EJN fens EUROPEAN JOURNAL OF NEUROSCIENCE

European Journal of Neuroscience, Vol. 38, pp. 3507–3512, 2013 doi:10.1111/ejn.12343

COGNITIVE NEUROSCIENCE

Goal or movement? Action representation within the primary motor cortex

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Keywords: action observation, goal coding, human, motor facilitation, reach to grasp movement, transcranial magnetic stimulation

Abstract

Although facilitation of the cortico-spinal system during action observation is widely accepted, it remains controversial whether this facilitation reflects a replica of the observed movements or the goal of the observed motor acts. In the present transcranial magnetic stimulation study, we recorded motor evoked potentials from two hand muscles (first dorsal interosseous and abductor digiti minimi) while 22 healthy participants observed a hand reaching towards and grasping a bottle. To test for alternative coding levels (goal vs. movement), three relevant aspects were systematically manipulated: the type of observed movement (precision grip or whole hand grasping), situational context (bottle positioned in front of or behind a wall-like barrier), and processing stage (transcranial magnetic stimulation pulse delivered at the onset of the movement or at the moment of contact between the fingers and the object). At movement onset, motor evoked potential responses reflected the program necessary to achieve the action goal within the situational context. During movement observation, however, the type of observed movement was taken into account and a transition towards a movement-related modulation was observed. These results suggest that, rather than being exclusive alternatives, goal coding and movement coding may relate to different processing stages.

Introduction

Observation of other people's actions has been shown to selectively facilitate the brain's motor circuits for executing the same actions (Grafton, 2009; Rizzolatti & Sinigaglia, 2010). But how exactly are observed actions mapped on the observer's motor system? The same motor behavior can be described at different levels: the goal level, the kinematics of the executed movement and the specific motor commands that activate the muscles in a coordinated sequence (Grafton & Hamilton, 2007). Which level of the hierarchy is relevant for motor facilitation? When a goal is present, is the pattern of muscle recruitment linked to the observed movements or to the goal of the observed motor act?

Action goals have been shown to influence response properties across different levels of the parieto-frontal network for action observation (for review see Grafton, 2009, 2010; Rizzolatti & Sinigaglia, 2010). Within the primary motor cortex (M1), sensitivity to action goals is suggested by the finding that transcranial magnetic stimulation (TMS)-induced motor evoked potentials (MEPs) vary depending on whether or not a goal is present (Cattaneo *et al.*, 2009). When there was no goal in the observed behavior (i.e. the experimenter merely opened and closed classic or reverse pliers), MEPs reflected the movements performed by the agent. However, when a goal was present (i.e. the experimenter grasped and dropped a peanut using the classic or reverse pliers), MEPs no longer reflected the observed movements, but the movements necessary to achieve the goal, suggesting that observed movements were remapped on the same goal-directed motor act. Others studies seeking to dissociate goal and movement, however, failed to show goal-related modulation of M1 excitability, revealing instead a faithful replica of the observed movement (Borroni *et al.*, 2011; Cavallo *et al.*, 2012; Sartori *et al.*, 2012a,b). For example, Cavallo *et al.* (2012) found that MEPs recorded from hand muscles during observation of tool actions reflected the observed hand movement, rather than the movement of the tool or the distal goal of the action. Therefore, it remains an open question whether the excitability of the M1 modulates according to the goal or the observed movements.

To elucidate the specificity of the visuo-motor response, Lago & Fernandez-del-Olmo (2011) recorded MEPs from hand muscles during observation of grasping actions performed with the hand or foot. When participants observed a static effector in front of the object, MEP enhancement was similar for observation of hand and foot actions. During the observation of the effector–object interaction, however, the initial facilitation observed for foot actions was abolished, suggesting a transition towards a more specific movement-related modulation of MEP amplitude.

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Received 15 March 2013, accepted 24 July 2013

In this perspective, one possibility is that the properties of motor responses to observed actions differ according to the processing stage. Before the to-be-observed action starts, contextual factors might dictate a motor facilitation reflecting the motor program necessary to achieve an action goal. During movement observation, computation of the specific features of the movement would then over-ride the initial goal representation, providing a refined matching of the unfolding movement. If this is correct, then one would expect a reversal in muscle-specific MEP enhancement when the observed movement does not correspond to the motor program initially facilitated.

