

# Motor Facilitation While Observing Hand Actions: Specificity of the Effect and Role of Observer's Orientation

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**Maeda, Fumiko, Galit Kleiner-Fisman, and Alvaro Pascual-Leone.** Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. *J Neurophysiol* 87: 1329–1335, 2002; 10.1152/jn.00773.2000. Action observation enhances cortico-spinal excitability. Here we tested the specificity of this effect and the role played by the orientation of the observer. Ten normal subjects observed video clips of right hand performing three different finger movements (*thumb ab-/adduction, index ab-/adduction, index extens-/flexion*) in two different orientations (*Away*, i.e., natural hand-orientation facing out from the observer; or *Toward*, i.e., unnatural hand-orientation facing toward the observer). Motor-evoked potentials (MEPs) induced by transcranial magnetic stimulation (TMS) were recorded from the abductor pollicis brevis (APB) and the first dorsal interosseus (FDI) muscles. Movement direction of the index finger was recorded using force transducers. Facilitation of MEP size was significantly greater for APB during observation of thumb movements and for FDI during observation of index finger movements. Facilitation of MEP size was significantly greater when the hand presented on screen was facing out from and corresponding to that of the observer (*Away* orientation). The direction of the index finger movement evoked by TMS shifted toward extension/flexion versus *ab-/adduction* matching the observed movement. Our results give further evidence that observation of a movement enhances motor output to the muscles involved in the movement and facilitates the observed action. In addition, we provide novel evidence about the high degree of specificity of this observation-induced motor cortical modulation. The degree of modulation depends on hand orientation. The modulation is maximal when the observed action corresponds to the orientation of the observer.

## INTRODUCTION

Neural circuitry for action execution (Binkofski et al. 1999; Rizzolatti et al. 1996b; Roth et al. 1996), action imagination (Decety et al. 1994; Kosslyn et al. 1995; Roland and Gulyas 1995), and action observation (Decety et al. 1997; Grafton et al. 1996; Grezes et al. 1998) appear to overlap extensively. Elements of this common circuitry involve the supplementary motor area (SMA), the premotor cortex, the superior temporal sulcus, the inferior frontal cortex (area 45), and the inferior parietal cortex (area 40). More recently, modulation of the activity of the primary motor cortex (M1) during mental imagery (Beisteiner et al. 1995; Fadiga et al. 1999; Pascual-Leone

et al. 1993, 1997; Porro et al. 1996; Roth et al. 1996) and observation of hands or actions (Fadiga et al. 1995; Ganis et al. 2000; Hari et al. 1998; Nishitani and Hari 2000; Strafella and Paus 2000) has been reported in neurophysiologic studies. One of the techniques that has been used in these studies is transcranial magnetic stimulation (TMS) (Abbruzzese et al. 1996; Fadiga et al. 1995, 1999; Hashimoto and Rothwell 1999; Ikai et al. 1996; Kasai et al. 1997; Pascual-Leone et al. 1993, 1997). TMS induces electrical current by rapid oscillations of a magnetic field. This can cause depolarization of cortical neurons underlying the electromagnetic coil when the induced current is sufficient. This technique allows us to study the motor system and explore intracortical and cortico-spinal excitability (see Pascual-Leone et al. 1998).

In this study, we used TMS to further investigate the selectivity of modulation of cortico-spinal activity when subjects observe different finger movements in different hand orientations. The study had several aims:

