Grasping with the Foot: Goal and Motor Expertise in Action Observation

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Abstract: Action observation typically induces an online inner simulation of the observed movements. Here we investigate whether action observation merely activates, in the observer, the muscles involved in the observed movement or also muscles that are typically used to achieve the observed action goal. In a first experiment, hand and foot motor areas were stimulated by means of transcranial magnetic stimulation, while participants viewed a typical hand action (grasping) or a nonspecific action (stepping over an object) performed by either a hand or a foot. Hand motor evoked potentials (MEPs) increased for grasping and stepping over actions performed by the hand and for grasping actions performed by the foot. Conversely, foot MEPs increased only for actions performed by the foot. In a second experiment, participants viewed a typical hand action (grasping a pencil) and a typical foot action (pressing a foot-pedal) performed by either a hand or a foot. Again, hand MEPs increased not only during the observation of both actions performed by the hand but also for grasping actions performed by the foot. Foot MEPs increased not only during the observation of grasping and pressing actions performed by the foot but also for pressing actions performed by the hand. This evidence indicates that motor activations by action observation occur also in the muscles typically used to perform the observed action, even when the action is executed by an unusual effector, hence suggesting a double coding of observed actions: a strict somatotopic coding and an action goal coding based on the observer's motor expertise. *Hum Brain Mapp* 35:1750–1760, 2014. © 2013 Wiley Periodicals, Inc.

Key words: action observation; action goals; motor expertise; transcranial magnetic stimulation; motor evoked potentials

INTRODUCTION

Several studies in human and non-human primates show that action observation covertly activates the observer's motor system in a fashion which roughly corresponds

to that shown when the same action is actually executed by the observer [e.g., Rizzolatti and Craighero, 2004]. One of the hypotheses which has been put forward to explain such phenomenon comes from neurophysiological studies in monkeys, which demonstrate the existence of a class of neurons in the premotor and parietal cortices that respond to both action execution and action observation. It has been hypothesized that this system, known as the "Mirror Neuron System" (MNS), may contribute to action understanding through a matching mechanism that maps the observed actions onto the motor repertoire of the observer [Di Pellegrino et al., 1992; Fogassi et al., 1998; Gallese et al., 1996]. Recent evidence suggests that a cortical fronto-parietal network with similar properties may also exist in humans [Cochin et al., 1999; Fadiga et al., 1995; Hari et al., 1998; Rizzolatti et al., 1996]. A still open key

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question is whether such sensorimotor activations induced by action observation strictly mimic the observed action or whether they reflect a more abstract representation of the goal of the action. In other words, does action observation induce, in the observer, the recruitment of the same motor program exactly involved in the observed action or the recruitment of the motor program habitually required to reach the goal of that action?

Neuroimaging studies suggest that only actions belonging to the observer's motor repertoire are mapped on the observer's motor system [Buccino et al., 2004], and that motor activation contingent upon action observation is modulated by the specific expertise of the observer [Calvo-Merino et al., 2005]. Additionally, during the observation of actions performed with different body parts, premotor and parietal activations show a somatotopic organization similar to that found when the same body parts are actually moved [Buccino et al., 2001; Sakreida et al., 2005; Wheaton et al., 2004]. Similarly, transcranial magnetic stimulation (TMS) studies demonstrate that action observation increases the amplitude of TMS-induced motor evoked potentials (MEPs) only in those muscles that are involved in the execution of the observed movements [Fadiga et al., 1995; Strafella and Paus, 2000].

On the other hand, recent evidence shows that motor activations occur also during the observation of motor acts performed by an effector that is unfamiliar or even not human, as long as the observed action has a familiar goal. For example, sensorimotor activations were observed during the observation of grasping actions performed by a robotic arm [Gazzola et al., 2007a]. Furthermore, individuals with congenital aplasia of the upper limbs show the activation of regions which are classically considered part of the putative human MNS following the observation of hand grasping [Gazzola et al., 2007b]. Aplasic individuals, although supposedly lacking the motor program to achieve hand grasping, typically have motor programs to achieve the same goal through different effectors (i.e., the foot or the mouth). In this case, the activation of regions involved in the execution of foot and mouth actions could be related to the goal of the action, rather than to the effector. This suggests that, during action observation, what is activated in the observer is not merely an anatomical inner replica of the observed sequence of muscular activations. Rather, the observed action seems to be also remapped in accordance with the observers' typical way of performing it.