In the present study we explored this prediction using a novel paradigm adapted from infant research. In violation-of-expectation studies, goal-directed actions are demonstrated to infants within different situational constraints in order to test for alternative encoding of unusual actions (Phillips & Wellman, 2005; Csibra & Gergely, 2009). By following the same logic, in our study we varied the presentation of different types of action movements and situational constraints to examine the modulation of M1 excitability by goal and movement. Participants observed a hand reaching towards and grasping a bottle positioned in front of or behind a wall-like barrier in three conditions. For the 'precision grip constrained' (PG_constrained) condition, the bottle was placed behind the barrier, so that the barrier prevented direct reach of the bottle. Participants observed a model's hand reaching over the barrier and grasping the bottle using a precision grip (Fig. 1A). For the 'precision grip unconstrained' (PG_unconstrained) condition, participants observed the model's hand grasping the bottle, located in front of the barrier, with a precision grip (Fig. 1B). Finally, there was a 'whole hand grasp' (WHG) condition in which participants observed the model's hand grasping the bottle, placed in front of the barrier, with a WHG (Fig. 1C). We expected that MEP responses recorded at the time that the observed movement started should be similar for the PG_unconstrained and WHG conditions. This is because the situational context (bottle in front of the barrier) should facilitate the same goal-directed motor program for both conditions. During movement unfolding, however, a transition towards a more specific movement-related modulation of MEP amplitude should be observed. If this is the case, then, at the time that the hand enters into contact with the object, MEP responses for the PG_unconstrained condition would be expected to reverse so as to match the specific features of the observed movement. This should not occur for the WHG and the PG_constrained condition, in which the movement unfolds in accordance with the initially facilitated motor program.

Materials and methods

Participants

Twenty-two healthy volunteers (seven men and 15 women, aged 20–36 years, mean age 24.3 years) took part in the experiment. All were right-handed, had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Wassermann, 1998; Rossi *et al.*, 2009). None of them had a history of neurological, major medical, or psychiatric disorders. The experimental procedures were approved by the ethical committee of the University of Padova and were carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association General Assembly, 2008). Written informed consent was obtained from each subject prior to experimentation. None of the individuals taking part in the experiment experienced discomfort or adverse effects

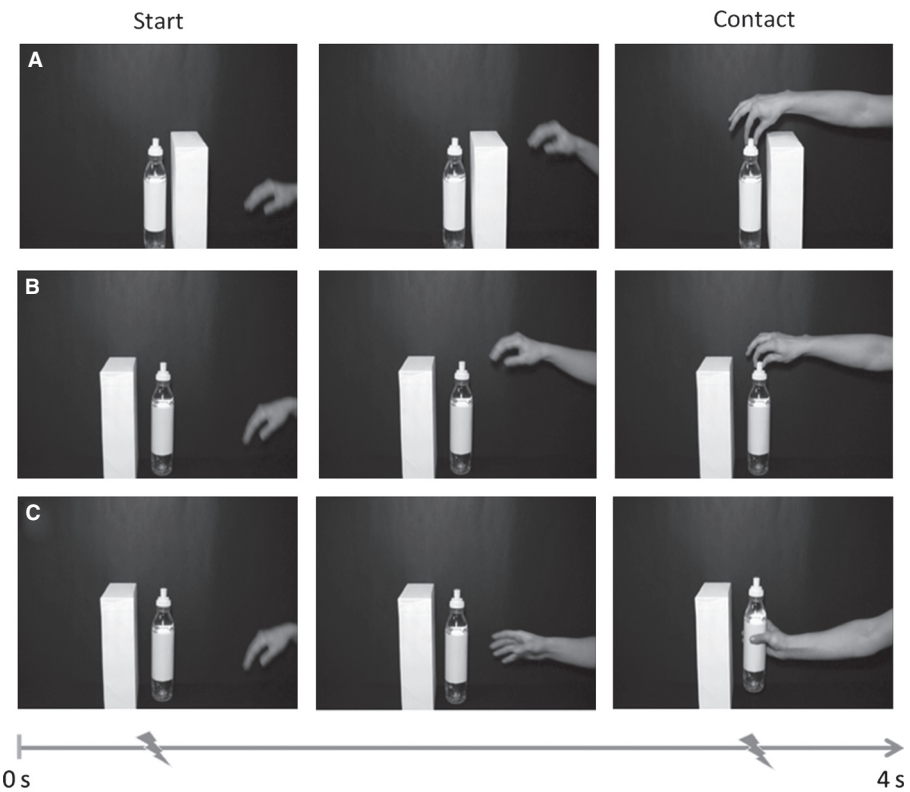

FIG. 1. Schematic representation of event sequencing during PG_constrained (A), PG_unconstrained (B) and WHG (C) actions. The TMS pulse could be delivered at the onset of the movement [when the hand started the action ('Start')] or at the moment of contact between the fingers and the object ('Contact').

during TMS acquisitions. Experiments were conducted in accordance with the ethical guidelines.

Stimuli

The experimental stimuli consisted of video clips representing three types of action sequences in which a human right hand reached towards, grasped, and lifted a bottle positioned in front of or behind a wall-like barrier. For the PG_constrained condition, the bottle was placed behind the barrier. The model's hand reached over the barrier and grasped the bottle by the cap with a precision grip, i.e. by opposing the thumb with the index finger (Fig. 1A). For the PG_unconstrained condition, although the bottle was in front of the barrier, the model's hand moved in the same manner as for the PG_constrained condition grasping the bottle by the cap with a precision grip (Fig. 1B). For the 'WHG' condition, the hand reached, grasped and lifted the bottle positioned in front of the barrier using a WHG, i.e. by using the thumb and hand palm (Fig. 1C). At the beginning of each sequence, the hand of the model was shown resting on a table in a prone position. The reaching movements started 500 ms after the onset of the action sequence. Video clips in which the hands moved towards the bottle but no hand–object interaction was displayed were also included as 'catch' trials. Each video clip lasted 4000 ms and the animation effect was obtained by presenting series of single frames each lasting 33 ms except for the first and last frame, which lasted 500 and 893 ms, respectively.