1) We studied the specificity of the changes in motor cortico-spinal excitability induced by the observation of an action. Studies by Fadiga et al. (1995) and Strafella and Paus (2000) have shown that observation of complex actions, such as grasping and writing, induces changes in intracortical and/or cortico-spinal excitability. This may be produced by a neural system matching action observation and execution in humans (Fadiga et al. 1995; Iacoboni et al. 1999), a concept supported by single-cell recordings in monkeys (di Pellegrino et al. 1992; Rizzolatti et al. 1996a). Although studies of ventral premotor cortex in monkeys required a goal and an interaction between the agency and the object for an increased neuronal discharge (Gallese et al. 1996), TMS studies of the primary motor cortex in humans seem to be controversial. Whereas Fadiga et al. (1995) found no significant differences in cortico-spinal excitability between goal-oriented transitive versus intransitive hand actions with no significant goals, a small but significant difference was found between the two types of action (Maeda, unpublished data). It may be that what is thought to be intransitive actions in monkeys may be transitive in humans. Alternatively, the presence of a goal may not affect cortico-spinal excitability in humans. In this study, we focused on simple movements and explored in greater detail the specificity of the

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modulatory effect of action observation on motor cortical excitability. For this purpose we asked subjects to observe single, elementary finger movements (index flexion/extension, index ab-/adduction, thumb ab-/adduction) rather than complex actions.

2) We explored whether action observation influences the direction of a finger movement evoked by TMS. We compared the angle of the index finger movement induced by TMS when the subject was observing the index finger moving up-down or side-to-side. Assuming a high degree of specificity of the modulatory effects of action observation on motor cortex excitability, we predicted that observation of an action would cause selective activation of the neurons within the motor cortex involved in that movement. Hence, observation of an index finger moving up and down was predicted to cause the subject's finger to move more vertically following the nonspecific activation by TMS and vice versa for observation of a side-to-side, horizontal movement.

3) Finally, we explored whether hand orientation would affect the amount of cortico-spinal excitability. Some studies have suggested that subjects may use an egocentric/allocentric frame of reference in the interpretation of an observed hand movement. Many groups have reported that to identify the handedness, subjects mentally rotate their own hand until it matches with the presented one (Ganis et al. 2000; Gentilucci et al. 1998; Parsons 1987). Gentilucci et al. (2000) also reported that anchoring of the hand to the agent (hence the hand facing away rather than toward) is the features of the grasp representations in the hand-recognition process. However, no studies to date have addressed the role that orientation may have in the motor facilitation produced by action observation, particularly when subjects simply watch without having to "interpret" anything. This is not a trivial question, in that in principle action observation may be used as a form of rehabilitation, and it would be important to know which are the most effective forms of stimulation of the motor system during observation of actions.

## METHODS

The experimental design is schematically summarized in Fig. 1, providing a flow chart of the study procedure.

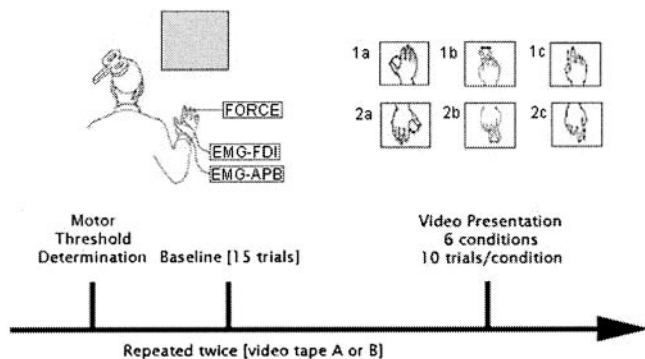


FIG. 1. A schematic illustration of the experimental design (set-up). *Left*: subject with electrodes and force transducer attached to fingers, facing the monitor. *Right*: 6 conditions are shown below (Conditions: 1a, Away-Thumb; 1b, Away-Index; 1c, Away-Index- $\perp$ ; 2a, Toward-Thumb; 2b, Toward-Index- $\parallel$ ; 2c, Toward-Index- $\perp$ ). *Bottom*: schematic flow chart of the experimental design (procedure).

## Subjects

Ten healthy volunteers (4 males, 6 females) with a mean age of 29.8 yr (range 19–51 yr) were recruited. All were right-handed according to the Oldfield Questionnaire (Oldfield 1971) and all were naive to the purpose of the study. The study was approved by the local Institutional Review Board, and written informed consent was obtained from all subjects. None of the subjects had neurological, psychiatric, or other medical problems, nor had any contraindications to TMS (Wassermann 1998).