It is also worth noting that in humans, at variance with monkeys, the network recruited following action observation also responds to the observation of intransitive movements [i.e., non-goal-directed movements, e.g., Fadiga et al., 1995], suggesting that in humans this network encodes both goal-directed motor acts and simple movements without a goal [Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010]. Thus, since the observed actions can be coded both in terms of goal and means to reach the goal [Rizzolatti and Sinigaglia, 2010], it is critical to assess the effects of viewing actions performed by an unusual

effector. If observed actions are translated into the *vocabulary* of the observer's actions [Rizzolatti and Craighero, 2004], and referred to the individual's own motor repertoire [Calvo-Merino et al., 2005], one could think that a highly familiar action, such as grasping an object, should activate the typical effector for that action (i.e., the hand) in a similar way when the body part that performs the observed action is either the hand actions, or an atypical effector such as the foot. Indeed, even if the observed action of grasping with the foot is potentially feasible for the observer, it is habitually performed with the hand and may, thus, automatically activate the typical hand grasping motor pattern.

Based on these considerations, we run two experiments on healthy humans to explore the selective modulation of the corticospinal excitability by action observation, with respect to the habitual correspondence between a given action and the effector that is seen performing that action. To this aim, motor facilitation was measured by recording MEPs evoked by TMS, contingent upon action observation [Fadiga et al., 1995], by varying across conditions the goal of the actions and the effectors used to perform such actions. In the first experiment, participants were presented with a typical hand action (i.e., grasping an object), performed by either the hand or the foot, and an unspecific action for both effectors (i.e., stepping over an object and then landing on it) performed by either the hand or the foot. In the second experiment, we presented an action typically performed with the hand (i.e., grasping an object) and an action that is specific for the foot (i.e., pressing a foot pedal of a car); both actions were executed with the hand or the foot. If observing a familiar action performed by an unusual effector activates only effector-specific motor programs in the observer, we should find an increase in MEP amplitude only in the muscles involved in the observed action. Conversely, if a goal-related action is remapped with respect to the observer's typical way of achieving the same goal, regardless of the specific muscles involved, we should find an increase in MEP amplitude only for the effector habitually used by the observer to perform that action. Finally, if observing a common action performed by an uncommon effector activates both kinds of motor mapping, we should find a modulation of MEP amplitude both in the muscles corresponding to the observed effector as well as in the muscles corresponding to the effector habitually used to perform that action.

EXPERIMENT I

Methods

Participants

Ten healthy individuals (eight women; mean age: 25 years, range: 21–33 years), with normal or corrected-to-normal vision, took part in the study. All participants were right-handed and right-footed, as assessed by the Oldfield handedness questionnaire [Oldfield, 1971] and the

Figure 1.

Experimental stimuli of Experiment 1. Video-clip frames depicting the four actions: (a) grasping with the hand; (b) grasping with the foot; (c) stepping over with the hand; (d) stepping over with the foot. sTMS was delivered after a random interval between 1,006 and 1,982 ms from the beginning of each video-clip. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

laterality preference inventory of Coren [1993]. None of the participants had neurological, psychiatric, or other medical problems nor had any additional contraindication to TMS [Wassermann, 1998]. All participants were naïve to the purpose of the study and gave written informed consent prior to their participation. The experiment was carried out in accordance to the ethical standards of the Declaration of Helsinki and was approved by the ethical committee of the University of Milano-Bicocca. No discomfort or other adverse effects were reported during TMS.

Experimental task

Participants sat at a distance of 80 cm in front of a PC monitor (Samsung SyncMaster 1200NF) and they watched a series of videos, displaying six situations, two static, namely: a right *static hand* and a right *static foot*; and four dynamic, namely: a right *hand grasping* and then lifting a pencil, a right *foot grasping* and then lifting a pencil, a right *hand stepping over* a pencil, landing with the wrist over it, and then rising up, and a right *foot stepping over* a pencil, landing with the heel over it and then rising up (Fig. 1). The actions were chosen because they are all potentially executable by the participants (i.e., they are part of their

motor repertoire), as explicitly confirmed by subjective reports at the end of the experimental session.

