

# Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker's posture

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## Abstract

Transcranial magnetic stimulation (TMS) studies report that viewing a given action performed by a model activates the neural representation of the onlooker's muscles that are activated during the actual execution of the observed action. Here we sought to determine whether this mirror observation-execution facilitation reflects only muscular specificity or whether it is also influenced by postural congruency between onlooker/model body parts. We recorded motor potentials evoked by single-pulse TMS from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles during observation of the right index and little finger abduction/adduction movements of models who kept their hands in a palm-down or palm-up position. Moreover, in different experiments observers kept their right hand palm down or palm up. Selective motor facilitation was observed during observation of movements that map the motor function of the targeted muscles, regardless of the posture of the observed hand. Modulation of FDI, however, was obtained only when participants kept their hand palm down; by contrast, modulation of ADM was obtained only when participants kept their hand palm up. Interestingly, electromyographic recordings showed that FDI is mostly active when index abduction/adduction movements are performed in the palm-down position, whereas ADM is mostly active when little finger abduction/adduction movements are performed in the palm-up position. Results show that the influence of the onlooker's hand posture is comparable in action execution and observation, thus indicating a fine-grain functional correspondence between these two processes.

## Introduction

The notion of motor mirroring is based on the striking result that viewing actions performed by other individuals activates neural circuits typically involved in motor planning and execution of the very same actions (Rizzolatti & Craighero, 2004). Neuroimaging studies suggest that the mirror-neuron system in humans includes a large, mainly fronto-parietal, neural network that matches action observation and execution (e.g. Hari *et al.*, 1998; Iacoboni *et al.*, 1999; Buccino *et al.*, 2001). By using single-pulse transcranial magnetic stimulation (TMS) it has been shown that action observation triggers specific mirror activation of the muscles that would be involved in the actual execution of the very same action (Fadiga *et al.*, 2005). Such a specific muscular facilitation supports the notion of a direct mapping of the observed actions onto the observer's motor system. The facilitation effect, however, might be linked to the process of mapping not only the motor commands but also the proprioceptive feedback that is inherently linked to action execution. In keeping with this view is the finding that mirror motor mapping occurs also for biomechanically impossible movements that cannot be coded in terms of stored motor commands (Romani *et al.*, 2005). In a similar vein, action observation activates primary sensorimotor parietal areas (Rossi *et al.*, 2002;

Avikainen *et al.*, 2002) and impossible actions engender higher activation of parietal areas with respect to possible actions (Costantini *et al.*, 2005). Moreover, the observer's actual body posture affects behavioural performance (Parsons, 1994; Sirigu & Duhamel, 2001) as well as neural responses (Vargas *et al.*, 2004) in motor imagery tasks that are known to activate cortical motor areas also active during action observation and execution (Jeannerod & Frak, 1999). Thus, it is plausible that the amount of motor facilitation during action observation might be influenced by the postural congruency between the onlooker's and the model's hands. It is also worth noting that the presence or absence of postural congruency would or would not imply a spatial correspondence between the observed movement and the movement resulting from the observer's contraction of the very same muscle while holding a specific hand posture.

The present study was aimed at testing whether activation of specific muscles during movement observation reflects the mirror motor mapping of the observed movements or the spatial congruency between the onlooker's/model's hand postures. To test the influence of these variables on motor facilitation contingent upon action observation, participants were asked to keep their hand palm down (Experiment 1) or palm up (Experiment 2) while watching video clips of palm-up or palm-down hands in which the index or the little finger performed abduction/adduction movements. Moreover, in Experiment 3, we recorded muscular activity during the actual execution of the same movements observed in Experiments 1 and 2. Thus, we tested

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the effect of both the observer's and of the observed hand posture on motor facilitation during action observation and compared it with the influence of hand posture during action execution.

## Materials and methods

### Participants

Sixteen healthy individuals (seven women and nine men) aged 18–26 (mean age 21.9 years) participated in Experiment 1; 12 healthy individuals (eight women and four men) aged 19–29 (mean 23.5 years) participated in Experiment 2. Eight healthy volunteers (six women and two men) aged 20–28 years (mean 23.9 years) participated in Experiment 3. None of participants were recruited for more than one experiment. A standard handedness inventory (Briggs & Nebes, 1975) allowed us to ascertain that all participants were right-handed. The participants were native Italian speakers with normal or corrected-to-normal visual acuity in both eyes; none had neurological, psychiatric or other medical problems or any contraindication to TMS (Wasserman, 1998). They were naïve as to the purposes of the study, and information about the experimental hypothesis was provided only after the experimental tests were completed. Participants gave their written informed consent and received 15 Euros for taking part in the TMS experiments. The procedures were approved by the ethical committee of the University of Verona and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No participants complained of any discomfort or presented with any adverse effects during TMS.

### Electromyographic recording and TMS

Motor-evoked potentials (MEPs) were recorded simultaneously from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles of the right hand. Electromyographic (EMG) recordings were performed with surface Ag/AgCl cup electrodes (1 cm diameter) placed in a belly tendon montage with active electrodes over the motor point and the reference electrodes over the interphalangeal joint. Responses were amplified, band-pass filtered (5 Hz–5 kHz), and digitized by means of a Viking IV electromyography apparatus (Nicolet Biomedical, Madison, WI, USA). The sampling rate of the EMG signal was 20 kHz. A prestimulus recording of 20 ms was used to assess the presence of EMG activity before the TMS pulse. To further control for the absence of unwanted background EMG activity before the magnetic pulse, the signal from both muscles was additionally displayed in separate channels set at high sensitivity (50  $\mu$ V). Moreover, during the preliminary session, EMG signals were sent to loudspeakers in order to provide participants with an auditory feedback of their muscular relaxation.