## Preparation and devices

Subjects were seated in a comfortable reclining chair. They were instructed to keep their hands still and as relaxed as possible. Their hands were supported on the arm of the chair and were pronated with their elbows flexed in a vertical angle from the subjects. Their hand positions matched the *Away* condition. Tightly fitting white lycra swimming caps were placed on their head to mark the site for stimulation. Stimulation was delivered to the "optimal scalp site," defined as the scalp position from which TMS induced motor-evoked potentials (MEPs) of maximal amplitude in the contralateral (right-sided) target hand muscles simultaneously (abductor pollicis brevis, APB, and first dorsal interosseous, FDI).

Four disposable self-adhesive electrodes (Nicolet Biomedical) were placed on the belly and tendon of the subjects' right APB and FDI muscles. Circular ground electrodes with a diameter of 30 mm were placed on their wrists. All of these sites were prepared appropriately before the electrodes were attached. MEPs were amplified using a Dantec Counterpoint electromyograph (EMG) with a band pass of 20–1000 Hz (Dantec, Skovlunde, Denmark). A ring, connected to two strain gauges to measure isometric forces in vertical (range  $\pm 0.45$  kg) and horizontal (range  $\pm 0.9$  kg) directions, was placed to fit between the proximal and distal interphalangeal joints (PIP and DIP) of the right index finger. The signals were amplified using bridge amplifiers (AD Instruments, Hastings, UK) with a band pass of 20–1000 Hz. The preamplified signals ( $\times 1000$ ) from both amplifiers were digitized using two PowerLab 16Ss devices (AD Instruments) with a sampling rate of 2 kHz per channel and stored on a Macintosh G3/300 Power PCs (Apple Computers) for off-line analysis.

## TMS procedure

TMS was performed with a commercially available 70-mm figure-of-eight coil and a Magstim Super Rapid Transcranial Magnetic Stimulator (Magstim). Single-pulse TMS was delivered to the optimal scalp position of the left hemisphere and the motor potentials evoked in the contralateral right APB and FDI were recorded. The coil was positioned tangentially to the scalp with the handle of the coil 45° from the mid-sagittal axis of the subject's head and pointing anteriorly; hence the maximal induced current was in the antero-medial direction. This orientation was chosen based on the finding that the lowest motor threshold (MT) was achieved when the induced electric current in the brain was flowing approximately perpendicular to the central sulcus (Brasil-Neto et al. 1992a; Mills et al. 1992). The coil was held with both hands bracing the coil against the head. This method has previously been shown to have a similar amount of variability as using a coil holder (Ellaway et al. 1998). The MT was defined as the minimal intensity of stimulation capable of inducing MEPs  $> 50 \mu\text{V}$  peak-to-peak amplitude in  $\geq 6$  of 10 trials for the APB or FDI muscle. Stimulation was started well above threshold intensity (generally 90% of the stimulator output) and decreased in steps of 2% of the stimulator output. The threshold determination was made during complete muscle relaxation that was monitored through audio and EMG signals for 100 ms prior to the application of the TMS.

Fifteen baseline MEPs were collected by applying single-pulse TMS to the optimal site at 120% of the subjects' MT, the inter-

stimulus interval being approximately 10 s ( $\pm 1$  s). This choice of inter-stimulus interval was based on the data from Chen et al. (1997), who found no change in cortico-spinal excitability after 1 h of 0.1 Hz (1 pulse per 10 s) repetitive TMS. The pulses were not spaced out equally to avoid any priming effects that may affect the MEP size. The optimal position was determined at the very beginning of the study as the scalp site from which MEPs of maximal amplitude were evoked by TMS. MTs and baseline MEPs were collected at the beginning of each video presentation (before tape A and tape B), while the subjects kept their eyes closed and their body relaxed. The devices, coils, and instruments, and the investigator (both for stimulation and analysis), were kept constant throughout the study.

