

## Competing Mechanisms for Mapping Action-Related Categorical Knowledge and Observed Actions

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**Responses to pictures of famous tennis and soccer athletes are slower when the responding effector is a hand or foot, respectively, indicating that visual recognition of individuals characterized by skilled motor behavior interferes with the motor reactivity of nonproficient observers. By contrast, directly viewing actions induces motor facilitation, suggesting that actions are mapped in the observers' motor system. Here, we used single-pulse Transcranial Magnetic Stimulation to determine 1) whether observing and recognizing the identity of famous tennis and soccer athletes selectively reduce the corticospinal excitability of arm and leg representations (categorization), 2) whether any athlete-related inhibition effect contrasts the facilitation associated with direct action observation (categorization + action), and 3) whether the classic action observation-related facilitation effect is found when viewing "in action" nonathlete models (action). In 3 experiments, we found that amplitude of motor evoked potentials (MEPs) recorded from leg and arm muscles gradually shifted from reduction to facilitation, moving from the categorization to the action observation tasks. Thus, semantic derivation of motor skills is reflected in limb-specific reduction of MEP amplitude, indicating that even abstract action knowledge is embodied in the motor system and that mapping others' actions on the basis of categorization or of their direct observation relies on competing functional mechanisms.**

**Keywords:** action simulation, grounded cognition, motor evoked potentials, motor expertise, semantic knowledge, TMS

### Introduction

Standard cognitive science theories assume that conceptual knowledge about experience relies on amodal symbols stored in a modular semantic memory system. By contrast, embodied cognition theories posit that semantic knowledge is grounded in the brain's modal systems for perception, action, and affect. These systems would be automatically engaged during online conceptual processing, thus allowing the reenactment of modality-specific patterns of activity similar to those called into play during the actual experience of perception, action, and emotion (Barsalou et al. 2003; Barsalou 2008). A clear view of the heated debate over these issues and evidence of the upsurge of interest in the embodied cognition hypothesis are provided by the many studies published on the topic (see, e.g., 2 recent journal issues entirely dedicated to the links between language and action processing; Fischer and Zwaan 2008; Nazir et al. 2008). Although it should be noted that strong forms of grounded cognition might not grasp the complexity of the issue at stake (Mahon and Caramazza 2008), several studies

suggest that dealing with semantic knowledge derived from one's own experience in the world reactivates specific sensorimotor neural traces (Barsalou 2008). Indeed, neurophysiological and neuroimaging studies indicate that retrieving words (Oliveri et al. 2004) and listening to verbs (Buccino et al. 2005) and sentences (Glenberg and Kaschak 2002) that convey motor information activate motor and premotor cortices in a rapid, automatic, and somatotopically organized manner (Pulvermüller et al. 2001; Barsalou et al. 2003; Hauk et al. 2004; Pulvermüller 2005). Moreover, convergent neurophysiological and behavioral results show that listening to limb action verbs (e.g., grasp or kick) inhibits the corticomotor representation of the limb involved in the execution of the represented action (Buccino et al. 2005). In addition, reaction times (RTs) for semantic judgments when subjects responded with the limb (hand or foot) associated with the verb were also delayed (Buccino et al. 2005).

This neural and behavioral inhibition may seem at odds with action observation studies in which facilitation was found (e.g., Rizzolatti and Craighero 2004). For example, single-pulse Transcranial Magnetic Stimulation (s-p TMS) of actual (Fadiga et al. 1995, 2005; Romani et al. 2005; Urgesi et al. 2006a; Avenanti et al. 2007) or implied (Urgesi et al. 2006b, 2010) action observation revealed an increase in corticospinal excitability. The facilitation effect was highly specific for the muscles that would be involved in actual execution of the observed action (Fadiga et al. 1995, 2005; Romani et al. 2005; Urgesi et al. 2006a) and has been attributed to the activity of the frontoparietal mirror system (Rizzolatti and Craighero 2004; Fogassi et al. 2005; Avenanti et al. 2007) underlying the mapping of motor and somatic components of observed actions (Avikainen et al. 2002; Raos et al. 2004; Costantini et al. 2005; Avenanti et al. 2007; Chong et al. 2008).

One way of reconciling the discrepancy between these seemingly contrasting lines of evidence is to consider that while the latter condition typically provides explicit cues about the properties of a given action (e.g., movement direction or the specific muscle involved in the action), no specific cues are provided by action verbs. Therefore, while the facilitation during direct observation may derive from a resonant mirror mapping between model and onlooker, the inhibition during semantic derivation may arise from competition between different motor schemata associated with the word that was heard or read (Buccino et al. 2005). The possible involvement of the motor system not only in action observation and execution but also in more abstract action representations is also supported by studies in which categorization of a given individual was based on representation of her/his motor skills.

Indeed, attribution of motor skills to a given category (e.g., athletes) is based on semantic knowledge that defines the person's identity (Macrae and Bodenhausen 2000). In a recent behavioral study, subjects were instructed to respond to pictures of famous tennis and soccer athletes, who were portrayed both within and outside their context of expertise, using the hand or foot as effectors. An increase in RTs (i.e., an inhibition of overt motor reactivity) when responding to tennis and soccer athletes was found when participants used the hand and foot, respectively (Bach and Tipper 2006). This result indicates that visual categorization of athletes influences observer reactivity according to the relationship between the effector used by the observer and the model's supposed expertise in using the same effector. Moreover, the study indicates that semantic knowledge concerning the observed model's expertise is mapped in the motor system of naive observers, thus suggesting that abstract person categorization also conveys information about conspicuous sensorimotor features attributed to the same person. More recently, the same research group (Tipper and Bach 2010) provided behavioral data showing that while indirect derivation of the motor expertise implies increase of RTs (inhibitory person-based motor priming), the direct vision of expert models performing specific actions facilitates RTs (facilitatory person-based motor priming).

However, until now no information has been provided about the possible neurophysiological correlates of this behavioral inhibition. In sum, conceptual semantic categorization of stimuli evoking body actions and motor simulation triggered by direct observation or imagination of a given action may represent 2 independent processes that contribute to suppressive and facilitatory corticospinal modulation, respectively. We explored these issues in 3 s-p TMS experiments. In the first experiment, we investigated whether the visual categorization of surnames and faces of models with motor expertise (tennis and soccer athletes), that is, a task that likely implies the semantic derivation of motor expertise (Young et al. 1988; Bodenhausen and Macrae 1998; Bach and Tipper 2006, 2007), is reflected in a reduction of the arm and leg corticospinal motor excitability of naive observers. In the second experiment, we measured corticospinal excitability of arm and leg muscles when subjects performed the same categorization task of Experiment 1 in response to visual presentation of the same tennis and soccer athletes, full body portrayed while executing a prototypical action ("in action" athlete stimuli), of the sport they were experts in. In the third experiment, we explored whether the corticospinal representation of arm and leg muscles was facilitated during observation of out-of-context lay people performing the same movements as the athletes in Experiment 2. Our experimental design allowed us to explore any modulation of an onlooker's corticospinal representations contingent upon different features of the model, namely: 1) semantic knowledge about his motor expertise (Experiment 1), 2) combination of expertise-related knowledge and action-related contextual information (Experiment 2), and 3) non-contextual action-related information (Experiment 3).