In Experiment 3, the EMG was recorded simultaneously from the FDI and ADM muscles of the dominant hand during execution of the movements that were observed in the previous experiments. To control for changes contingent upon hand posture in muscles that are not specifically involved in the execution of finger movements, the EMG was also recorded from the extensor carpi radialis (ECR) muscle. The EMG signal was amplified at a gain of 1000 by a Digitimer D360 amplifier (Digitimer, Hertfordshire, UK), band-pass filtered (20 Hz–2.5 kHz), and digitized by a CED Power 1401 controlled by means of the Spike2 software (Cambridge Electronic Design, Cambridge, UK). The sampling rate was set at 5 kHz.

Focal TMS was performed by means of a 70-mm figure-eight stimulation coil (Magstim polyurethane-coated coil) connected to a Magstim 200 Rapid (The Magstim Company, Carmarthen, UK),

producing a maximum output of 2 T at the coil surface (pulse duration, 250  $\mu$ s; rise time, 60  $\mu$ s). The coil was placed tangentially to the scalp, with the handle pointing backward and laterally at 45° away from the midline, approximately perpendicular to the line of the central sulcus. This orientation induced a posterior-anterior current in the brain and was chosen on the basis of the finding 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). The coil was positioned over the optimal scalp position (OSP), defined as the position from which MEPs with maximal amplitude were recorded simultaneously from the FDI and ADM muscles. With this coil position, a stable signal was obtained from both muscles in all participants, and is in keeping with TMS studies showing that the distance between the OSPs for the two muscles is within the spatial resolution of the employed coil (approximately 1 cm; Krings *et al.*, 1998; Facchini *et al.*, 2002). The OSP was detected by moving the intersection of the coil in steps of 1 cm around the motor-hand area of the left motor cortex and by delivering TMS pulses with constant intensity. Participants wore a tight-fitting bathing cap on which the scalp positions for stimulation were marked. The coil was held by hand, and its position with respect to the marks was checked continuously. The resting motor threshold (rMT), defined as the lowest stimulus intensity able to evoke five out of 10 MEPs with an amplitude of at least 50  $\mu$ V in both of the targeted muscles, was determined by holding the stimulation coil over the OSP. During the recording session, the stimulation intensity was 130% of the rMT and ranged from 62% to 88% (mean 75.8%) of the maximum stimulator output in Experiment 1 and from 47% to 98% (mean 73.9%) of the maximum stimulator output in Experiment 2. The peak-to-peak amplitudes of the MEPs (in mV) were collected and stored on a computer for offline analysis.

### Stimuli and procedure

Experimental stimuli consisted of colour video clips representing abduction/adduction movements of the right index and little finger of a male (aged 26) and female (aged 29) model. The models' hands were viewed in both palm-down and palm-up postures, and the angular displacement of the finger movements in both postures ranged from 0° to 30°. We also showed the static image of the models' still hands in both postures. Thus, for each model six video clips were created corresponding to the factorial combination of movement (still hand, index finger abduction/adduction, little finger abduction/adduction) and posture (palm down, palm up). Video clips lasted 3300 ms and showed two cycles of abduction/adduction movements of the fingers with a frequency of 0.6 Hz. The animation effect was obtained by presenting series of single frames each lasting 33 ms. Static hand images had the same duration as the moving stimuli. Participants sat 80 cm away from a 19-inch monitor (resolution, 640  $\times$  480 pixels; refresh frequency, 85 Hz) on which stimuli appeared on a uniform background and subtended a visual angle of 11.4°  $\times$  12.1°. Stimulus-presentation timing, EMG recording and TMS triggering, and randomization were controlled by using E-prime V1.1 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC.

Each participant was tested in one experimental session lasting approximately 90 min. Participants sat in a comfortable armchair in a dimly illuminated room with their right hand resting on a pillow; they were instructed to keep their hand still and to fully relax with the help of the auditory feedback. To explore the possible effect of the spatial congruency between the model's posture and that of the observer, MEPs were recorded while participants kept their hand palm down

(Experiment 1) or palm up (Experiment 2). In both experiments, the left hand was always kept in a palm-down position. Muscular relaxation of the right hand, from which MEPs were recorded, was complete in both hand postures. Participants were instructed to pay attention to the stimuli presented on the screen and were informed that, when requested at a given point during the experiment, they were to report the gender of the hand presented in the trial. In each block, the experimenter requested reports at the end of six randomly selected trials. No overt response was required at any time during stimuli presentation and data collection. The six types of video clips were presented in separate blocks counterbalanced according to a Latin square design. Each block consisted of 16 trials with a random presentation of male and female hand stimuli; a short rest was allowed before proceeding to a different block. At the beginning and at the end of the experimental session, 16 MEPs were recorded while participants had their eyes closed to ensure that no change in corticospinal excitability related to TMS *per se* occurred. In each trial, the magnetic pulse was delivered between 660 and 990 ms before the end of the movie to avoid any priming effects that could affect MEP size and a blank screen lasting 7.7 s was presented before the next trial (time between pulses, 10.01–10.34 s). The choice of the interstimulus interval was based on research by Chen *et al.* (1997) that demonstrated no change in corticospinal excitability with repetitive TMS at 0.1 Hz for 1 h.

In Experiment 3, EMG activity was recorded from two hand muscles (FDI, ADM) and from a forearm muscle (ECR) that is not involved in the actual execution of the index and little finger abduction/adduction movements. The EMG was recorded while participants executed index and little finger abduction/adduction movements with the moving hand in both palm-down and palm-up posture. The four types of movements were tested in separate blocks and the order of the four blocks was counterbalanced across participants; for each block, 16 cycles of two movements were performed. Before each block, the experimenter showed the movement to be executed; to maximize analogies between the executed and the observed movements, angular displacement and pace of movements during execution was identical to that of the observation conditions.