### Video presentation

A video screen was placed 100 cm from the subject so that the hand-size on screen was approximately the actual size of a hand. The subjects were instructed to attend to the video screen and to the movements that were shown.

Subjects viewed three actions in two conformations (Fig. 1), as follows: 1) a right hand presented in the same orientation as the subject's hand with the thumb abducting (1a, *Away-Thumb*), the index finger abducting (1b, *Away-Index-||*), or the index finger moving vertically (1c, *Away-Index-⊥*); and 2) a right hand presented in the opposite orientation to the subject's hand, with the thumb abducting (2a, *Toward-Thumb*), the index finger abducting (2b, *Toward-Index-||*), or the index finger moving vertically (2c, *Toward-Index-⊥*).

Each trial lasted 10 s with the finger moving at a rate of two movements per second. Single-pulse TMS was applied randomly between 4–6 s after the initiation of a given trial. The timing of TMS was random to avoid any phase-dependent effect, since the effect of TMS on the precise position of the presented finger during the movement was unknown and unpredictable. Overall we collected 20 trials for each condition (total of 120 trials), which were in pseudo-random order. We prepared two videotapes with 60 trials (10 trials per condition, 6 conditions) per tape (tape A and B). The order in which the tapes were shown was alternated and counterbalanced among subjects.

### Data analysis

**APB AND FDI MEP SIZE.** Data were collected on 10 subjects and the MEPs were analyzed off-line on a Macintosh G3/300 Power PC using PowerLab software. Area-under-the-curve of the MEPs was calculated after rectification, and the percentage change ( $\Delta\%$ ) of averaged baseline MEP area to each MEP during the video observation was calculated. These values (20 for each of the 6 conditions and for both APB and FDI) were then averaged separately for further analysis. Data were analyzed employing repeated measures analysis of variance (ANOVA) examining differences between the APB and FDI across the six stimuli (1a, *Away-Thumb*; 1b, *Away-Index-||*; 1c, *Away-Index-⊥*; 2a, *Toward-Thumb*; 2b, *Toward-Index-||*; 2c, *Toward-Index-⊥*). Subsequent planned comparisons were made such that the effects of three different video conditions all with different finger movements (a, *Thumb*; b, *Index-||*; c, *Index-⊥*) could be examined.

### Angle of index finger movement

Data were collected on eight subjects. The peak force exerted in the horizontal and vertical axis between 0–100 ms after application of TMS was analyzed off-line on a Macintosh G3/300 Power PC using PowerLab software. From the peak force exerted in the two directions, the angle was calculated for each trial (angle of 0° indicates that the finger was moving in a complete horizontal direction toward the thumb). Again, as per the MEP analysis, the baseline angle of the index finger was averaged for each tape to calculate the  $\Delta\%$  in the angle for each trial. These values (20 for each of the 6 conditions)

were then averaged for further analysis. Data were analyzed employing a one-way repeated measure ANOVA examining the angle of the index finger from the horizontal plane across the presentations of different finger movements (1a, *Away-Thumb*; 1b, *Away-Index-||*; 1c, *Away-Index-⊥*).

All statistical analysis was carried out by Statistical Packages for Social Sciences (SPSS 6.0/9.0; SPSS, Chicago, IL).

## RESULTS

All subjects tolerated the study well without any adverse effects.

### Motor thresholds

MT of all subjects was measured at the beginning of the study as well as at mid-point (before collecting the second baseline MEPs prior to presentation of the second video tape) and was found to be on average 60.4% (SE = 3.6) and 59.7% (SE = 3.5) of maximum stimulator output, respectively. This repeated determination of MT was carried out to control for any changes in cortico-spinal excitability over the course of the experimental session and to minimize the variability of the MEP size. There were no significant differences between the two MT determinations (and hence the stimulation intensity) within each subject [ $t(9) = 1.21$ ,  $P > 0.05$ ], indicating no significant, nonspecific change in motor cortico-spinal excitability during the study that could have confounded the results.

