but not in the OP muscle.

These findings are in conflict with the conclusions but not with the results reported by Cattaneo et al. (2009), who investigated grasping action performed with different tools. They recorded MEPs from the contralateral OP muscle while participants observed grasping action performed using classic and reverse pliers. Although opposite hand movements were necessary as to operate classic and reverse pliers, a similar pattern of motor activation was observed. This led the authors to conclude that when a goal is present, CS excitability reflects the ultimate effects of the observed movements over the object, regardless of which body part is actually moved as to achieve it.

Differently from Cattaneo et al. (2009), in the present study, we recorded MEP activity from 2 muscles simultaneously, the OP muscle and the FDI muscle. Furthermore, here, we used 3 rather than 2 types of pliers: classic pliers, reverse pliers, and magnetic pliers. Therefore, we have been able to dissociate between hand movements, tool movements, and action goals. If CS excitability represented the ultimate effect of the observed behavior, a similar modulation of MEP amplitude should have been observed regardless of the observed hand–tool movements. In contrast, we observed a statistically significant effect of type of movement for both the OP and the FDI muscle. In keeping with the results by Cattaneo et al. (2009), no significant difference was observed between MEPs recorded from OP during the observation of grasping actions performed with classic and reverse pliers. Crucially, however, MEPs recorded from FDI were greater for grasping with classic pliers than for grasping with reverse or magnetic pliers. In contrast to the hypothesis that CS facilitation reflects the action goal regardless of the movements necessary to achieve it, this finding suggests that CS facilitation reflects the observed hand movements.

Tool-Related Modulation of CS Excitability

For both the OP and the FDI muscle, a significant linear effect of type of movement was observed. One possible interpretation for these findings is that observed tool movements contribute, at least partly, to CS facilitation. With classic pliers, the object was grasped by means of a closing movement of the hand and a closing movement of the tool. With reverse pliers, the object

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was grasped by means of an opening movement of the hand and a closing movement of the tool. With magnetic pliers, the object was grasped by means of an opening movement of the hand and an opening movement of the pliers. If MEP amplitude increases during the closing phase of the hand and/or the tool, this would indeed explain why the strongest response occurred during the observation of a grasping action performed with classic pliers, followed by the observation of a grasping action performed with reverse pliers, and lastly by the observation of a grasping action performed with magnetic pliers.

An alternative yet not mutually exclusive interpretation is that modulation of MEPs during action observation is based on a "natural motor template": The more similar the observed motor act to the natural motor template, that is, grasping by the hand, the more pronounced the modulation in CS excitability. In monkeys, intensity of mirror neuron responses during grasping observation is strongest during the observation of grasping actions performed by hand, weaker for observation of grasping using reverse pliers, and weakest for observation of spearing with a stick (Rochat et al. 2010). Because grasping with reverse pliers resembles hand grasping, whereas spearing with a stick implies a motor act that radically differs from hand grasping, it has been proposed that visual mirror responses in premotor area F5 are stronger when the effector–object interaction resembles more faithfully that performed by the natural effector. Similarly, our results might be interpreted as indicating that modulation of CS facilitation reflects the similarity between the observed motor act and grasping by hand. In this interpretation, the same resonant motor plan would be activated by the observation of grasping action performed by different effectors, whereas the degree of activation might depend upon the resemblance of the observed motor act with the natural motor template.

Finally, it should be considered that although using the magnetic pliers was similar to using the reverse pliers—both types of pliers requiring an opening movement of the hand—this does not necessarily imply that the FDI and the OP muscles were activated to a similar extent and with the same timing in the 2 grasping conditions. This raises the question of whether modulation of MEPs during tool action observation might reflect differential involvement of the FDI and the OP muscles during execution of the corresponding grasping actions. Experiments recording EMG activity during execution of tool actions using reverse and magnetic pliers are needed to clarify this issue.

Representation of Observed Actions in M1

It has been proposed that within the human motor system, action representation is hierarchically distributed across a set of interconnected brain areas that are differently recruited for different aspects of goal-oriented behavior (Grafton and Hamilton 2007; Grafton 2009). In particular, whereas the parietal node of the action observation network, namely the inferior parietal lobule, is assumed to provide a goal description of the observed motor act (Hamilton and Grafton 2006; Grafton and Hamilton 2007; Tunik et al. 2007; Hamilton and Grafton 2008), the frontal node, namely the inferior frontal gyrus, is suggested to represent the kinematic features of the observed movement (Pobric and Hamilton 2006; Grafton and Hamilton 2007). In the present study, we investigated which level of the hierarchy—observed movements or action goal—does CS excitability in M1 reflect. TMS experiments typically fail to show goal-related modulation in the observer's motor cortex. Instead, they reveal a processing of the observed movement in a strictly time-locked and muscle-specific fashion (Gangitano et al. 2001; Borroni et al. 2005; Montagna et al. 2005; Borroni and Baldissera 2008; Alaerts et al. 2009; Alaerts, Senot, et al. 2010; Alaerts, Swinnen, et al. 2010; Cavallo et al. 2011; Urgesi et al. 2010). Our results add to this literature suggesting that during observation of tool actions modulation of M1 excitability reflects the observed movements, rather than the action goal.

To conclude, the present results demonstrate that during observation of tool actions, detailed motor matching recruits online the same muscles as those used in the observed action. These findings are directly relevant for theories of action observation and motor cognition as they suggest that observed and executed actions might be linked at a movement level. Sensorimotor learning (Heyes 2001, 2010a, 2010b) provides a plausible explanation for this link: Experiences in which observation and execution of the same movement occur in contingent manner, including observing one's own actions and being imitated, forge strong links between visual and motor neurons coding similar movements. Given sufficient "mirror" experience, motor areas with appropriate neuroanatomical connections with sensory areas may acquire as well as loose (e.g., Catmur et al. 2007, 2011) visuomotor matching properties.

More generally, detailed motor matching of the observed movement might be relevant to the understanding of motor learning (Mattar and Gribble 2005; Stefan et al. 2005, 2008; Cross et al. 2006; Frey and Gerry 2006) and to the developing of interventions that seek to stimulate and improve motor functions via action observation (Celnik et al. 2006, 2008; for review, see Mulder 2007). Acting "with objects" (i.e., tool use) involves motor schemata that often differ dramatically from those involved in acting "on objects" (reaching, grasping, manipulation; Johnson-Frey and Grafton 2003; see also Johnson-Frey 2004). The fact that movement-specific motor matching extends to tool actions suggests that action observation might be beneficial for learning (and re-learning) not only object-directed hand action but also tool actions.

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