### Data handling

Task compliance was good in both TMS experiments, as assessed by immediate verbal report of the gender of the presented hand. The absence of background EMG activity was confirmed through visual inspection of the data. Individual mean peak-to-peak MEP amplitudes were calculated separately for each block (16 trials per cell) and each muscle. Trials with background activity preceding the TMS pulse or with an MEP amplitude that could not be distinguished clearly from

background EMG activity ( $< 90 \mu\text{V}$ ) were discarded (3.2% and 3.9% of the total in Experiments 1 and 2, respectively). To compare the baseline level of corticospinal excitability of the participants in Experiments 1 and 2, rMT and the raw amplitudes of MEPs recorded during the two eyes-closed conditions were compared further by means of series of independent-sample *t*-tests (two-tailed). For each participant, raw amplitudes of MEPs recorded from each muscle were *z*-transformed to control for the interindividual variability of the absolute level of MEPs amplitude. The individual mean *z*-scores were calculated for the two eyes-closed and the six observation conditions. To check whether any corticospinal excitability change occurred during the experiment, we compared the two eyes-closed conditions at the beginning and at the end of the experiment by means of paired-sample *t*-tests (two-tailed). Moreover, normalized MEP amplitudes for each muscle during the observation conditions were entered in repeated-measures analyses of variance (ANOVAS) with posture (palm down, palm up) and movement (still hand, index finger abduction/adduction, little finger abduction/adduction) as within-subjects variables.

In Experiment 3, the raw maximal EMG amplitude (MEA; in mV) from each muscle (FDI, ADM, ECR) was computed for each trial and each type of movement. For each muscle, MEA was entered in two-way repeated-measures ANOVAS with participants' posture (palm-down, palm-up) and type of movement (index finger abduction/adduction, little finger abduction/adduction) as within-subjects variables. *Post hoc* multiple comparisons were performed using the Tukey test.

## Results

### Experiment 1

Raw mean MEP amplitudes during the eyes-closed conditions and the six observation conditions are reported in Table 1. No difference was observed between normalized MEP amplitudes during the eyes-closed condition blocks performed at the beginning and at the end of the experiment. This was true for both the FDI ( $t_{15} = 0.97$ ,  $P = 0.346$ ) and the ADM muscle ( $t_{15} = -0.70$ ,  $P = 0.494$ ).

Analysis of normalized MEP amplitudes recorded from the FDI during the observation conditions yielded a significant main effect of movement ( $F_{2,30} = 9.20$ ,  $P = 0.001$ ). A *post hoc* test showed that the MEP amplitude was higher during the index finger abduction/adduction condition than during the still hand ( $P = 0.001$ ) and the little finger abduction/adduction conditions ( $P = 0.026$ ), which in turn did not differ from one another ( $P = 0.325$ ). The main effect of posture ( $F_{1,15} = 2.46$ ,  $P = 0.137$ ) and the interaction movement  $\times$  posture ( $F_{2,30} = 0.03$ ,  $P = 0.972$ ) were nonsignificant, thus showing that the somatotopic mapping of the observed movement was scarcely influenced by the spatial congruency between the model's and the

TABLE 1. Potential amplitudes from the FDI and ADM muscles during the two eyes-closed condition blocks in Experiment 1

	Potential amplitude (mV)							
	Eyes-closed		Palm-down			Palm-up		
	B1	B2	Static	Index finger	Little finger	Static	Index finger	Little finger
FDI	2.82 $\pm$ 0.29	2.61 $\pm$ 0.3	2.91 $\pm$ 0.37	3.31 $\pm$ 0.39	3.18 $\pm$ 0.44	2.69 $\pm$ 0.31	3.28 $\pm$ 0.44	2.88 $\pm$ 0.39
ADM	1.7 $\pm$ 0.24	1.89 $\pm$ 0.32	1.93 $\pm$ 0.28	1.97 $\pm$ 0.24	2.1 $\pm$ 0.35	1.7 $\pm$ 0.22	1.96 $\pm$ 0.23	2.1 $\pm$ 0.31

Values are given as means  $\pm$  SEM. Recordings were made at the beginning (B1), at the end of the experimental session (B2) and during the six observation condition blocks in Experiment 1. ADM, abductor digiti minimi; FDI, first dorsal interosseous muscle.