### APB and FDI MEP size

Figure 2 provides a representative example of rectified APB and FDI MEPs for one block of trials.

### Influence of observing specific hand orientations and finger movements

A  $2 \times 2 \times 3$  repeated measures ANOVA examining the  $\Delta\%$  in MEP area across “different muscles (2: APB  $\times$  FDI),” “observation of different hand orientations (2: *Away*  $\times$  *Toward*),” and “observation of different finger movements (3: *Thumb*  $\times$  *Index-||*  $\times$  *Index-⊥*)” was performed. A significant three-way interaction was found across these comparisons

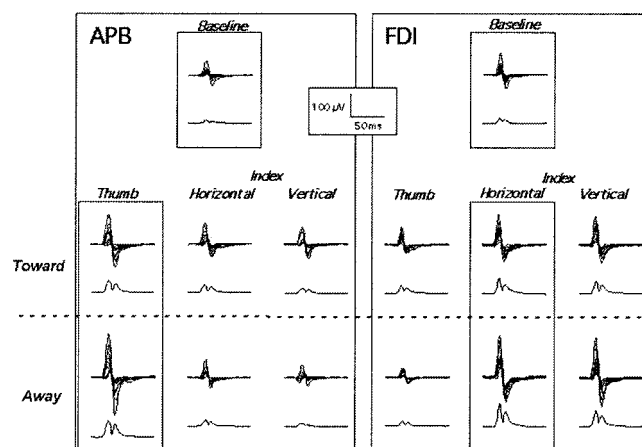


FIG. 2. A representative example of abductor pollicis brevis (APB) and first dorsal interosseus (FDI) motor-evoked potentials (MEPs) of 1 block. In each condition, the top figures are overlays of all MEPs and the bottom figures show the mean rectified MEPs.

[ $F(2,18) = 6.969, P = 0.006; \eta^2 = 0.436$ ]. In addition, a significant two-way interaction was found between different muscles and observation of different finger movements [ $F(2,18) = 11.895, P = 0.001; \eta^2 = 0.569$ ], and a significant main effect was found for observation of different hand orientations [ $F(1,9) = 28.941, P = 0.001; \eta^2 = 0.763$ ]. A series of planned comparisons was then performed with the goal of determining if there was a different pattern of activation between the APB and FDI muscles across the video conditions, i.e., the observed movements.

#### Influence of observing thumb ab-/adduction

For the Thumb condition,  $\partial\%$  of the APB MEP size was significantly greater than that of the FDI. Specifically, the Away-Thumb presentation produced significantly greater  $\partial\%$  in APB MEP size than the FDI MEP size when observing the Thumb condition in either orientation (Away-Thumb:  $P = 0.006$ ; Toward-Thumb:  $P = 0.002$ ) (Fig. 3A). Further,  $\partial\%$  of APB MEP size differed between observing Away-Thumb and Toward-Thumb conditions ( $P = 0.003$ ), whereas Away-Thumb and Toward-Thumb conditions did not differentiate  $\partial\%$  of FDI MEP size ( $P > 0.05$ ). Finally, it is interesting to note that when the orientation of the hand was Toward, the Thumb condition did not differ from the Index-|| nor the Index- $\perp$  condition ( $P > 0.05$ ). In other words, the only significant difference in this analysis was found between the Away-Thumb condition and all other conditions. These results demonstrate that viewing movements of a thumb results in a significant increase in MEP size of the APB, but not FDI muscles. However, this effect is highly dependent on the orientation of the observed action (and hence on the observer's view point): increase in MEP size only occurs when the observed hand was in the same orientation as the subject's hand (i.e., Away condition).