Each trial started with a central cross presented for 1 s, followed by the video-clip presented for 2.1 s (70 frames, inter-frame interval of 30.5 ms). The four videos displaying a dynamic situation were carefully matched for the timing of each main component of the action; for all the actions, from the onset of the trial, the effector started to move after 250 ms, it was reshaped after 1,006 ms, got in contact with the object after 1,300 ms, and lifted it or raised up after 2,000 ms. Luminance, contrast, hue, and saturation were kept constant between frames in each video-clip, and between different video-clips. The intertrial interval was 8,500 ms, during which a blank screen was presented. Each of the four videos displaying dynamic actions was repeated 30 times during each experimental session, thus yielding 120 trials, equally divided in six blocks. The four action conditions were presented in a random order within each block. Static conditions were presented in two blocks of 30 trials each, one at the beginning and one at the end of the experimental session, for a total of 60 trials. In each block, 15 trials for each static effector were presented randomly and they served as baseline. Sequence and timing of the video-clips and the TMS pulses were under computer control (E-prime software, Psychology Software Tools, Pittsburgh, PA).

During the experimental sessions, participants were asked to pay attention to the video-clips, while remaining relaxed. To ensure attention to the video-clips, participants were told that, at the end of the experiment, they had to provide a detailed description of both the actions and the objects featured in the videos. Overall, participants provided accurate descriptions. Moreover, at the end of the experiment, they were asked if they were able to perform the observed actions, and in particular how often they used to execute the grasping-with-the foot action. Every subject reported to be able to perform the observed hand and foot actions, but they also unanimously reported that the grasping-with-the foot actions were highly unusual, hence confirming that the grasping-with-the foot action, although feasible, was uncommon for the participants.

TMS protocol

Participants sat comfortably in an armchair, in a dimly lit room. They were instructed to relax and keep their right hand and leg on a pillow. The hand was kept supine on the pillow. The leg rested with the knee slightly bent, and the foot laid with the heel on a comfortable footrest. Two experimental sessions were conducted for each participant, in two different days. In one session, single-pulse TMS (sTMS) was applied over the hand area of the left primary motor cortex (M1), while in the other session sTMS was delivered over the foot area of the left M1. The order of the two sessions was counterbalanced across participants.

To stimulate the hand motor region, sTMS was delivered by a 70-mm figure-of-eight coil connected to a Magstim 200 stimulator (Magstim, Whitland, UK). For each subject, we first identified the optimal scalp position for inducing MEPs in the contralateral, right first dorsal interosseus (FDI) muscle. After localizing the area, the target site was marked on a tightly fitting Lycra cap worn by the participant. Throughout the experimental session, the coil was maintained in the optimal position with a mechanical device. The coil was positioned tangentially to the scalp, pointing anteriorly, 45° from the midsagittal axis [Mills et al., 1992].

To stimulate the foot motor region, a 110 mm double cone coil was placed over the vertex, oriented perpendicular to the head. Being designed for inducing a stronger magnetic field, as compared to the figure-of-eight coil, this coil is better suited for stimulating the foot area, which is located medially inside the central sulcus [Hovey and Jalinos, 2008]. For each participant, we identified the optimal scalp position for inducing MEPs in the contralateral, right abductor hallucis (AH). The orientation of the coil inducing the strongest AH activation was individually determined for each subject by assessing the amplitude of MEPs by moving the coil relative to the midsagittal plane.

For the electromyographic (EMG) recording, two pairs of silver-silver chloride surface electrodes were placed over the belly of the target muscles: the active electrodes were placed over FDI and AH, and the reference electrodes over the associated joints, that is, the metacarpophal-

angeal joint of the index finger for the FDI, and the first metatarsophalangeal joint for the AH. EMG signals were acquired using a BrainAmp MR recorder and Vision Recorder software (Brainproducts, Munich, Germany) at a sampling rate of 5,000 Hz, band-pass filtered (0.015–1,000 Hz), and stored for offline analysis.