## Materials and Methods

### Experiment 1

#### Subjects

Thirteen healthy subjects (all males, mean age  $25.0 \pm$  standard deviation [SD] 6.5 years) participated in this experiment. All subjects except one

were right-handed according to the Standard Handedness Inventory (Briggs and Nebes 1975) and had normal or corrected-to-normal visual acuity. All subjects gave their written informed consent prior to their inclusion in the study and were naive as to its purpose. Subjects were compensated for their time, and specific information concerning the study was provided only after the subject had finished all experimental sessions. The experimental procedures were approved by the Fondazione Santa Lucia Ethics Committee and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. None of the participants had a history of neurological, psychiatric, or other medical problems or any contraindication to TMS (Wasserman 1998). No discomfort or adverse effects during TMS were noticed or reported. Since the present research was not focused on the expertise of the observers, which by all means shapes resonant reactivity (Aglioti et al. 2008; Beilock et al. 2008; Fourkas et al. 2008), no professional or semiprofessional tennis or soccer players were recruited for the study. To be included in this experiment, each participant had to recognize all the famous athletes portrayed in the series of face and surname stimuli.

#### Electromyographic and TMS Recording

Electromyographic (EMG) recording was performed with a Viking IV (Nicolet Biomedical) electromyograph. EMG signal was band filtered (20 Hz–2.5 kHz, sampling rate 10 kHz), digitalized, and stored for off-line analysis. Pairs of Ag–AgCl surface electrodes (1 cm diameter) were placed over the muscle belly (active electrode) and over the associated joint or tendon (reference electrode) in a classical belly-tendon montage. The ground electrode was placed over the knee for tibialis anterior/soleus (TA/SOL) and over the dorsal part of the elbow for extensor carpi radialis/flexor carpi radialis (ECR/FCR) recordings. Leg and arm muscle activity was recorded in different experimental blocks. We recorded from the gravitational/antigravitational muscles of both limbs to specifically control for the muscle specificity of any modulatory effects related to the different observation conditions.

TMS of ECR/FCR was performed using a 70-mm figure-of-eight coil connected to a Magstim Super Rapid Transcranial Magnetic Stimulator (The Magstim Company) placed over the left motor cortex. The coil was held tangentially to the scalp with the handle pointing  $45^\circ$  away from the nasion-inion line in a posterolateral direction (Brasil-Neto et al. 1992; Mills et al. 1992). For the TA/SOL muscles, as their motor cortical representation is located deep along the interhemispheric sulcus and difficult to reach with the magnetic pulse, a double-cone coil was used. To find individual optimal scalp positions (OSPs, i.e., the stimulation position that induces motor evoked potentials [MEPs] of maximal amplitude) for each muscle, 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 subjects. Once the OSP was found, the resting motor threshold (rMT) was defined as the lowest intensity of stimulation that produced 5 MEPs out of 10 consecutive magnetic pulses with at least 50  $\mu$ V of amplitude. We defined the rMT by targeting the ECR (using the figure-of-eight coil for the upper limb) and TA (using the double-cone coil for the lower limb) gravitational muscles. TMS studies in which 2 muscles are recorded simultaneously (as in this study ECR/FCR and TA/SOL) determined rMT by targeting those presenting a higher threshold to avoid the loss of any differential modulations involving the less excitable muscle (Romani et al. 2005; Fourkas et al. 2006; Avenanti et al. 2007). Here, we chose the lower threshold muscle to allow using stimulation intensities 20% above rMT without saturating the stimulators also in subjects with high thresholds. Importantly, the chosen scalp positions allowed us to record a clear and stable simultaneous EMG signal (10 MEPs out of 10 TMS pulses) from FCR during ECR stimulation and from SOL during TA stimulation (Krings et al. 1998). Mean rMT was  $67.3 \pm$  SD 9.46% for TA and  $55.8 \pm$  SD 10.17% for ECR. During the experimental sessions, s-p TMS with 120% intensity of individual rMT was delivered over the marked OSP. EMG recording started 100 ms before the magnetic pulse in order to control for the absence of muscular preactivation in each trial. MEPs' peak-to-peak amplitudes (in millivolts) were collected and stored in a computer for off-line analysis.

#### Visual Stimuli

The experimental visual stimuli consisted of 10 famous athletes' surnames and faces (5 tennis players and 5 soccer players). The stimuli

subtended a visual angle of about  $9.3^\circ$  and were perceived effortlessly by the participants. The full set of experimental stimuli can be found in the Supplementary Material.

### Procedure

Participants were tested in 2 sessions of approximately 90 min each. In each session, MEP amplitudes were recorded from either arm (simultaneously from ECR/FCR) or leg (simultaneously from TA/SOL) muscles. Upper and lower limb stimulation order was counterbalanced across subjects. During the experimental blocks, the subjects were comfortably seated in a dimly lit room at a distance of 80 cm from a computer screen (SONY Trinitron CPD-E400P, 60 Hz refresh rate). Each session consisted of 4 experimental blocks of 20 trials each. At the beginning of the experiment, subjects were instructed to pay attention to the visual stimuli presented on the screen and to categorize the stimuli verbally (saying "soccer player" or "tennis player") in a self-paced manner during the intertrial interval (9000 ms). During each experimental block, participants were presented twice with 5 tennis and 5 soccer randomized stimuli. Thus, 20 MEPs per block were obtained. Surname and face stimuli were presented in separate blocks counterbalanced for each subject and limb and repeated twice. As MEPs' amplitude may be greatly influenced by the format of the stimuli, the block procedure allowed optimizing the signal-to-noise ratio. Importantly, tennis- and soccer-related items were presented randomly within each block, which allowed excluding that this crucial comparison was influenced by habituation effects. Each stimulus appeared at the center of the screen for 1500 ms. During stimulus presentation, a single pulse of TMS was delivered over the subjects' muscle OSP at 120% of rMT (examples of athletes' surnames and faces are shown in Fig. 1, left part). The magnetic stimulation was delivered at random times ranging between 1100 and 1400 ms from stimulus onset to avoid any priming effects that might influence MEP amplitude. TMS frequency during experimental blocks was  $<0.1$  Hz to avoid that TMS per se would influence motor cortex excitability (Chen et al. 1997).