#### Influence of observing index finger ab-/adduction

The Index-|| condition was then examined. It was found that for the Away condition, the  $\partial\%$  in FDI MEP size was signif-

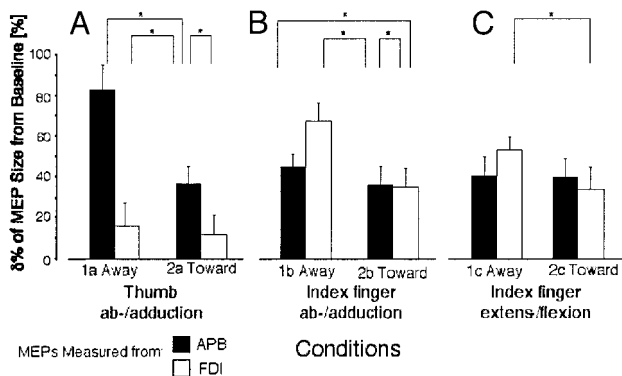


FIG. 3. A: percentage change ( $\partial\%$ ) of MEPs when either Away or Toward Thumb condition was presented. Bars indicate standard errors. \*Compared with  $\partial\%$  of APB MEP size when observing Away-Thumb condition,  $P < 0.05$ . B:  $\partial\%$  of MEPs when either Away or Toward Index-Horizontal (||) condition was presented. \*Compared with  $\partial\%$  of FDI MEP size when observing Away-Index-|| condition,  $P < 0.05$ . C:  $\partial\%$  of MEPs when either Away or Toward Index-Vertical ( $\perp$ ) condition was presented. Bars indicate standard errors. \*Compared with  $\partial\%$  of FDI MEP size when observing Away-Index- $\perp$  condition,  $P < 0.05$ .

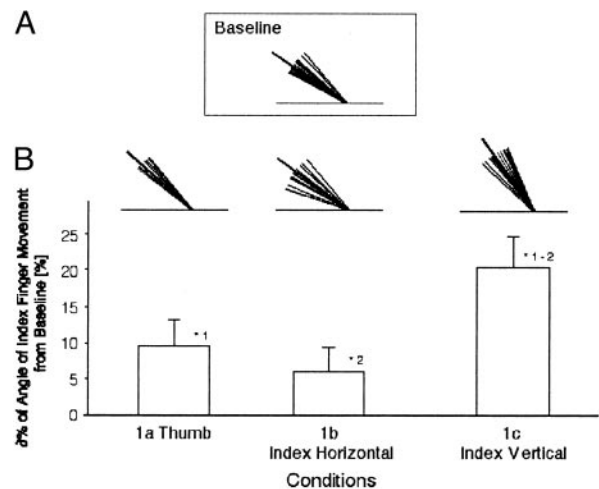


FIG. 4. A: a representative example of the directions of peak force evoked in the index finger (calculated from the 2 force transducers) of 1 block. The long thick line for baseline or each condition shows the mean value. B:  $\partial\%$  of the mean angle (Away and Toward) of each condition [Thumb, Index-Horizontal (||), Index-Vertical ( $\perp$ )] from the mean baseline angle in the right index finger. Bars indicate standard errors. \*Compared with  $\partial\%$  of index finger angle when observing Index- $\perp$  condition,  $P < 0.05$ .

icantly different from conditions that involved different orientation and different fingers ( $\partial\%$  of FDI when observing Toward-Index-||:  $P = 0.001$ ;  $\partial\%$  of APB when observing Away-Index-||:  $P = 0.015$ ;  $\partial\%$  of APB when observing Toward-Index-||:  $P = 0.002$ ) (Fig. 3B). Across these three  $\partial\%$  in MEPs from baselines, there were no significant differences (all  $P$ 's  $> 0.05$ ). The data indicate that viewing a finger movement that mainly involves FDI contraction will increase FDI activity, but only when the orientation of the hand being viewed is in the same orientation as the recording hand (i.e., Away condition). These results are equivalent to those found for the Thumb condition described above with the muscle of interest being the FDI instead of APB.