For each area, we determined the resting motor threshold (rMT), corresponding to the lowest stimulation intensity inducing MEPs with peak-to-peak amplitude of at least 50 μ V in 5 out of 10 sTMS stimuli [Rossini et al., 1994]. During each experimental session, stimulation intensity was set at 120% of the individual rMT and kept constant throughout the experiment. For the hand area, the mean ($\pm$ standard deviation, S.D.) rMT was 66% ($\pm$ 7.8) of the maximum stimulator output; for the foot area, the mean rMT was 60% ($\pm$ 10.7).

During each experimental session, MEPs were recorded during the observation of the video-clips. Each trial started with the presentation of a video-clip, followed by a sTMS pulse delivered after a random interval between 1,006 and 1,982 ms from the beginning of the video-clip. This temporal window, on the total duration of 2.1 s of each video, corresponded, respectively, to the moment immediately before the effector got in contact with the object (i.e., in which the fingers were already preshaped for the grasping or the stepping over action), and the moment immediately before the effector lifted the object (in the grasping actions) or raised up from the object (in the stepping over actions) after having interacted with it. The interval between sTMS pulses ranged from 10.5 to 11.48 s, to rule out any carryover effects of sTMS on cortical excitability [Chen et al., 1997].

The amplitude of the MEPs evoked at an intensity of 120% of the individual resting motor threshold, calculated in terms of areas, was, on average, 3.8 (S.D. $\pm$ 2) mV*ms in FDI and 3.3 ($\pm$ 2.5) mV*ms in AH.

Statistical analysis

The analysis was conducted on 9 out of 10 participants. One participant was excluded from the analysis, due to an excess of muscular contraction following unrequested postural adjustments throughout the experiment, which interfered with the pattern of the EMG responses. The EMG trace was rectified and the areas underlying the MEPs were calculated for each trial. The pre-TMS EMG activity, recorded in the 200 ms preceding the TMS pulse, was used as a baseline to check for the presence of EMG activity before the TMS pulse. Trials ($\approx$ 20%) where such activity was present were discarded from further analysis. Motor facilitation by action observation was calculated by dividing the average MEPs' area in each experimental condition by that of the homologous static condition for each participant (i.e., hand grasping and stepping-over conditions divided by static hand; foot grasping and stepping-over divided by static foot). A repeated-measures analysis of variance (ANOVA) was conducted with three within-subjects factors: action (grasping, stepping-over), effector (hand, foot), and TMS-site (hand

Figure 2.

Mirror facilitation by action observation on MEPs in Experiment I. (a–d) Depict the main effects of action (a, c) and effector (b, d) on MEPs recorded from the muscle FDI (upper panel) and AH (lower panel). Error bars represent the standard error. Asterisks indicate statistical significance at $\alpha = 0.05$.

motor area, foot motor area). For all analyses, the level of significance was set at $P < 0.05$. Whenever necessary, post hoc comparisons were run with the Newman-Keuls test.

Results and Discussion

The ANOVA showed significant effects of action ($F_{1,8} = 7.6$, $P < 0.02$), TMS-site by effector interaction ($F_{1,8} = 26.6$, $P < 0.001$), and TMS-site by action interaction ($F_{1,8} = 11$, $P < 0.01$). Furthermore, the significant action by effector by TMS-site interaction ($F_{1,8} = 8.3$, $P < 0.02$) highlighted the specific effect of the action goal and the motor program used to reach it. Other effects were not significant (all P s > 0.5). The action by effector by TMS-site interaction was explored via two separate two-way ANOVAs, one for each TMS-site (hand motor area, foot motor area), with action and effector as main factors. With respect to the stimulation of the motor hand area (i.e., MEPs recorded from the FDI), a significant main effect of the effector ($F_{1,8} = 21.3$, $P < 0.002$) was found, indicating that the MEP amplitude was greater during the observation of actions performed by the hand (mean $\pm$ S.D.: 1.13 ± 0.4), as compared to actions performed by the foot (0.94 ± 0.3), regardless of the type of action. The main effect of action ($F_{1,8} = 11.5$, $P < 0.01$) showed that MEPs amplitude was

greater when the subjects observed grasping actions (1.13 ± 0.4), as compared to stepping over actions (0.94 ± 0.3), regardless of the effector. The effector by action interaction was not significant ($F_{1,8} = 2.8$, $P = 0.13$) (Fig. 2a,b). These results indicate that the hand motor cortex is activated by observed grasping actions performed not only by a hand but also by a foot.