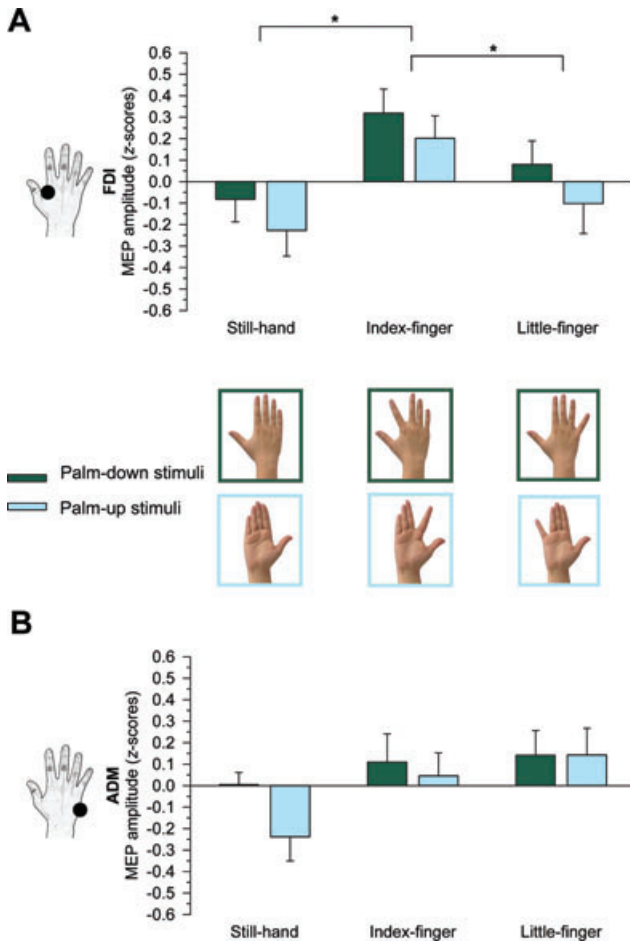


FIG. 1. Mean amplitudes (z-scores) of motor-evoked potentials (MEPs) recorded from the first dorsal interosseus (FDI; A) and abductor digiti minimi (ADM; B) muscle in Experiment 1 in which participants kept their hands in the palm-down position. Hand figurines show the observer's hand posture. The dot on each figurine indicates the muscle from which motor potentials were recorded. Pictures of hands in the middle row show the female model's hands presented during the observational conditions of palm-down (dark bars) and palm-up (light bars) stimuli. Error bars indicate standard errors; \* $P < 0.05$ .

observer's hand (Fig. 1A). Planned comparisons confirmed results of the main analysis by showing that MEP amplitude during observation of index finger abduction/adduction movements significantly differed from MEP amplitude during observation of the still hand, both when the hand stimulus was in palm-down ( $F_{1,15} = 4.71, P = 0.046$ ) and in palm-up ( $F_{1,15} = 7.46, P = 0.015$ ) positions. By contrast, the MEP

amplitude during observation of little finger abduction/adduction movements did not significantly differ from the MEP amplitude during observation of the still hand in the palm-down ( $F_{1,15} = 1.38, P = 0.259$ ) as well as in the palm-up posture condition ( $F_{1,15} = 0.38, P = 0.545$ ).

Analysis of normalized MEP amplitudes recorded from the ADM during the observation conditions showed nonsignificant main effects of movement ( $F_{2,30} = 2.36, P = 0.11$ ) and posture ( $F_{1,15} = 1.04, P = 0.323$ ), as well as a nonsignificant movement–posture interaction (Fig. 1B;  $F_{2,30} = 0.79, P = 0.461$ ).

Experiment 2

In this experiment, all procedures and stimuli were identical to those of Experiment 1 except that the participants kept their hands in the palm-up position. Raw mean MEP amplitudes during the two eyes-closed blocks and the six observations in Experiment 2 are reported in Table 2. No difference was observed between MEP amplitudes during the two eyes-closed blocks run at the beginning and at the end of the experiment for either the FDI ( $t_{11} = -0.67, P = 0.516$ ) or the ADM muscle ( $t_{11} = 0.46, P = 0.652$ ), thus confirming that no change in the excitability of the corticospinal system related to TMS *per se* occurred during the experimental session.

A between-experiments comparison showed no across-group difference in raw MEPs amplitudes in the eyes-closed conditions run at the beginning (FDI:  $t_{26} = 1.63, P = 0.115$ ; ADM:  $t_{26} = 0.35, P = 0.726$ ) and at the end of the experiment (FDI:  $t_{26} = 1.31, P = 0.2$ ; ADM:  $t_{26} = 0.24, P = 0.813$ ). Moreover, there was no rMT difference in observers who kept their hand in the palm-down (Experiment 1) or the palm-up (Experiment 2) position ( $t_{26} = 0.16, P = 0.872$ ). These results indicate that the observer's hand posture did not modify corticospinal excitability at rest. However, the observer's posture affected the modulation of the two target muscles during movement observation. Indeed, in striking contrast with the results of Experiment 1, analysis of normalized MEP amplitudes recorded from FDI during the observation conditions showed that the main effect of movement ( $F_{2,22} = 1.21, P = 0.318$ ) and posture ( $F_{1,11} = 0.54, P = 0.478$ ), as well as the movement–posture interaction ( $F_{2,22} = 1.10, P = 0.35$ ) were nonsignificant (Fig. 2A). Analysis of normalized MEP amplitudes recorded from ADM during the observation conditions yielded a highly significant main effect of movement ( $F_{2,22} = 12.15, P = 0.001$ ), because MEP amplitude was higher during observation of little finger abduction/adduction movements than during observation of the still hand ( $P = 0.001$ ) and of the index finger abduction/adduction movements ( $P = 0.004$ ), which in turn did not differ from one another ( $P = 0.591$ ). The main effect of posture ( $F_{1,11} = 0.39, P = 0.545$ ) and the movement–posture interaction ( $F_{2,22} = 0.4, P = 0.678$ ) were nonsignificant, thus showing

TABLE 2. Potential amplitudes from the FDI and ADM muscles during the two eyes-closed condition blocks in Experiment 2

	Potential amplitude (mV)							
	Eyes-closed		Palm-down			Palm-up		
	B1	B2	Static	Index finger	Little finger	Static	Index finger	Little finger
FDI	1.92 ± 0.51	1.90 ± 0.49	2.44 ± 0.64	2.25 ± 0.58	2.47 ± 0.64	1.88 ± 0.39	2.42 ± 0.59	2.43 ± 0.57
ADM	1.57 ± 0.28	1.77 ± 0.41	1.82 ± 0.35	1.97 ± 0.41	2.42 ± 0.53	1.8 ± 0.34	1.99 ± 0.44	2.49 ± 0.46

Values are given as means ± SEM. Recordings were made at the beginning (B1), at the end of the experimental session (B2) and during the six observation condition blocks in Experiment 2. ADM, abductor digiti minimi; FDI, first dorsal interosseus muscle.