#### Influence of observing index finger in extens-/flexion (vertical movements)

We then examined the Index- $\perp$  condition. Although the  $\partial\%$  of APB MEP size did not differ significantly based on hand orientation, the  $\partial\%$  of FDI MEP size differed significantly between different orientations ( $P = 0.05$ ) (Fig. 3C). The  $\partial\%$  of FDI MEP size, however, did not differ from the  $\partial\%$  of APB MEP size across either level of hand orientations ( $P > 0.05$ ). These data imply that unlike horizontal (||) movements, viewing vertical ( $\perp$ ) index finger movements do not differentiate APB and FDI MEP size. Rather, viewing vertical movements differentiates Away and Toward conditions as was examined by the  $\partial\%$  of FDI MEP size.

#### Direction of index finger movement

Figure 4A provides a representative example of the directions of force pulses evoked in the index finger (calculated from the 2 force transducers) in one block of trials.

To determine if there was a significant difference across the variables, a one-way repeated measures ANOVA was performed across observation of different finger movements (3: Thumb  $\times$  Index-||  $\times$  Index- $\perp$ ). There was a significant effect

between these conditions [ $F(2,14) = 7.331, P = 0.007; \eta^2 = 0.512$ ]. Employing post hoc Bonferroni corrected contrasts, it was found that the Index- $\perp$  condition had a significantly greater increase in angle than either the Thumb condition ( $P = 0.007$ ) or the Index- $\parallel$  condition ( $P = 0.008$ ) (Fig. 4B). There was no significant difference between the Thumb condition and the Index- $\parallel$  condition ( $P > 0.05$ ). These data indicate that observation of the Index- $\perp$  condition significantly increases the angle of motion of the index finger.

## DISCUSSION

In the present study we have replicated previous findings that cortico-spinal excitability is increased during observation of hand movements and have provided novel demonstration about the specificity of this facilitation to the muscles involved in the observed simple actions and about the critical role played by observer orientation. The facilitation is greater during observation of natural (Away) hand orientations than of unnatural (Toward) hand orientations.

The finding of increased cortico-spinal excitability during observation of hand movements specific to the involved muscles is consistent to what has been shown by Fadiga et al. (1995) and Strafella and Paus (2000). When the subject observed index finger ab-/adduction, there was significant selective facilitation of MEP size in FDI as compared with APB. Conversely, significant preferential facilitation of MEP size in APB relative to FDI was found during observation of thumb ab-/adduction. Observation of index finger extens-/flexion (vertical movement) resulted in smaller but significant facilitation of the FDI muscle.

Unlike observation of index finger ab-/adduction, extens-/flexion did not differentiate the amount of facilitation between APB and FDI MEP size. Perhaps this is due to the only partial contribution of the FDI to a vertical index finger motion. Alternative differential effects of observation of horizontal and vertical biological motion might be entertained.

In any case, these results are consistent with the hypothesis that in humans there is a system matching action observation and execution (Fadiga et al. 1995). The existence of such a matching system in the premotor and parietal cortex was recently suggested by a functional magnetic resonance imaging (fMRI) study of action observation and imitation (Iacoboni et al. 1999). Activation of premotor and parietal areas is likely to influence motor cortical outputs *trans*-synaptically, hence shifting motor cortical output excitability (as measured by TMS-induced MEP).