The MEPs recorded from the AH after the stimulation of the foot motor region only showed a significant main effect of the effector ($F_{1,8} = 11.6$, $P < 0.01$), with MEPs amplitude greater during the observation of actions performed by the foot (1.11 ± 0.22), as compared to actions performed by the hand (0.92 ± 0.18). Instead, the effects of action ($F_{1,8} = 0.02$, $P = 0.87$) and the effector by action interaction ($F_{1,8} = 0.34$, $P = 0.57$) did not reach statistical significance (Fig. 2c,d).

These results show a specific facilitation of corticospinal excitability contingent upon action observation for the muscles that would be involved in the execution of the observed movements. In fact, the observation of actions performed by the hand increased MEP amplitude in FDI, while observing actions executed by the foot increased MEP amplitude in AH, compatibly with a motor resonance of the observed action mapped in somatotopic coordinates. However, MEP amplitude recorded from FDI was enhanced not only by the observation of actions performed with the hand but also by grasping actions performed with

Figure 3.

Experimental stimuli of Experiment 2. Video-clip frames depicting the four action: (a) grasping with the hand; (b) grasping with the foot; (c) pressing with the hand; (d) pressing with the foot. sTMS was delivered after a random interval between 1,006 and 1,982 ms from the beginning of each video-clip. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the foot. Conversely, the excitability of the foot motor area was increased only by the observation of grasping actions performed with the foot, but not with the hand. This last result shows that the observation of a familiar action (i.e., grasping) executed by an atypical effector (i.e., foot) induces a motor facilitation also in those muscles that are habitually used to reach the same goal (i.e., hand). The stepping-over action with the foot, being not typical for both the hand and the foot, did not induce any activation of the FDI.

However, the control action (i.e., *stepping over*) critically differs from the grasping action, not only for being unspecific for both the hand and the foot but also for not being a goal-directed action. Therefore, we run a second experiment in which two familiar and common goal-directed actions for the hand and the foot were shown.

EXPERIMENT 2

In this experiment, participants were presented with two familiar, goal-directed actions, one typically performed with the hand (i.e., grasping) and one typically executed with the foot (i.e., pressing a car foot pedal). The actions had both a clear goal, as they were insert in an unambiguous context and were both familiar to the viewers. By presenting typical and familiar transitive actions

for both the hand and the foot, this experiment aimed at investigating whether the foot motor area might be modulated by the observation of a typical foot action performed by an atypical effector (i.e., the hand), in the same way as the hand motor area was modulated by the observation of a grasping action performed by the foot in Experiment 1.

Methods

Participants

Ten healthy participants (all women; mean age: 27.7 years, range: 23–33 years), with normal or corrected-to-normal vision, took part in the study. Two participants took part also in the first experiment. Subjects' selection criteria were the same as in Experiment 1.

Experimental task, TMS protocol, and statistical analysis

Experimental task, sTMS protocol, and data analysis were the same as in Experiment 1, but now participants observed the following video-clips: (1) a right *static hand*; (2) a right *static foot*; (3) a right *hand grasping* and then lifting a pencil; (4) a right *foot grasping* and then lifting a pencil; (5) a right *hand pressing* and then releasing a foot pedal

Figure 4.

Mirror facilitation by action observation on MEPs in Experiment 2. (a–d) Depict the main effects of action (a, c) and effector (b, d) on MEPs recorded from the muscle FDI (upper panel) and AH (lower panel). Error bars represent the standard error. Asterisks indicate statistical significance at $\alpha = 0.05$.

of a car; (6) a right *foot pressing* and then releasing a foot pedal of a car (Fig. 3). These actions were all potentially executable by the participants, as explicitly confirmed by subjective reports at the end of the experiment, although grasping with the foot or pressing a foot pedal with the hand were rated as totally unfamiliar actions. The temporal pattern of the two dynamic stimuli was matched frame by frame, in the same fashion as Experiment 1, so that the effectors started to move, reached the object, and lifted or released it in the same moments in the four videos.