### Data Analysis

MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition or single trials contaminated by muscular preactivation were excluded as outliers and precontracted trials, respectively (7.83% of total). Raw MEP amplitudes were entered in a  $(2 \times 2 \times 2 \times 2)$  factorial design with Stimulus (face and surname), Sport (soccer and tennis), Limb (arm and leg), and Muscle (ECR/TA gravitational and FCR/SOL antigravity) as main factors. Post hoc comparisons were performed with Newman-Keuls test.

### Experiment 2

The same 13 subjects of Experiment 1 underwent Experiment 2 in a separate testing session performed on the same day. The order of experiments was counterbalanced across subjects. Experiment 2 differed from Experiment 1 for the type of observed stimuli (see Fig. 1). The

experimental procedures and data handling were identical in these 2 experiments (outliers and precontracted trials, 7.44% of total).

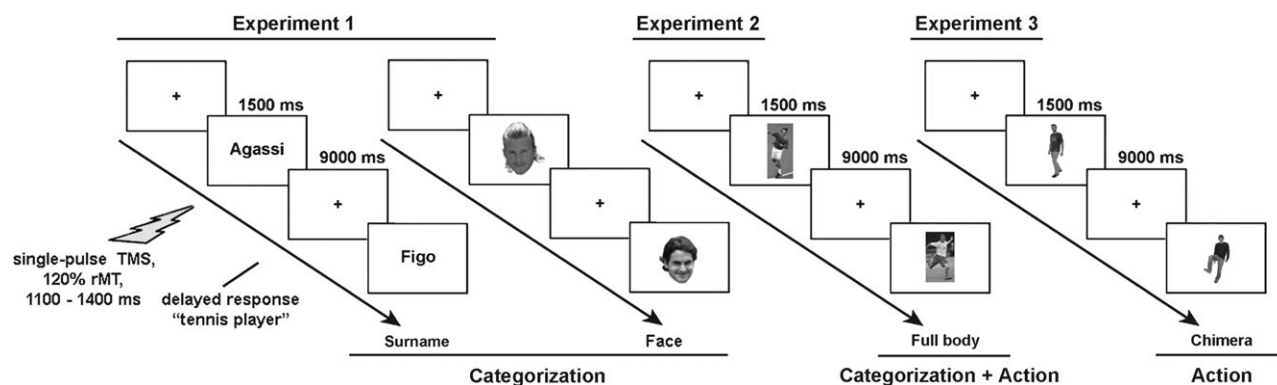
We chose full-body "in action" snapshots of the same 10 athletes presented in Experiment 1. The images portrayed the athletes performing a "typical" sport movement (examples in Fig. 1). As only the still image of the middle phase of an ongoing action has been proven effective in facilitating motor cortex excitability (Urgesi et al. 2006b), we selected snapshots of tennis players that showed the middle phase of a service or forearm shot and snapshots of soccer players that depicted the athletes as they kicked a ball. The tennis racquet and soccer ball were removed from the images because tool observation per se might facilitate the excitability of the motor system (Chao and Martin 2000; Beauchamp et al. 2002). The amount of implied motion in each image was controlled by asking 10 independent participants to rate the implied motion in a set of 20 tennis and 20 soccer still images by marking a 10-cm vertical visual analogue scale (VAS). The upper and the lower extremities of the VAS indicated "maximal implied movement" and "no implied movement," respectively. Participants were explicitly asked to rate the motion implied in the upper limbs, lower limbs, and entire body in separate blocks presented in counter-balanced order. Based on the subjective ratings of implied motion, a subset of 5 images was selected for each sport (full set in Supplementary Material). As the aim of Experiment 2 was to test whether action facilitation for implied motion perception contrasts the possible MEP amplitude reduction related to categorization of the model's motor expertise, in the final stimuli subset, we included the tennis and soccer snapshots with higher implied motion for the upper and lower limbs, respectively (see Results). It is worth noting that the tennis and soccer snapshots in the final set did not differ for the ratings of global implied motion (i.e., the motion implied by the entire image, see Results).

Raw MEP amplitudes were entered in a  $(2 \times 2 \times 2)$  factorial design with Sport (soccer and tennis), Limb (arm and leg), and Muscle (ECR/TA gravitational and FCR/SOL antigravity) as main factors. Post hoc comparisons were performed with the Newman-Keuls test.

### Experiment 3

Fourteen right-handed participants (Briggs and Nebes 1975) with normal or corrected-to-normal vision took part in this experiment (12 females, mean age  $21.9 \pm$  SD 2.21 years). Following the same line of reasoning of Experiments 1 and 2, no professional or semiprofessional tennis or soccer players were recruited for the study (Aglioti et al. 2008; Beilock et al. 2008; Fourkas et al. 2008).

The experimental stimuli consisted of full-body "in action" snapshots in which no contextual sport-related information was available. Black and white pictures were taken from individuals in everyday clothing assuming the same postures as the athletes in Experiment 2 or standing still. In order to be sure that the attention of the observer would be focused on the motion of the upper or lower limbs (Bach et al. 2007; Chong et al. 2009), we used Adobe Photoshop CS software (Adobe Systems Incorporated) to merge the initial images and create "motor chimeric" snapshots in which the upper or lower half of the body (upper or lower chimeras) was in motion and the other half was static



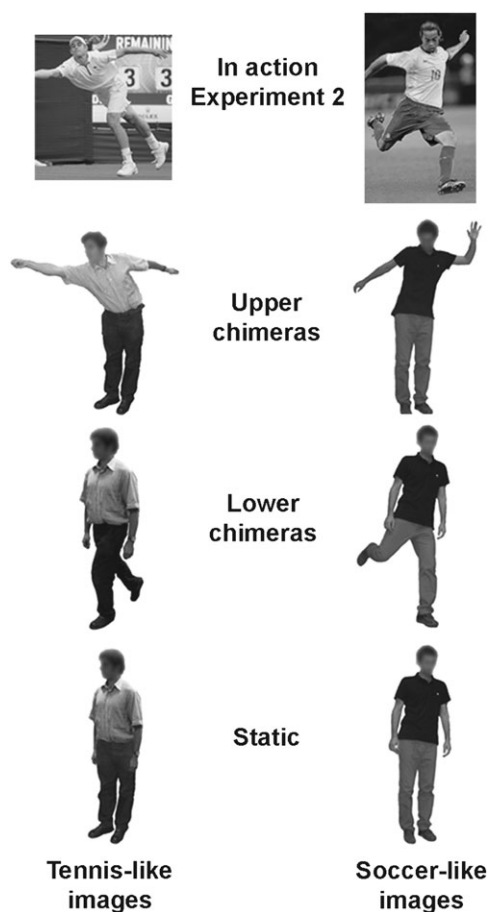
**Figure 1.** Examples of typical event trials for "surname" and "face" (Experiment 1) "in action" (Experiment 2) and "lower chimeras" (Experiment 3) stimuli.