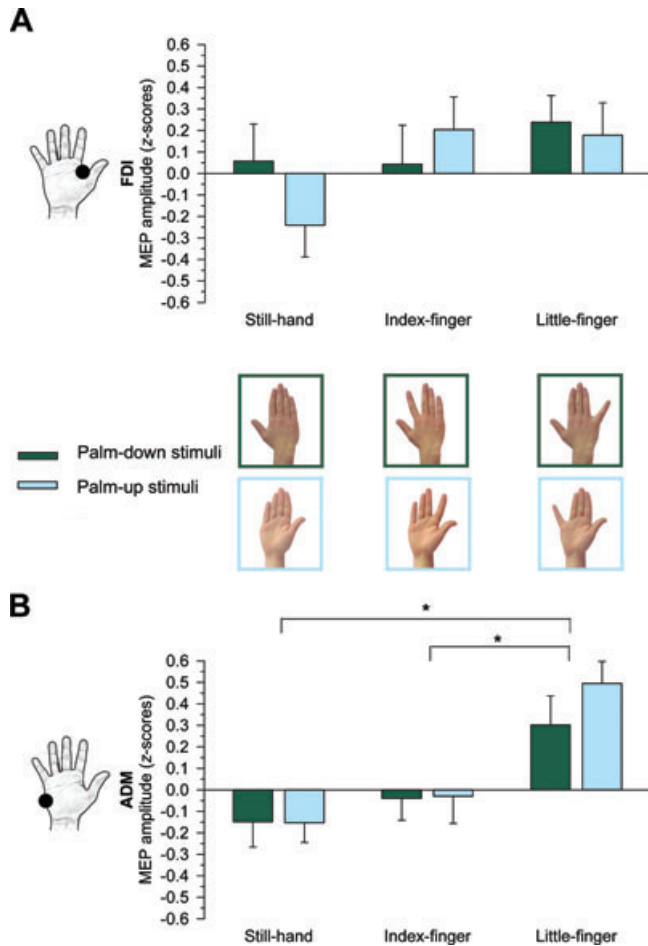


FIG. 2. Mean amplitudes (z-scores) of motor-evoked potentials (MEPs) recorded from the first dorsal interosseus (FDI; A) and abductor digiti minimi (ADM; B) muscle in Experiment 2 in which participants kept their hands in the palm-up position. Hand figurines show the observer's hand posture. The dot on each hand figurine indicates the muscle from which motor potentials were recorded. Pictures of hands in the middle row show the male model's hands presented during the observational conditions of palm-down (dark bars) and palm-up (light bars) stimuli. Error bars indicate standard errors;  $*P < 0.05$ .

that modulation of the ADM muscle contingent upon observation was not influenced by the spatial congruency between the model's and the observer's hand (Fig. 2B). Planned comparisons confirmed the significant facilitation of MEPs recorded from the ADM muscle during observation of little finger movements compared to observation of the still hand, both with palm-down ( $F_{1,11} = 4.82$ ,  $P = 0.05$ ) and palm-up hand stimuli ( $F_{1,11} = 18.02$ ,  $P = 0.001$ ). No significant difference emerged between observation of index finger movements and observation of the still hand in either posture condition ( $F_{1,11} < 1$ ).

### Experiment 3

The MEA data related to execution of the four types of finger movements observed in Experiments 1 and 2 are presented in Fig. 3, separately for each muscle (FDI, ADM, ECR).

Analysis of MEAs recorded from the FDI muscle (Fig. 3A) showed a significant main effect of type of movement ( $F_{1,7} = 26.13$ ,  $P = 0.001$ ), because the MEA was higher during execution of index