During each experimental session, stimulation intensity was set at 120% of the individual rMT and was kept constant throughout the experiment. For the hand area, the mean ($\pm$ S.D.) rMT was 63% (± 7.6) of the maximum stimulator output; for the foot area, the mean rMT was 60% (± 8). Trials in which EMG activity in the 200 ms preceding the TMS stimulus was present (22%) were discarded from the analysis.

The amplitude of the MEPs evoked at an intensity of 120% of the individual resting motor threshold, calculated in terms of areas, was, on average, 2.2 (± 1.9) mV*ms in FDI and 1.7 (± 1.5) mV*ms in AH.

Results and Discussion

A repeated-measures ANOVA was conducted with three within-subjects factors: action (grasping, pressing),

effector (hand, foot), and TMS-site (hand motor area, foot motor area). The analysis showed a significant TMS-site by effector interaction ($F_{1,9} = 30$, $P < 0.001$) and a significant TMS-site by action interaction ($F_{1,9} = 10.6$, $P < 0.01$). Other effects were not significant (all P s > 0.3). To further explore these interactions, and to test for the specific predictions made on this experiment on the light of the results of the first experiment, we ran a set of planned comparisons. On FDI, the MEP amplitude was greater during the observation of actions performed by the hand (mean $\pm$ S.D.: 1.21 ± 0.45), as compared to actions performed by the foot (1 ± 0.43), regardless of the type of action ($F_{1,9} = 17$, $P < 0.003$). Moreover, MEP amplitude was greater when the subjects observed grasping (1.18 ± 0.45), as compared to pressing actions (1 ± 0.44), regardless of the effector ($F_{1,9} = 11$, $P < 0.01$) (Fig. 4a,b).

MEPs recorded from AH after the stimulation of the foot motor region were greater for the observation of actions performed by the foot (1.16 ± 0.32), as compared to actions performed by the hand (1 ± 0.26) ($F_{1,9} = 8$, $P < 0.02$). Finally, MEP amplitude increased when participants observed pressing actions (1.16 ± 0.03), as compared to grasping actions (1 ± 0.25), regardless of the effector ($F_{1,9} = 6$, $P < 0.03$) (Fig. 4c,d).

The results of Experiment 2 confirmed the results found in the first experiment, revealing a motor facilitation specific for the muscles that would be involved in the

execution of the observed movements, with an increase in the amplitude of MEPs recorded from FDI during the observation of actions performed by the hand and an increase of MEP amplitude in AH for the observation of actions executed with the foot. Moreover, we found an enhancement in MEP amplitude recorded from FDI also for the observation of a grasping action performed with either the hand or the foot, thus replicating the results of Experiment 1. The novel finding of Experiment 2 is that observing either a foot or a hand pressing a foot pedal, an action typically executed with the foot, induced an increase in MEP amplitude recorded from AH only. These results confirm and extend the results of Experiment 1, showing that the excitability of both hand and foot motor areas is modulated by the observation of a familiar action executed by an unusual effector.

DISCUSSION

In this study, we recorded MEPs from hand (FDI) and foot (AH) muscles, induced by sTMS delivered to the hand or foot motor areas, respectively, during the observation of actions performed by different effectors (i.e., hand or foot). In line with previous studies [e.g., Fadiga et al., 1995; Strafella and Paus, 2000], we have found a facilitation of corticospinal excitability by action observation, which was specific for the effector involved in the actual execution of the observed movements. Indeed, observing an action performed by the hand increased MEP amplitude in FDI, while observing an action executed by the foot increased MEP amplitude in AH.