(examples of these kind of stimuli are given in Fig. 2). It is relevant that even though the chimeric stimuli were obtained from nonexpert out-of-context models that mimicked tennis or soccer actions, they were not easily categorized as tennis- or soccer-related postures. In view of this, in Experiment 3, we refer to the stimuli as tennis- and soccer-like images. Experiment 3 differed from Experiments 1 and 2 for the type of observed stimuli (see Fig. 1, rightmost part). The experimental procedures and data handling were identical to Experiments 1 and 2.

Subjective ratings of the motion implied by the different chimeric stimuli were obtained. In particular, VAS ratings for the whole image and for the upper and lower limbs were obtained in separate blocks counterbalanced across subjects. One subject was discarded from the VAS analysis because of a technical failure in recording his responses. During the TMS session, participants were presented with static upper or lower body chimeric images of both soccer- and tennis-like postures (15 trials per condition). The presentation order of the different images as well as the limb stimulation order was counterbalanced within and across subjects, respectively. The presentation of upper and lower body chimera occurred in separate blocks counterbalanced within subjects. Participants were asked to pay attention to the stimuli and were informed that questions about whether the model was depicted in a frontal or lateral view would be asked during testing.

Mean TMS intensities for ECR and TA muscles' stimulation were  $51.5 \pm \text{SD } 10.25\%$  and  $47.5 \pm \text{SD } 8.36\%$ , respectively. MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition or trials contaminated by muscular preactivation were excluded as outliers and precontracted trials, respectively (5.29% of total).

MEP amplitudes of upper and lower chimera conditions were normalized on static images (upper and lower chimera MEP amplitudes



**Figure 2.** Examples of lower and upper chimeras and static images of tennis- and soccer-related postures (Experiment 3) developed from "in action" images of Experiment 2.

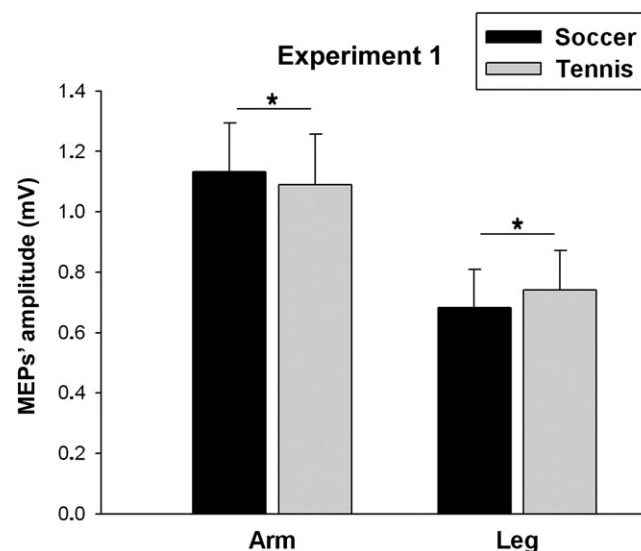
of soccer and tennis images were divided by MEP amplitudes of static images). Normalizing the data allows controlling for interindividual MEP variability and disentangling facilitatory from inhibitory modulations of corticospinal excitability.

Normalized MEP amplitudes of upper and lower chimera stimuli were entered in 2 separate repeated measures analyses of variance (ANOVAs) with Sport (tennis and soccer), Limb (arm and leg), and Muscle (ECR/TA gravitational and FCR/SOL antigravity) as main factors ( $2 \times 2 \times 2$ ). Post hoc comparisons were performed using the Newman-Keuls test.

## Results

### Experiment 1

MEP amplitude analysis showed a main effect of Limb factor ( $F_{1,12} = 26.467$ ), with arm muscles ( $1.112 \pm \text{SD } 0.588$  mV) more excitable than leg muscles ( $0.713 \pm \text{SD } 0.460$  mV,  $P < 0.000$ ). The Muscle factor also reached significance ( $F_{1,12} = 9.486$ ); MEP amplitudes were significantly higher for ECR/TA ( $0.983 \pm \text{SD } 0.517$  mV) than for FCR/SOL ( $0.841 \pm \text{SD } 0.599$  mV,  $P = 0.009$ ), probably because we used OSP for the former muscles and because of their larger corticospinal representation. The Stimulus factor (face/surname) did not reach statistical significance ( $F_{1,12} = 0.360$ ,  $P = 0.560$ ). Importantly, the only significant interaction was the one between Sport and Limb ( $F_{1,12} = 24.412$ ,  $P < 0.000$ ) (Fig. 3). Post hoc comparisons showed that the arm muscles' corticospinal motor excitability was reduced during presentation of the tennis stimuli ( $1.091 \pm \text{SD } 0.599$  mV) with respect to soccer stimuli ( $1.132 \pm \text{SD } 0.581$  mV,  $P = 0.013$ ). A complementary pattern of results was found for leg muscles' corticospinal motor excitability that was reduced during categorization of the soccer stimuli ( $0.683 \pm \text{SD } 0.457$  mV) with respect to the tennis stimuli ( $0.742 \pm \text{SD } 0.466$  mV,  $P = 0.002$ ). No other main effect or interaction was significant (all  $P$ s  $> 0.9$ ). No changes in the analysis were found



**Figure 3.** Interaction between Sport and Limb factors in Experiment 1. Raw amplitude in millivolts (mean  $\pm$  standard error of mean) of MEPs recorded from arm (ECR/FCR) and leg (TA/SOL) muscles. Histograms show that the excitability of arm muscles was reduced during "tennis player" stimuli presentation with respect to "soccer player" stimuli presentation. The opposite pattern was found for leg muscles (all  $P$ s  $< 0.013$ ). The difference between arm and leg muscles was likely due to the larger corticospinal motor representation of arm muscles. \*denote  $P$  values  $< 0.05$ .

when taking out data from the mild left-handed subject. The significance of the interaction between Sport and Limb factors in the comparison of raw MEP amplitudes indicates that the pattern of relative reduction for the limb muscles associated with the sport is independent from MEP absolute amplitude.