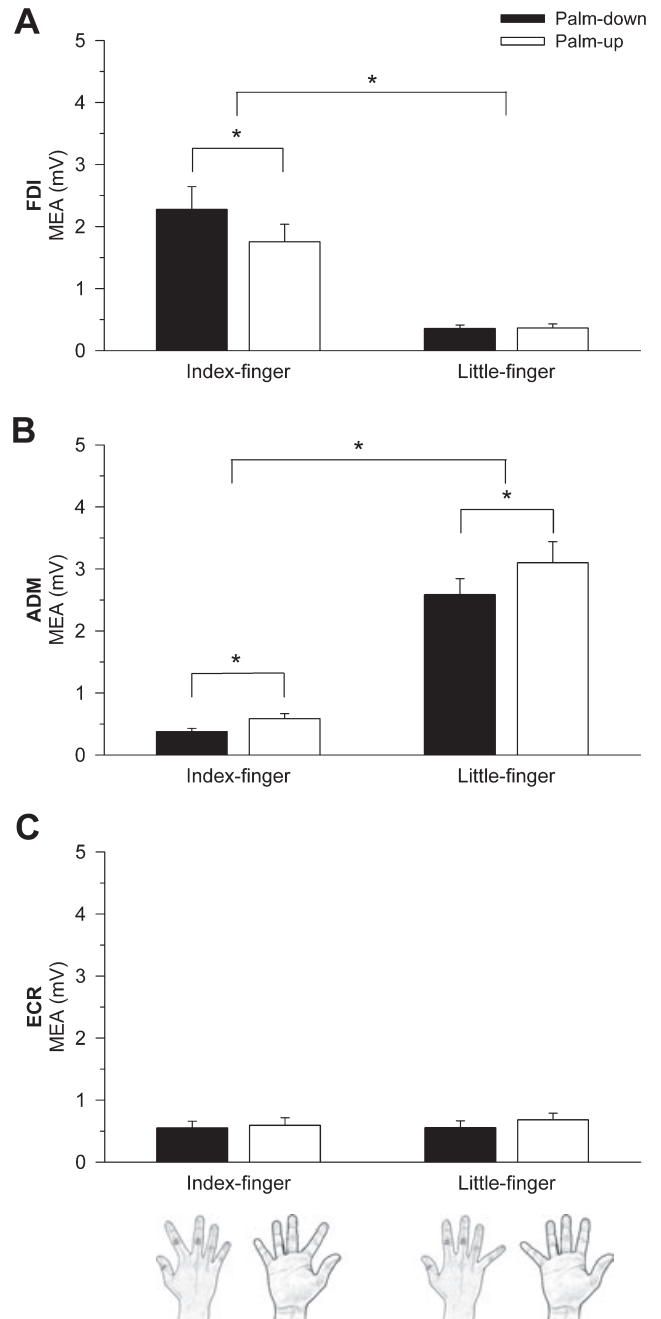


FIG. 3. Maximal electromyographic activity (MEA) recorded from the first dorsal interosseus (FDI; A), abductor digiti minimi (ADM; B), and extensor carpi radialis (ECR; C) muscles while participants of Experiment 3 executed index finger and little finger abduction/adduction movements in palm-down and palm-up hand postures. Hand figurines show the moving finger and the participant's hand posture during movement execution. Error bars indicate standard errors;  $*P < 0.05$ .

finger ( $2.01 \text{ mV} \pm 0.32 \text{ mV}$ ) than little finger abduction/adduction movements ( $0.36 \text{ mV} \pm 0.06 \text{ mV}$ ), and a significant main effect of participants' posture ( $F_{1,7} = 11.02$ ,  $P = 0.013$ ), because MEA was higher when participants kept their hand palm down ( $1.31 \text{ mV} \pm 0.19 \text{ mV}$ ) than palm up ( $1.06 \text{ mV} \pm 0.14 \text{ mV}$ ). A significant type of movement-participants' posture interaction was also observed ( $F_{1,7} = 8.57$ ,  $P = 0.022$ ). A *post hoc* test showed that the MEA was higher when participants executed index finger

abduction/adduction movements than when they executed little finger abduction/adduction movements, both when their hand was palm down ( $P < 0.001$ ) and palm up ( $P < 0.001$ ). It is important to note that a significantly higher MEA was observed when participants executed index finger abduction/adduction movements with palm-down posture than when they executed the corresponding movement with palm-up posture ( $P = 0.001$ ). No such posture-related effect was observed during execution of little finger abduction/adduction movements ( $P = 0.999$ ), in which the FDI has no role.

Analysis of MEAs from the ADM muscle (Fig. 3B) showed a significant main effect of type of movement ( $F_{1,7} = 113.89$ ,  $P < 0.001$ ), because the MEA recorded from the ADM muscle was higher during execution of little finger abduction/adduction movements ( $2.84 \text{ mV} \pm 0.27 \text{ mV}$ ) than during execution of index finger abduction/adduction movements ( $0.48 \text{ mV} \pm 0.06 \text{ mV}$ ). The main effect of participants' posture was significant ( $F_{1,7} = 7.97$ ,  $P = 0.023$ ), because the MEA was higher when participants kept their hand palm up ( $1.84 \text{ mV} \pm 0.2 \text{ mV}$ ) than palm down ( $1.48 \text{ mV} \pm 0.15 \text{ mV}$ ). A nonsignificant type of movement-participant posture interaction was obtained for the ADM muscle ( $F_{1,7} = 1.25$ ,  $P = 0.3$ ), thus showing that a significantly higher MEA was recorded when participants had their hand palm up while executing both index finger and little finger abduction/adduction movements.

Nonsignificant main effects of type of movement ( $F_{1,7} = 1.54$ ,  $P = 0.254$ ) and participants' posture ( $F_{1,7} = 2.26$ ,  $P = 0.177$ ), as well as non significant interaction ( $F_{1,7} = 1.67$ ,  $P = 0.237$ ) were obtained from the ECR muscle (Fig. 3C), which is not involved in either of the two types of movement executed by the participants.

## Discussion

In the present research, we expanded previous single-pulse TMS studies by showing that motor facilitation during action observation occurs for muscles that are actually involved in executing the observed movements (e.g. Fadiga *et al.*, 1995; Strafella & Paus, 2000; Gangitano *et al.*, 2001; Maeda *et al.*, 2002; Romani *et al.*, 2005). We investigated the influence of the observer's and the model's hand posture on the facilitation of potentials recorded from hand muscles during the observation of finger movements. Specifically, we tested whether modulation of a given muscle is related to its functional involvement in executing the observed movements or to the postural congruency between the model's hand and that of the observer. For this purpose, we manipulated the posture (palm down, palm up) of the model's moving hand. Moreover, in different experiments the observer's hand was kept in a palm-down (Experiment 1) or palm-up (Experiment 2) position.

A strictly topographic account postulates that the observation-related motor facilitation should involve only the muscles that would be activated during the actual execution of the observed movements, independently from the spatial congruency of the model's moving finger and the observer's corresponding body part. Facilitation of FDI motor representation, for example, should occur when observing index movements performed by hands in both palm-up and palm-down positions, independently from the observer's hand posture. In the same vein, facilitation of the ADM muscle should occur during observation of little finger movements with the model's hand in both palm-up and palm-down positions, no matter what the observer's posture. By contrast, if the motor facilitation contingent upon action observation is not only a result of the mapping of motor commands but also of the mapping of ongoing proprioceptive feedback, then MEP facilitation should be lower during the observation of palm-up than palm-down

hand stimuli in participants who are holding their hand palm down. The opposite is expected in participants who are holding their hand palm up. Finally, the influence of a spatial correspondence between the space of the model's movement (left or right with respect to the main axis of the moving hand) should predict, in participants who are holding their hand in the palm-down position, facilitation of FDI during observation of index movements performed by a hand in the palm-down position and of little finger movements performed by a hand in the palm-up position. Conversely, facilitation of the ADM muscle should be found during observation of the model's abduction/adduction movements of the little finger with palm-down hand posture and of the index finger with palm-up hand posture. The opposite pattern of muscle-movement correspondence is expected in participants who are holding their hand in the palm-up position.