The crucial finding was that the excitability of the hand motor area was modulated not only by actions performed by the hand but also by grasping actions in general, regardless of the effector used to execute them. Likewise, the foot motor area was modulated not only by actions performed by the foot but also by the observation of either the foot or the hand pressing a foot pedal. The observation of an action unspecific for both hand and foot (i.e., stepping over) did not modulate specifically neither the hand nor the foot area. This evidence demonstrates that motor facilitation contingent upon action observation is not restricted to the same muscles involved in the observed action, but it occurs even in the muscles typically used to achieve the same action goal. Indeed, when a recognizable action goal (e.g., grasping) is performed through an unusual effector (e.g., the foot), a motor facilitation can be observed also in the muscles that are typically used to accomplish the observed action goal (i.e., the hand). If the observed effector did not perform a goal-directed action typically achieved by using a different effector, the imitative motor facilitation is restricted to the observed effector. This is indeed the case of the stepping-over action, which is unspecific for both hand and foot and, therefore, induces only an increase of the MEPs recorded from the muscle actually involved in the observed action.

Previous evidence in monkeys showed that mirror neurons in premotor and parietal cortices discharge for both action execution and observation of motor acts (i.e., goal-directed movements). [Rizzolatti and Craighero, 2004]. Critically, F5 premotor neurons hold surprising properties of interpreting the goal of the action, inferring it from partial visual cues [Umiltà et al., 2001], auditory cues [Kohler et al., 2002] or even selectively responding to a contingent motor act, strictly depending on its action goal [Umiltà et al., 2008]. Similarly, mirror neurons in inferior parietal lobe encode the goal of an action, showing a different activity when the same motor act is part of different actions [Fogassi et al., 2005].

Likewise, neuroimaging and neurophysiological studies in humans suggest the existence of a parieto-frontal network encoding the goals of the observed actions. For instance, frontal and parietal areas are activated by the observation of grasping actions performed by a real arm as well as by a robotic arm, although human and robotic body parts differ both in terms of kinematics and visual features [Gazzola et al., 2007a]. TMS evidence also suggests that when subjects observe a goal-directed action (i.e., grasping an object), what is coded is the action goal rather than the different movements to reach it [Cattaneo et al., 2009]. On the other hand, unlike monkeys, the human action-observation network is activated not only by goal-directed actions but also by intransitive actions, such as arm movements or finger flexion [Fadiga et al., 1995; Romani et al., 2005; Avenanti et al., 2007]. Given these features of the human putative MNS, Rizzolatti and Sinigaglia [2010] argued that sensorimotor activations in humans during action observation might reflect a double encoding mechanism for action observation. A first mechanism would be related to the coding of the motor components of the observed action, namely the displacements of body parts (i.e., movement mirroring). In this case, there would be a mapping of the observed movements onto the observer's inner representation of the same movements. The second mechanism involves a mapping of the observed action goal (i.e., goal mirroring), and would be more functional to action understanding. These two mechanisms appear to be also mediated by different brain regions [Cattaneo et al., 2010; Jastorff et al., 2010]. For instance, in a recent fMRI study, Jastorff and colleagues [2010] presented participants with various motor acts performed by different effectors (i.e., hand, mouth, foot) and found that the motor acts were coded differently in premotor and parietal cortices according to the effector used or the motor act shown. In particular, in the premotor cortex, motor acts are clustered on the basis of the effector, regardless of the type of motor act; conversely, in the parietal cortex, motor acts are clustered according to the goal, irrespective of the effector used. Therefore, an observed action is encoded firstly in terms of body displacements in the superior temporal sulcus [see also Cattaneo et al., 2010], and then the visual information is sent to the parietal cortex, where the action is abstractly encoded at a higher level in terms of

its goal, regardless of the effector involved to achieve it. Finally, the information is sent to the premotor cortex, where the specific program involved in the observed actions, both in terms of goal and effector, is recruited [Jastorff et al., 2010]. The recruitment of the muscles typically involved in the observed action found in our study might therefore reflect the parietal role in categorizing motor acts according to their functional meaning and in generalizing the observed actions across effectors.