### Experiment 2

The subjective ratings of the motion implied in “in action” sport snapshots were compared using a repeated measure ANOVA with Body part judged (whole body and lower or upper limbs) and Sport (tennis and soccer) as within-subjects factor ( $3 \times 2$ ). No main effect reached statistical significance (all  $P$ s > 0.08). Crucially, the interaction between Body part judged and Sport was significant ( $F_{2,18} = 38.420$ ,  $P < 0.000$ ). Post hoc comparisons revealed that the perceived implied motion in the upper limbs was higher for tennis images ( $72.060 \pm \text{SD } 14.787$  mm) compared with soccer images ( $49.180 \pm \text{SD } 11.732$  mm,  $P < 0.000$ ). Conversely, the perceived implied motion in the lower limbs was higher for soccer images ( $70.900 \pm \text{SD } 14.282$  mm) compared with tennis images ( $43.840 \pm \text{SD } 9.858$  mm,  $P < 0.000$ ). Whole-body implied motion did not differ between soccer ( $68.820 \pm \text{SD } 15.200$  mm) and tennis ( $62.740 \pm \text{SD } 17.566$  mm) stimuli ( $P = 0.150$ ) (Fig. 4).

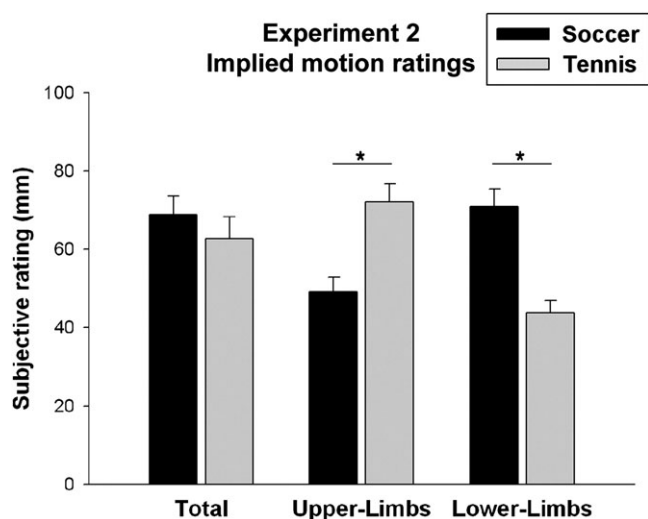
The ANOVA on raw MEP amplitudes revealed a main effect of Limb factor ( $F_{1,12} = 24.614$ ,  $P < 0.000$ ), which was explained by the higher excitability of arm muscles ( $1.168 \pm \text{SD } 0.564$  mV) with respect to leg muscles ( $0.772 \pm \text{SD } 0.547$  mV). The Muscle factor also reached significance ( $F_{1,12} = 6.265$ ,  $P = 0.028$ ), with ECR/TA muscles being more excitable ( $1.046 \pm \text{SD } 0.576$  mV) than FCR/SOL ( $0.895 \pm \text{SD } 0.596$  mV). No other factor or interaction was significant (all  $P$ s > 0.052). Importantly, unlike Experiment 1 where surnames and faces of soccer or tennis athletes were used, the interaction between Sport and Limb did not reach significance in this experiment ( $F_{1,12} = 0.815$ ,  $P = 0.385$ ) where “in action” stimuli were used (MEP amplitudes of all experimental conditions are provided in Supplementary

Material). To test whether “in action” stimuli were effective in modulating motor cortex excitability, we used a dependent samples  $t$ -test to compare MEP amplitudes for “no action” items (surname and face conditions collapsed together) with the “in action” items. MEP amplitudes resulted higher during “in action” experiment ( $0.970 \pm \text{SD } 0.511$  mV) compared with the face/surname “no action” experiment ( $0.911 \pm \text{SD } 0.493$  mV,  $t_{13} = 2.392$ ,  $P = 0.034$ ) (Fig. 5), suggesting that the possible MEP facilitation associated to direct action observation contrasted with the suppressive effect of expertise-related categorization.

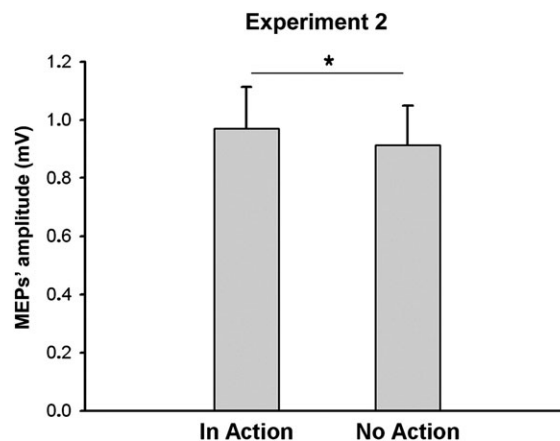
### Experiment 3

The subjective ratings of the motion implied by upper and lower chimeras and still snapshots were compared using a repeated measure ANOVA with Moving body part (upper or lower chimeras), Sport (tennis like and soccer like), and Body part judged (lower limbs, upper limbs, and whole body) as within-subjects factor ( $2 \times 2 \times 3$ ). All factors reached statistical significance as main effects: Body part judged ( $F_{2,24} = 23.542$ ,  $P < 0.000$ , whole = upper limbs > lower limbs), Sport ( $F_{1,12} = 27.315$ ,  $P < 0.000$ , soccer like > tennis like), and Moving body part ( $F_{1,12} = 7.828$ ,  $P = 0.016$ , upper > lower chimeras). All interactions reached significance (all  $P$ s < 0.020). Crucial to this experiment, the triple interaction between Moving body part  $\times$  Sport  $\times$  Body part judged was significant ( $F_{2,24} = 4.643$ ,  $P = 0.019$ ). Post hoc testing revealed that when rating lower chimeras, implied action was higher for soccer-like images than for tennis-like images in lower limbs ( $63.67 \pm \text{SD } 25.38$  vs.  $35.43 \pm \text{SD } 19.28$  mm,  $P < 0.000$ ) and total movement conditions ( $60.58 \pm \text{SD } 22.49$  vs.  $27.52 \pm \text{SD } 15.56$  mm) ( $P < 0.000$ ). By contrast, implied action ratings for soccer- and tennis-like images were not significantly different in the upper limb condition ( $21.69 \pm \text{SD } 18.85$  vs.  $10.43 \pm \text{SD } 8.29$  mm,  $P = 0.232$ ) (Fig. 6, lower panel). Ratings of upper chimeras showed no difference between the tennis- and soccer-like conditions for all the Body parts judged ( $P > 0.991$ ) (Fig. 6, upper panel).