### *Topographic mapping on the observer's motor system of the model's moving muscle*

In Experiment 1, observation of index finger movements brought about a significant facilitation that was comparable in the model's palm-down and palm-up positions. Thus, a facilitation of the FDI muscle was obtained only during observation of index finger movements that would imply FDI contraction if actually performed. A novel experimental manipulation of the present study was the recording of MEPs while observers performed the action observation task with their hand in the palm-up position (Experiment 2). In this experiment, we observed a selective modulation of the ADM muscle contingent upon observation of little finger movements whether they were performed by hands in the palm-down or palm-up posture. The FDI facilitation in Experiment 1 and the ADM facilitation in Experiment 2 seem to reflect a topographic matching of the model's movement onto the observer's corticospinal system, regardless of the model's hand posture.

The absence of modulation of mirror motor facilitation according to onlooker-model postural congruency may seem at odds with a study by Maeda *et al.* (2002). Authors found greater TMS facilitation contingent upon action observation when the model's hand posture was congruent (facing away) with the observer's hand than when it was incongruent (facing toward). In that study, the inversion of the hand orientation not only changed the side of space where the finger movements were directed, but also the perspective from which the hand stimuli were viewed. Indeed, the model's hand was viewed from an egocentric perspective in the facing-away condition and from an allocentric perspective in the facing-toward condition. Thus, the study of Maeda *et al.* could not determine whether the reduction of motor facilitation in the facing toward condition was because of the spatial incongruence between the model's and the observer's hand posture or the fact that the model's hand was viewed from an allocentric perspective. By contrast, in our experiment the manipulation of the model's hand posture does not change the observer's perspective, which remains egocentric. In these conditions, there is no effect of the spatial congruency between the observed and the observer's hand posture on motor facilitation contingent upon action observation. The occurrence of motor facilitation only during observation of movements that map the motor function of the probed muscle supports the notion that observed actions are directly matched onto the observer's motor system (Fadiga & Craighero, 2004; Rizzolatti & Craighero, 2004). If observed and executed actions are mapped onto overlapping neural circuitry, action observation should interfere with the execution of incongruent actions and facilitate the execution of congruent actions. Behavioural studies showing that observation of actions performed by other individuals directly influences the execution of

one's own actions (visuomotor priming) are in accordance with this hypothesis. These studies show that participants are faster in initiating finger movements during observation of congruent movements performed by other individuals than during observation of incongruent finger movements (Sturmer *et al.*, 2000; Brass *et al.*, 2001; Craighero *et al.*, 2002; Kilner *et al.*, 2003). It is worth noting that the spatial congruency between the direction of the executed and observed movements does not explain visuomotor priming. Indeed, when the observed images are inverted, for example flipped upside down (Brass *et al.*, 2001) or presented in an orthogonal plane compared with the observer's hand (Heyes *et al.*, 2005), the facilitation effect reflects the action pattern and not the spatial congruency between the directions of executed and observed movements. These behavioural results and the facilitation of FDI in Experiment 1 and ADM in Experiment 2 of the present study hint at a specific motor mapping of observed movements onto the observer's motor system.

#### *Possible postural influences on mirror motor activation*

As noted, the model's hand posture does not seem to modulate MEP facilitation, which, when present, was comparable during observation of palm-up and palm-down hands. However, the absence of ADM modulation during observation of little finger abduction/adduction movements in Experiment 1 and of FDI modulation during observation of index finger movements in Experiment 2 cannot be explained by a strict somatotopic mapping hypothesis because these two muscles would be active during the actual execution of little finger and index finger abduction/adduction movements, respectively. Indeed, selective mirror motor facilitation of the FDI muscle was found only in Experiment 1 (observer's hand was palm down) and of the ADM muscle only in Experiment 2 (observer's hand was palm up). Although derived from the comparison of two different groups, the symmetric inversion of MEP modulation would indicate that the observer's hand posture might influence mirror motor activation. This hypothesis is in keeping with the notion that motor facilitation during action observation reflects neural processing carried out not only in higher-order motor areas (Fadiga *et al.*, 1995; Strafella & Paus, 2000) but also in primary sensorimotor parietal areas (Avikainen *et al.*, 2002; Rossi *et al.*, 2002; Costantini *et al.*, 2005).

Moreover, both voluntary movements (Shimura & Kasai, 2002) and movements evoked by stimulation of primary motor cortex (Wassermann *et al.*, 1998; Graziano *et al.*, 2004) are influenced by the actual limb posture. Wassermann *et al.* (1998) demonstrated that finger movements induced by TMS pulses over the hand representation in primary motor cortex changed contingent upon the posture assumed by the hand. Abduction movements of the index finger were obtained when the hand was in a semiflexed position, whereas mainly flexion movements were observed when the thumb and the index fingers were opposed in a pincer grip. Such a proprioceptive neuromuscular facilitation is reflected by changes in the amplitude of MEPs recorded from the muscles that are proximal to the manipulated joint (Shimura & Kasai, 2002). The observer's actual body posture might also affect the execution of mental motor imagery tasks (Parsons, 1994; Sirigu & Duhamel, 2001) that rely on neural circuits largely overlapping those involved in motor execution (Jeannerod & Frak, 1999). The time needed to mentally rotate hand stimuli in order to judge their laterality is increased when the observer's hand posture is compatible with the hand stimulus to be mentally rotated than when it is incompatible (Parsons, 1994; Sirigu & Duhamel, 2001). The influence of proprioceptive information signalling the position of one's own body parts may be reflected in the reduction of facilitation of MEPs recorded from hand muscles during imagery of finger movements that

are incompatible with the observer's hand posture (Vargas *et al.*, 2004). In agreement with these studies, our results might suggest that the body posture of the model, but not that of the observer, influences the muscular selectivity of motor activation contingent upon action observation.