A previous TMS study, which investigated the muscle specificity of the motor programs activated during action observation, demonstrated that when participants observed a static effector in front of an object, before grasping it, the cortical excitability was enhanced even in muscles belonging to an effector not involved in that action, as long as it was potentially able to achieve the goal [Lago and Fernandez-del-Olmo, 2011]. When participants subsequently saw the effector interacting with the object, the motor facilitation was muscle specific. For instance, when the object was grasped with the foot, there was a decrease of MEP amplitude recorded from the hand, as compared to the static phase. The authors' account is that only at the beginning of the action the motor program is activated on the basis of the goal of the action, while during effector-object interaction the program is transformed into a muscle-specific program [Lago and Fernandez-del-Olmo, 2011]. The different effects found here may be likely due to the different timing of the sTMS with respect to the phase of the observed action. Indeed, while in the study by Lago and Fernandez-del-Olmo [2011], sTMS was delivered during static phases (i.e., before the effector started to move or after the action was completed), here the sTMS was delivered during the effector-object dynamic interaction. An early timing of the TMS pulse with respect to the static effector may have captured affordance-like activations, while our later stimulation may have interacted with the coding of dynamic goal-related aspects of the observed action. This view is further supported by a second main difference between the two studies, related to the overall duration of the observed action: here TMS pulses were delivered during faster actions (2 s), as compared to those of Lago and Fernandez-del-Olmo (10 s).

Our results support the hypothesis of two parallel coding of actions, that is, movement mirroring and action mirroring, that are both activated whenever a person observes an action. In daily life, the motor activations expressed by such a double coding of observed actions typically coincide: we generally see people achieving goals using the very same effectors that we would normally use to execute the same actions [see Gazzola et al., 2007b]. In line with the idea of a hierarchical organization of the motor system involving different descriptive levels of the action [i.e., goal, kinematic, muscular levels, see Grafton and Hamilton, 2007], it might be possible that, whenever the effector involved in the observed action differs from the one that is typically used to execute that action, the brain activates

not only the motor program corresponding to the observed effector, but also, at a higher level, the motor program of the effector commonly used to reach that goal, even when it is not actually implicated in the observed action. In fact, the activation of the action-observation network may reflect the recruitment of an effector-specific motor program, as well as the recruitment of a more abstract motor program useful for achieving the goal of the observed action. This is in line with previous evidence (e.g., Hamilton and Grafton, 2006; Jastorff et al., 2010] showing the role of parietal regions in the representation of the action goal in an effector-independent fashion, and in turn in the representation of action plans and goals, rather than in the recognition of the observed movement pattern, which appears more linked to temporal and frontal activity [e.g., Hamilton and Grafton, 2006; Jastorff et al., 2010]. Given that the same goal can be achieved in different ways, the effector-independent coding of the observed action may be functional to recognize the action goal, regardless of the specific way used to achieve it. Our findings indicate that changes in cortical-spinal activation by the sight of actions may reflect both the coding of the observed action goal, and the coding of the single movements involved in the action.

Our findings are also in line with recent studies on action priming (see Heyes, 2011, for a review), which suggest that automatic imitation may be mediated by the putative human MNS through a direct link between perception and action. In automatic imitation paradigms, a motor response is facilitated by the observation of a task-irrelevant action that is similar to the required motor response in terms of body part involved and/or type of movement [e.g., Bach et al., 2007; Heyes et al., 2005; Gillmeister et al., 2008; Leighton and Heyes, 2010]. These studies suggest that automatic imitation is influenced by the matching of both the effector and the movement type, likely through the recruitment of excitatory links between the corresponding sensory and motor representations, emerging from repeated visuo-motor experience of familiar actions [Heyes 2001; 2010]. In line with the associative sequence learning theory [e.g., Heyes et al., 2005], these automatic stimulus-response connections can be a product of learning, depending on the repeated experience of observing actions, both self-generated or executed by others and observed during social interactions. In this contest, our findings suggest that, during the observation of a familiar action performed by an atypical effector, our motor system recruits, on one hand, the motor program corresponding to the observed effector by mapping the observed movement on his/her own body schema [Bach et al., 2007]. On the other hand, the motor program of the typical effector used to achieve the same goal might be simultaneously recruited through learning-dependent excitatory links depending on our typical sensory-motor experience (as in the case of grasping an object which is typically performed by the hand).

In conclusion, while the motor matching of an observed moving body part would allow to simulate the efferent components of the observed action in a strictly congruent fashion, the simultaneous, automatic, matching of the observed action on its prototypical effectors would be of more help to understand the action goal based on our experience. This complex mechanism of motor coding would increase our abilities in social interactions.

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