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

Matteo Candidi, Carmelo Mario Vicario, Ana Maria Abreu and Salvatore Maria Aglioti

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 naïve 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 naïve 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 ± 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 naïve 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; Bellock 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 offline 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° away from the nasion-inion line in a postcorticalateral 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 µV of amplitude. We defined the rMT by targeting the ERC (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 ERC/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 TMS stimulation and from SOL during TA stimulation (Kring and et al. 1998). Mean rMT was 67.3 ± SD 9.46% for TA and 55.8 ± SD 10.17% for ERC. 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
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).

Data Analysis
MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition or single trials contaminated by muscular MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition or single trials, were excluded as outliers and precontracted trials, 7.44% of total. Raw MEP amplitudes were entered in a (2 × 2 × 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 experiment.
(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 $51.5 \pm SD 10.25\%$ and $47.5 \pm SD 8.36\%$, 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 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 ($1.112 \pm SD 0.588\ mV$) more excitable than leg muscles ($0.713 \pm SD 0.460\ mV$, $P < 0.000$). The Muscle factor also reached significance ($F_{1,12} = 9.486$); MEP amplitudes were significantly higher for ECR/TA ($0.983 \pm SD 0.517\ mV$) than for FCR/SOL ($0.841 \pm SD 0.599\ mV$, $P = 0.009$), 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 ($1.091 \pm SD 0.599\ mV$) with respect to soccer stimuli ($1.132 \pm SD 0.581\ mV$, $P = 0.013$). A complementary pattern of results was found for leg muscles’ corticospinal motor excitability that was reduced during categorization of the soccer stimuli ($0.683 \pm SD 0.457\ mV$) with respect to the tennis stimuli ($0.742 \pm SD 0.466\ mV$, $P = 0.002$). No other main effect or interaction was significant (all $P$s $> 0.9$). No changes in the analysis were found

![Figure 2](image-url). 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.

![Figure 3](image-url). Interaction between Sport and Limb factors in Experiment 1. Raw amplitude in millivolts (mean ± 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 $< 0.05$. 

Cerebral Cortex December 2010, V 20 N 12 2835
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 × 2). No main effect reached statistical significance (all Ps > 0.08). Crucially, the interaction between Body part judged and Sport was significant (F2,18 = 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 ± SD 14.787 mm) compared with soccer images (49.180 ± SD 11.752 mm, P < 0.000). Conversely, the perceived implied motion in the lower limbs was higher for soccer images (70.900 ± SD 14.282 mm) compared with tennis images (43.840 ± SD 9.858 mm, P < 0.000). Whole-body implied motion did not differ between soccer (68.820 ± SD 15.200 mm) and tennis (62.740 ± SD 17.566 mm) stimuli (P = 0.150) (Fig. 4).

The ANOVA on raw MEP amplitudes revealed a main effect of Limb factor (F1,12 = 24.614, P < 0.000), which was explained by the higher excitability of arm muscles (1.168 ± SD 0.564 mV) with respect to leg muscles (0.772 ± SD 0.547 mV). The Muscle factor also reached significance (F1,12 = 6.265, P = 0.028), with ECR/TA muscles being more excitable (1.046 ± SD 0.576 mV) than FCR/SOL (0.895 ± SD 0.596 mV). No other factor or interaction was significant (all Ps > 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 (F1,12 = 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 (surnames and face conditions collapsed together) with the “in action” items. MEP amplitudes resulted higher during “in action” experiment (0.970 ± SD 0.511 mV) compared with the face/surname “no action” experiment (0.911 ± SD 0.493 mV, t13 = 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 × 3). All factors reached statistical significance as main effects: Body part judged (F2,24 = 23.542, P < 0.000, whole = upper limbs > lower limbs), Sport (F1,12 = 27.315, P < 0.000, soccer like > tennis like), and Moving body part (F1,12 = 7.828, P = 0.016, upper > lower chimeras). All interactions reached significance (all Ps < 0.020). Crucial to this experiment, the triple interaction between Moving body part × Sport × Body part judged was significant (F2,24 = 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 ± SD 25.38 vs. 35.43 ± SD 19.28 mm, P < 0.000) and total movement conditions (60.58 ± SD 22.49 vs. 27.52 ± 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 ± SD 18.85 vs. 10.43 ± 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
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 \( P > 0.117 \)). 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 ± SD 0.302 normalized) with respect to observation of tennis-related lower chimeras. *Denote \( P \) values < 0.05.

Conversely, the analysis of normalized MEPs’ amplitude during observation of upper chimeras showed that no factor or interaction reached statistical significance, indicating there was no corticospinal modulation in either arm or leg muscles (all \( P > 0.153 \)) (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 Thorophman 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 simultaneous cortical reactivity triggered by the movement properties of the stimuli (Taylor and Thorophman 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 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 coexistence 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 limb 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.

**Funding**

Ministero Istruzione Università e Ricerca (Progetti di Ricerca di Interesse Nazionale, PRIN 2007/MHRPTS_002); Istituto Italiano di Tecnologia SEED 2009 (Protocol Number 21538); the Italian Ministry of Health to S.M.A. A.M.A. is funded by Fundação para a Ciência e Tecnologia of Portugal (SFRH/BPD/36350/2007).
Supplementary Material

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

Notes

This study was conducted at the Fondazione Santa Lucia, IRCCS, Rome, Italy. Conflict of Interest: None declared.

References