Our study provides new data demonstrating that the facilitation of motor cortico-spinal excitability depends on the orientation of the observed hand. Facilitation of MEP size is greater during observation of natural (Away) hand orientations than unnatural (Toward) hand orientations. Under the framework of the "mirror system," it may be predicted that observation of actions with Toward orientation would result in larger MEPs, which was not the case in our study. The mirror system was proposed following recordings in monkeys to describe neurons in the ventral premotor cortex F5 that respond selectively to the observation of actions made by other individuals (di Pellegrino et al. 1992). This system has been interpreted as a way to match observation and execution of events (Gallese et al. 1996). There may be several possible interpretations of

the disparities of our results and the predictions from such studies. There may be neurons within the premotor or even motor cortex that are activated when observing one's "own hand." Such neurons could account for the results of our study, as they might be predicted to result in a greater facilitation when observing hands in a natural orientation to one's own. Another possible interpretation is that most previous studies have been conducted in the context of imitation and have used hands in a mirror configuration (Iacoboni et al. 1999). In our study, however, the hand was not in a mirror configuration, but rather, in a "rotated" configuration. Future studies on observation of "self" versus "other" hands, and mirror versus rotated hands, would help address these issues and aid in the understanding of our current results.

The other novel finding of our study is that there was a significant increase in angle when observing index finger extens-/flexion (vertical movements) compared with ab-/adduction (horizontal movement). As opposed to the traditional somatotopically ordered representational map for muscles outputs (Penfield and Rasmussen 1950; Woolsey et al. 1992), current data reveal that the internal organization of each body part is best described as a network having broadly distributed functions (Sanes and Donoghue 1997). Each neuron within M1 appears to participate in the projection to multiple muscles (Buys et al. 1986; Fetz et al. 1989) and motor actions (Schieber and Hibbard 1993). Evidence of this notion has been obtained not only from neural recordings and intracortical electrical stimulation, but also from pharmacological inactivation, connective studies, and neuroimaging studies (Sanes and Donoghue 2000). Our results are consistent with such a hypothesis of existing internal "functional" networks. Alternatively, apart from the "distributed function theory," this could be due to different cortico-spinal channels (and therefore different muscular synergies) reaching threshold for action potential generation. Thus the observed effect of specific deviation of the index finger could be the result of the collaboration of different hand muscles that are differentially involved during action observation.

This finding as well as the importance of hand orientation may have tangible repercussions for the rehabilitation of patients with neurological insults. A similar modulation of the angle of the movement evoked by TMS has been demonstrated following repeated active and passive motion (Classen et al. 1998). The present results expand these results on "short-term" plasticity of the motor cortical outputs by revealing that not only repeated motion, but also motion observation, can exert such effects. It would be of interest to evaluate whether mental simulation of movements also impacts on angle deviation from baseline in a similar manner.

It is important to note several points when interpreting our findings. First, the level of attentiveness at baseline and during the observation of finger movements is different, which may result in greater variability in MEP size at baseline. This was minimized by applying TMS at sufficiently high intensity at well above MT (Kiers et al. 1993) and by collecting a sufficiently large number of trials at baseline and for each condition (Brasil-Neto et al. 1992b). This difference in attentiveness may also result in smaller MEP size at baseline. We have hence computed MEP size of each condition in terms of percentage change from baseline and conducted between-condition comparisons. This analysis rules out changes in cortico-spinal

excitability across conditions that might be due to attention, alertness, interest, etc. Hence, the findings in this study are most likely due to specific changes due to observation of different hand orientations, fingers, and their movements.

Second, we do not know for sure whether the change in motor cortical output demonstrated is occurring within M1. There is indirect evidence, however, that change in cortical output excitability during action-observation is intracortical in origin (Strafella and Paus 2000). Strafella and Paus used the paired-pulse TMS technique in their study. Modulation of MEP size in this paired-pulse TMS paradigm is felt to represent intracortical mechanisms of facilitation and inhibition (Ziemann et al. 1996). Modulation of MEP size during imagery has similarly been shown to be intracortical in origin (Hashimoto and Rothwell 1999; Kasai et al. 1997; Roth et al. 1996). Hence, we propose that the findings in our study are also most likely due to “muscle, orientation, and action” observation-specific changes within the cortex. Experimental proof for this assertion is, however, not provided by the present results and certainly we cannot rule out that transsynaptic effects from the premotor or parietal cortical region may account for the change in motor cortical outputs documented (Iacoboni et al. 1999).

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