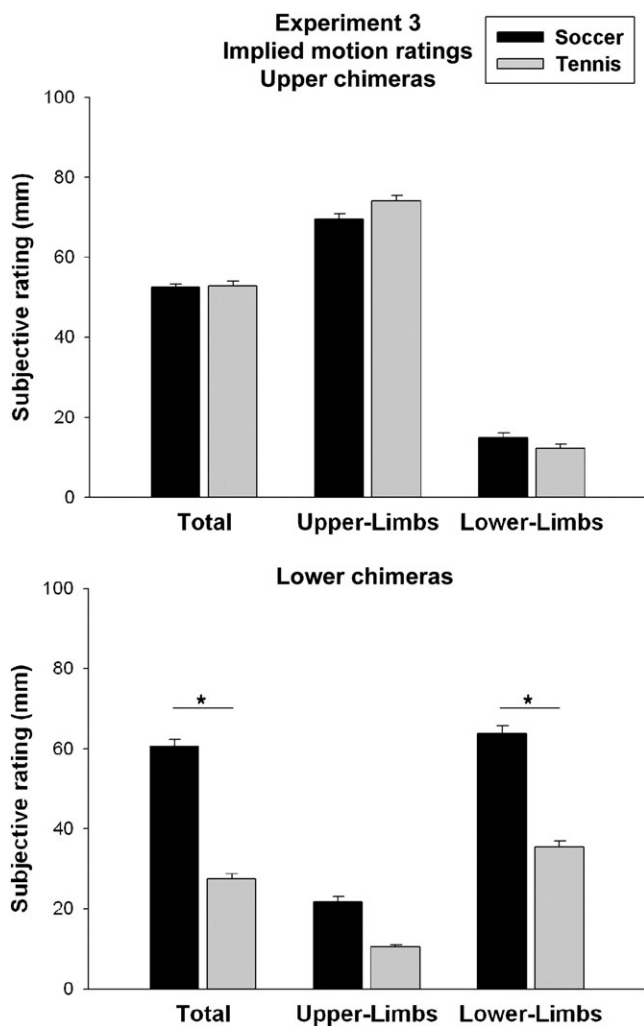
Thus, unlike Experiment 2 where expertise-related categorization was still at play, in Experiment 3, the dissociation of implied motion ratings of soccer- and tennis-like postures was found for lower limb movements but not for upper limb



**Figure 4.** Subjective ratings of the motion implied in tennis and soccer “in action” stimuli. Histograms represent mean VAS ratings (mean in millimeter  $\pm$  standard error of mean) of the amount of motion implied in the whole posture and in the upper and lower limbs of each image type. Implied upper limb motion ratings for tennis “in action” images were significantly higher than for soccer players; the opposite was true for the lower limb. Judgments about the motion implied in the whole posture did not differ between soccer and tennis “in action” stimuli. \*denote  $P$  values < 0.05.



**Figure 5.** Comparison of raw MEPs' amplitude (millivolts  $\pm$  standard error of mean) for “in action” (Experiment 2) and “no action” (Experiment 1) stimuli. “In action” stimuli evoked higher MEPs' amplitudes ( $P = 0.034$ ) than “no action” stimuli, thus indicating a general modulation toward corticospinal facilitation contingent upon implied action observation. \*denote  $P$  values < 0.05.

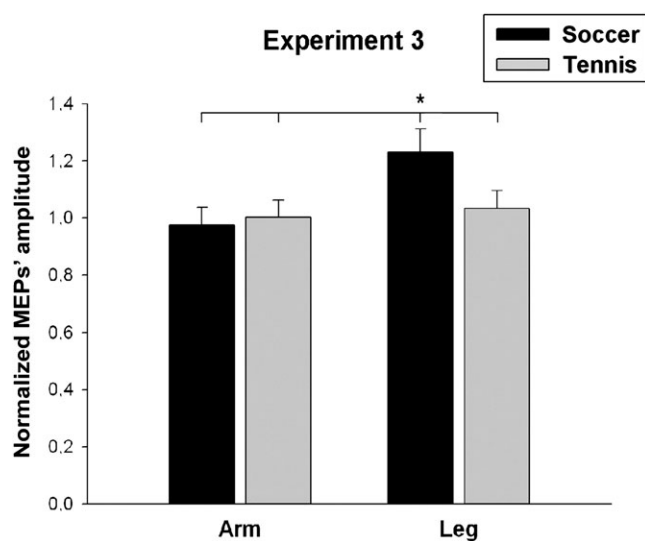


**Figure 6.** Subjective ratings of soccer- and tennis-related chimeric images. Histograms represent mean VAS ratings (mean in millimeter  $\pm$  standard error of mean) of the amount of perceived motion implied in upper and lower chimeras when subjects judged the implied motion conveyed by the whole image or by the upper or lower limbs. Crucially, the implied motion in the lower limbs of soccer-related images was higher than in tennis-related images when judging only the lower limbs or the whole image of lower chimeras. Conversely, tennis-related images did not evoke stronger sensations of implied motion when subjects judged either the upper limbs or the whole image of upper chimeras. \*denote  $P$  values  $< 0.05$ .

movements. This characteristic of the different stimuli allowed to test for the first time the effect of “pure” implied motion perception on lower limb corticospinal excitability.

The analysis of normalized MEPs recorded during observation of lower chimeras showed no main effect of Sport, Limb, or Muscle (all  $P$ s  $> 0.117$ ). Importantly, the interaction between Sport and Limb turned out to be significant ( $F_{1,13} = 5.956$ ,  $P = 0.029$ ). Post hoc analysis showed that excitability of leg muscles (both gravitational and antigravitational) was facilitated during observation of soccer-like lower chimeras ( $1.231 \pm$  SD 0.302 normalized) with respect to tennis-like ones ( $1.033 \pm$  SD 0.236 normalized,  $P = 0.010$ ). Excitability of the arm muscles did not differ during observation of soccer-like ( $0.975 \pm$  SD 0.230 normalized) and tennis-like ( $1.001 \pm$  SD 0.229 normalized) chimeras ( $P = 0.688$ ) (Fig. 6).

Conversely, the analysis of normalized MEPs’ amplitude during observation of upper chimeras showed that no factor or



**Figure 7.** Interaction of Sport and Limb factors in Experiment 3. Normalized MEPs’ amplitude (mean  $\pm$  standard error of mean) of MEPs recorded from arm (ECR/FCR) and leg (TA/SOL) muscles. Histograms show that leg muscles were facilitated during observation of soccer-related lower chimeras with respect to observation of tennis-related lower chimeras. \*denote  $P$  values  $< 0.05$ .

interaction reached statistical significance, indicating there was no corticospinal modulation in either arm or leg muscles (all  $P$ s  $> 0.153$ ) (Fig. 7) (raw MEP amplitudes of all experimental conditions are provided in Supplementary Material).