#### *Predominance of topographic mirroring over postural influences*

The absence of facilitation of muscles that would be involved in the actual execution of observed movement indicates that the observer's posture modulates motor mirroring in a rather complex way. One might wonder, for example, whether posture-related modulations of the motor system during action observation reflect an analogous modulation during execution of the observed movements. Results of our Experiment 3, in which we recorded EMG activity from FDI, ADM, and ECR muscles during the actual execution of right index and little finger abduction/adduction movements with the hand in both palm-down and palm-up positions, speak in favour of this possibility.

No posture-related modulation of ECR activity was found in that this muscle is not involved in index or little finger movements. Activation of the FDI was higher during execution of index finger than little finger abduction/adduction movements. In the same vein, activation of the ADM was higher during execution of little finger than index abduction/adduction movements. This occurred regardless of the participants' hand posture. Importantly, however, activation of the FDI when participants executed index finger abduction/adduction movements was higher in palm-down than palm-up hand posture. By contrast, activation of the ADM when participants executed little finger abduction/adduction movements was higher in palm-up than palm-down hand posture. It is important to note that in the observation tasks motor facilitation was found only for the FDI in Experiment 1 (where participants kept a palm-down position) and only for the ADM in Experiment 2 (where participants kept a palm-up position). As the ADM has little involvement in index movements, it might seem puzzling that the activity of the ADM was higher in the palm-up hand position during execution of index finger movements. A plausible explanation for this effect is that the ADM has a postural role also in performing index movements. The observed posture-related modulation of muscular activity during movement execution may reflect different degrees of subthreshold tonic contraction or biomechanical constraints on the strength exerted by the two muscles while keeping the hand in the palm-down or palm-up position. In any case, the postural effects found during action execution might help to explain the pattern of motor facilitation contingent upon action observation. As a matter of fact, the effect of the observer's hand posture on mirror motor facilitation was analogous to the effect on muscular activity during movement execution.

Visual monitoring of our own body parts interacts with the proprioceptive signals needed for the construction and maintenance of an on-line representation of the body (Berlucchi & Aglioti, 1997). The artificial induction of discrepancies between different sources of sensory information modulates activity of occipito-temporal, parietal and frontal areas in a specific way. For example, discrepancies between proprioceptive and visual feedback concerning the visual appearance of moving body parts do not modulate the activity of the motor and premotor cortex (Dohle *et al.*, 2004). This is demonstrated by functional magnetic resonance imaging (fMRI) study in which participants viewed their hand in a monitor while they executed specific hand movements. Subjects could see the actual movements of the observed hand or a reversed image that created the impression that movements were performed by the opposite, nonmoving hand (Dohle

*et al.*, 2004). A strong activation contingent upon this visuo-proprioceptive incongruence was observed in the visual cortex but not in frontal or parietal areas, thus showing that the mirror neuron system does not map sensory discrepancies concerning the spatial arrangement of moving body parts. By contrast, modulation of activity was observed in premotor and parietal cortex when the visuo-proprioceptive discrepancy was related to the trajectory of the movement and not only to the laterality or to the visual appearance of the moving body part (Farrer *et al.*, 2003; Balslev *et al.*, 2005). Thus, whereas action cues might be crucial in modulating activity in mirror-system areas, differences in the visual appearance of the moving body parts seem to modulate activity in temporal and parietal areas. Recent TMS (Romani *et al.*, 2005) and fMRI studies (Costantini *et al.*, 2005) showed comparable motor facilitation when participants observed movements that were within the limits of, or beyond, normal joint mobility. As movements that are beyond the normal range of joint mobility do not map normal motor functioning, motor facilitation during observation of biomechanically impossible movements would suggest that what is coded is not the precise kinematics of movements but their general meaning. In the same vein, the functional significance of finger abduction/adduction movements is not changed by the biomechanical extension of the joint limits. Thus, if gross variations in the visual appearance of the moving stimulus were ineffective, small differences in the amount of muscular activity during execution of movements with different hand postures would be reflected clearly in the degree of muscular facilitation during movement observation.

## Conclusions

The present study suggests that in our experimental conditions mirror motor activation is influenced more by the topographic matching of the model's movement on the observer's motor system than by the spatio-postural congruency between the model's moving hand and the observer's hand. Moreover, the results suggest that a fairly complex interplay of somatotopic and postural variables underlie the motor facilitation contingent upon action observation. Future studies are needed to clarify the complex combination of visual and proprioceptive factors that contribute to mirror motor activation. Comprehension of the relations between limb posture and mirror motor activations could be of assistance in rehabilitation treatments based on the use of action observation and/or motor imagery to improve movement execution.

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## Abbreviations

ADM, abductor digiti minimi; ECR, extensor carpi radialis; EMG, electromyography; FDI, first dorsal interosseous; fMRI, functional magnetic resonance imaging; MEA, maximal electromyography amplitude; MEP, motor evoked potential; OSP, optimal scalp position; rMT, resting motor threshold; TMS, transcranial magnetic stimulation.

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