## Discussion

Although concepts may be more than percepts (Bedny et al. 2008), mounting evidence suggests that semantic representations can be mapped onto modal sensorimotor cortices (Glenberg 1997; Goldberg et al. 2006; Barsalou 2008) and that this mapping can even take place according to somatotopic rules (Hauk et al. 2004; Pulvermüller et al. 2005; Aziz-Zadeh et al. 2006; Boulenger et al. 2009; but see also Bedny et al. 2008; Postle et al. 2008). Within the framework of grounded cognition theories (Glenberg 1997; Wilson 2002; Barsalou 2008), we tested nonathlete individuals in 3 s-p TMS experiments to explore the corticospinal motor reactivity of non-expert onlookers who 1) perceive and categorize surnames or faces of motorically expert individuals, namely, elite tennis and soccer athletes, a condition in which indirect category-related actions’ information is available; 2) observe the very same athletes performing an action in their domain of expertise, a condition in which both direct and category-derived information about actions is available; and 3) observe nonathlete individuals portrayed in the same postures of athletes, a condition in which direct action related but not categorical information is available.

### Categorical Derivation of Actions Influences Corticospinal Motor Representations

One of the main results of our study is that knowledge concerning the representation of skilled motor behavior that is not actually perceived but is an implicit characteristic of a well-known athlete model is mapped in the corticospinal motor excitability of nonskilled observers. This process is indexed by a reduction of MEPs recorded from the arm and leg when

subjects categorized tennis and soccer athletes, respectively. This effect was found for both extensor and flexor muscles of the limb associated with the athlete's domain of expertise, indicating that the relative inhibition of corticospinal motor representation associated to athlete categorization regarded the whole limb associated with a specific sport rather than with a specific muscle. These results expand the findings of behavioral studies showing that knowledge concerning soccer and tennis athletes has an effect on motor reactivity (Bach and Tipper 2006; Tipper and Bach 2010). Indeed, in a recognition task, the participants' responses were slower and less accurate when performed using the limb associated with the observed athlete's domain of motor expertise (Bach and Tipper 2006). As the effect was found both when the athletes were portrayed in sport activity and in everyday contexts, the authors suggested that identity representation of expert athletes automatically influences the observers' motor system. Social psychology studies show that mere viewing of a famous person automatically activates information concerning the person's profession (Bodenhausen and Macrae 1998). Specifically, it has been shown that RTs are faster in a semantic categorization task based on occupation than in a semantic categorization task based on people naming (Young et al. 1988). The physiological finding of Experiment 1 extends previous behavioral and social research by showing that recognizing an athlete's identity automatically inhibits the corticomotor representation of the limb semantically associated with that athlete's domain of motor expertise. The reduction of MEPs' amplitude contrasts with TMS studies in which direct viewing of actual (Fadiga et al. 1995, 2005; Romani et al. 2005; Urgesi et al. 2006a; Avenanti et al. 2007), implied (Urgesi et al. 2006b, 2010), or motorically imagined (Vargas et al. 2004; Fourkas et al. 2006) actions brought about an MEP facilitation that was specific for the muscle that would be involved in performing the same action. Moreover, during direct action observation, the facilitation of agonist and antagonist muscles followed the temporal progress of the observed action (Gangitano et al. 2001).

Our findings shed new light on the process involved in semantic derivation of categorization of others based on their motor expertise. Indeed, we show that this process differs from direct action observation because it induces 1) inhibitory rather than facilitatory MEP modulation and 2) simultaneous suppression of both agonist and antagonist muscles of the same limb rather than facilitation of the muscles that would be activated at specific instants during execution of the observed action. It is worth noting that while viewing an action may trigger the simulation of the very same action (Fadiga et al. 1995; Prinz 1997; Gangitano et al. 2001, 2004; Kilner et al. 2003), categorical knowledge linked to stimulus recognition (in our case, faces or surnames of famous athletes) may only allow the indirect derivation of implicit motor properties of the stimulus. A variety of complex sensory and motor information (e.g., the sensation of the racquet in the hand, the weight of the racquet, the movement necessary to hit the ball) may be evoked by action derivation. However, the inferential process does not provide any detail about the implementation of a specific action and can provide only abstract information about a category of actions. By contrast, direct observation of an action provides explicit information on the exact implementation of the very same action and thus implies a direct matching between observation and execution (Rizzolatti and Craighero 2004) as well as a consequent MEP facilitation

(Fadiga et al. 1995; Gangitano et al. 2001, 2004; Urgesi et al. 2006a, 2006b; Avenanti et al. 2007). Therefore, the suppression of motor representations during semantic derivation may arise from competition between different motor schemata associated to a series of different actions within the domain of expertise of the observed athlete (see Tipper and Bach 2010 for a similar proposal). This explanation is reminiscent of studies where listening to hand- or foot action-related sentences brought about a clear inhibition of MEPs recorded from the relative body part (Buccino et al. 2005). The above-mentioned difference may also explain why the derivative notion of the high motor skills of a model involves an embodiment process based on mapping the observers' whole limb and not specific muscles, like what happens in direct action observation tasks.

A partially different explanation of the MEP reduction related to semantic categorization calls into play the interactions between cognitive and motor systems (Redding et al. 1992; Taylor and Thoroughman 2007). Taylor and Thoroughman (2008) showed that changing the cognitive load of a semantic categorization task caused a reduction of motor adaptation. This result suggests that overlapping neural systems are recruited during early stages of motor learning and categorization tasks (Taylor and Thoroughman 2008). Our categorization task was delayed (i.e., there was a self-paced time gap between stimulus disappearance and response). Therefore, the need for cognitive monitoring processes may have altered the simulational cortical reactivity triggered by the movement properties of the stimuli (Taylor and Thoroughman 2008). This would be in keeping with an Event Related Potential (ERP) study in which a more negative deflection, generated in a specific part of the anterior cingulate cortex and possibly related to response inhibition, was elicited by delayed responses (Qiu et al. 2008).

Regardless of the possible explanations for suppressive mapping, the finding that derived information about actions is mapped in the motor system is also in keeping with previous behavioral, physiological, and neuroimaging studies showing that listening or reading action verbs related to a specific body part modulates motor response, corticomotor excitability, and blood oxygen level-dependent activity in motor areas that represent the same body part (Pulvermüller et al. 2001; Hauk et al. 2004; Buccino et al. 2005; Tettamanti et al. 2005; for a review see Hauk et al. 2008). The fact that semantic derivation is reflected in corticospinal activity suggests that knowledge representation as well as language comprehension may be based on the reactivation of sensorimotor features associated with concepts acquired in previous experiences in the world (Barsalou et al. 2003; Decety and Grèzes 2006; Barsalou 2008). Thus, conceptual processing may rely on motor, somatic, and visual regions not primarily concerned with linguistic processing (Barsalou et al. 2003; Havas et al. 2007). This is in accord with behavioral studies showing that when language specifies certain properties of an action (e.g., the direction of a movement), the motor system is automatically influenced in its efferent motor commands based on an action-sentence compatibility rule (i.e., movements are best executed when in the same direction implied in the verb, the so-called action compatibility effect) (Glenberg and Kaschak 2002).

In sum, corticospinal motor modulation was linked to semantic derivation of the athlete models' excellent skills as well as to body parts associated to sport-specific skills. This is in accord with grounded cognition theories suggesting that higher order, linguistic, and conceptual representations can

be mapped in one's own sensorimotor systems (Gallese and Lakoff 2005; Barsalou 2008).

### ***Derived Action Semantics and Action Observation Exert Opposite Influences on Corticospinal Excitability***

Experiment 1 indicates that processing abstract information concerning the skilled motor behavior of a model leads to somatotopic reduction of the corticospinal excitability of an onlooker. In Experiment 2, we investigated whether this derivation effect was influenced by direct action observation, which typically induces corticospinal facilitation (Fadiga et al. 2005; Romani et al. 2005; Urgesi et al. 2006a, 2006b; Avenanti et al. 2007). To this aim, we asked nonathlete subjects to categorize pictures of tennis and soccer athletes portrayed while performing a movement typical of their sport. It has been shown that images merely implying an action activate the motor system (Nishitani and Hari 2002; Grèzes et al. 2007) and facilitate motor cortex excitability (Urgesi et al. 2006b, 2010). Moreover, based on the notion that corticospinal facilitation during the observation of implied action is maximal for initial and middle action phase snapshots (Urgesi et al. 2006b, 2010), we chose images of tennis players portraying the middle phase of services/forehand shots and images of soccer players depicting the middle phase of ball kicking. Therefore, we used a type of "in action" stimulus that conveys both contextual categorical information about the athlete models and explicit information about the performed action. We aimed to investigate whether the reduction of corticospinal excitability related to the categorization task would survive the expected facilitation typically occurring for action simulation or whether the excitability reduction would diminish or even vanish given the supposed simulative facilitating phenomena. Subjective ratings of the quantity of motion implied in upper and lower limbs were higher in tennis and soccer images, respectively. This indicates that participants perceived upper limb and lower limb actions as more dynamic in tennis and soccer models, respectively. However, subjective ratings were dissociated from the physiological data. In fact, no specific cortical facilitation was found in arm and leg muscles during categorization of tennis and soccer implied action images. A possible explanation for this negative result was the co-existence of the categorization task, which reduced the corticospinal excitability of the same muscles and contrasted the possible facilitation contingent upon direct action observation. This result may seem in contrast with the behavioral findings that motor expertise-related priming may turn from inhibitory to facilitatory when moving from abstract categorization to direct action view (Tipper and Bach 2010). However, the difference may be explained by task (active responses vs. passive viewing) and type of measurement (RTs vs. MEPs) variables. It is known, for example, that preparing a motor response over short intervals (500–1000 ms) (like happens in Tipper and Bach 2010 but not in the present study) may induce opposite facilitatory and inhibitory effects on RTs and MEP amplitudes (Sinclair and Hammond 2008).

It could be suggested that the suppressive effect contingent upon athlete categorization was not due to difficulty in choosing among different schemata (Buccino et al. 2005) but might simply represent the undershoot phase of neural activity occurring after an excitatory peak. Were this the case, absence of the sport- and limb-specific MEP modulation reported in Experiment 2 would not reflect the synchronous competition

between facilitatory simulation and suppressive categorization but may be related to the complex interplay between the neuronal pools stimulated by the magnetic pulse. Different motor axons (i.e., axons with different length and conductance properties) present different recovery cycles, including the undershoot phase of action potential (Kuwabara et al. 2000). As both timing and site of stimulation were identical in Experiments 1 and 2, at least theoretically, we were measuring the same phase of neural firing occurring after stimulus presentation. Thus, any difference in the direction of modulation (suppression or facilitation) associated to the stimulus format should have originated from stimuli-specific processes occurring at the same time. Moreover, the TMS time window used in all the 3 experiments of the present study derived from our previous experience with implied action facilitatory effects (Urgesi et al. 2006b, 2010), further suggesting that timing had no specific role in the lack of specific MEP modulation in Experiment 2. It is also relevant that the analysis between "in action" and "no action" stimuli revealed that images portraying athletes during a kicking movement were effective in activating the observers' motor cortex, thus ruling out that cortical excitability might be insensitive to the presented images. In view of this, we posit that the limb-specific suppression of corticospinal motor representation associated to the semantic derivation of an athlete expertise and the mirror motor facilitation deriving from direct action observation compete for the same corticomotor substrate virtually at the same time. This interpretation is further supported by the results of Experiment 3 where the experimental stimuli portrayed actors with no specific motor expertise and whose implied action was limited to the upper or lower hemibody. It is worth noting that in Experiment 2, the implied motion ratings of "in action" stimuli indicated higher motion perception for upper and lower limbs in tennis and soccer snapshots, respectively. By contrast, while implied motion ratings of lower limb chimeras presented higher values for soccer-related images, no sport- and limb-related difference was found for upper limb chimeras. Therefore, we expected that only lower limb chimeras would be effective in triggering sport-specific modulation of leg muscles' excitability. In particular, we expected leg muscles' MEP amplitude to be higher during soccer-like compared to tennis-like lower chimera observation. Indeed, this is exactly what we found here, thus demonstrating a clear MEP facilitation contingent upon implied action when the observed model cannot be categorized on the basis of his motor expertise. Also, the fact that we found the effect only for lower chimeras, in which implied motion ratings were higher for soccer-like snapshots than for tennis-like snapshots, indicates a nice convergence between subjective and neurophysiological indices of motor reactivity. Moreover, the facilitation of leg muscles expands previous knowledge about hand muscles' facilitation (Urgesi et al. 2006b, 2010) and indicates the strong tendency of humans to simulate observed actions, even if just implied, according to somatotopic rules.

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## Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

## Notes

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