Electromyographic and transcranial magnetic stimulation recording

When subjects shape their hand to grasp an object there is a characteristic pattern of muscle activity in the intrinsic muscles of the hand that move the index finger [first dorsal interosseous (FDI)] and little finger [abductor digiti minimi (ADM)] (e.g. Cattaneo *et al.*, 2005). The FDI muscle abducts and flexes the index finger and is involved in precision grip and, to a lesser extent, in WHG; in contrast, the ADM muscle abducts the little finger and is significantly more active for WHG than precision grip. Because of this characteristic pattern of activation, the FDI and ADM are commonly considered when evaluating muscle-specific MEP enhancement during observation of precision grip and WHG actions (e.g. Fourkas *et al.*, 2006; Urgesi *et al.*, 2010; Sartori *et al.*, 2012a,b).

Following this logic, in the present study we recorded MEPs from the FDI and ADM. TMS pulses were administered by using the Master Magstim 200 Unit of a Magstim Bistim2 stimulator (Magstim, Whitlan, Dyfed, Wales, UK) connected to a 70 mm figure-of-eight coil. The coil was held tangentially to the scalp with the handle pointing backwards and laterally with a 45° angle to the midline. This orientation permits the lowest motor threshold, optimising the stimulation (Brasil-Neto *et al.*, 1992; Mills *et al.*, 1992). During the recording session, the coil was positioned in correspondence with the optimal scalp position (OSP), defined as the position from which MEPs with maximal amplitude were recorded simultaneously from the FDI and ADM. To find the individual OSP, 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 participants. Once the OSP was found, the individual resting motor threshold was determined as the lowest stimulus intensity able to generate reliable MEPs ($\geq$ 50 μV peak-to-peak amplitude) in the relaxed muscles in 5 out of 10 consecutive TMS pulses (Rossini *et al.*, 1994). During the recording sessions, the stimulation intensity was set at 115% of the resting motor threshold, which ranged from 38 to 62% (mean 47.14%) of the maximum stimulator intensity and the OSP was continuously checked during the whole experiment. MEPs were simultaneously recorded from the FDI and ADM muscles of the participant's right hand. Electromyographic (EMG) activity was recorded by pairs of Ag–AgCl surface electrodes (9 mm diameter) placed over the muscle belly (active electrode) and over the ipsilateral proximal interphalangeal joint (reference electrode) in a classical belly–tendon montage. Electrodes were connected to an isolated portable ExG input box linked to the main EMG amplifier for signal transmission via twin-fiber optic cable (Professional BrainAmp ExG MR, Brain Products, Munich, Germany). The ground electrode was placed over the participant's left wrist and connected to the common input of the ExG input box. In the recording session, EMG signals were sampled (5000 Hz), amplified, band-pass filtered (20 Hz–1 kHz), and stored on a PC for offline analysis. A pre-stimulus recording of 100 ms was used to check for the presence of EMG activity before the TMS pulse. In order to prevent contamination of MEP measurements by background EMG activity, trials with any background activity > 100 μV in the 100 ms window preceding the TMS pulse were excluded from the MEP analysis. EMG data were collected for 300 ms after the TMS pulse.

Procedure

Participants were tested in a single experimental session lasting approximately 45 min. Experimentation was carried out in a dimly illuminated room. Participants were seated in a comfortable armchair with a fixed chinrest. Stimuli were displayed on a 19-inch monitor (resolution 1280 × 1024 pixels, refresh frequency 75 Hz) at a viewing distance of 80 cm. Participants were instructed to pay attention to the displayed stimuli while keeping their right hand still and as relaxed as possible. As a control for attention, they were told that at the end of the experiment they would be debriefed about what they had seen during the experimental session. The magnetic pulse was delivered at the onset of the movement – when the hand started the action ('start') – or at the moment of contact between the fingers and the object ('contact'). During the TMS session, eight trials were presented for each type of action sequence (PG_constrained, PG_unconstrained and WHG) for each pulse delay (start and contact). Sixteen additional catch trials (eight for start and eight for contact delay) were shown for a total of 64 randomly presented trials. Two series of five MEPs were also recorded while participants were observing a white fixation cross presented on a black background. One series was recorded at the beginning, whereas the second was recorded at the end of the experimental session. Comparisons of MEP amplitudes for the two series allowed us to check for any cortico-spinal excitability change related to TMS *per se*. Following each action sequence, an intertrial interval of 9 s was given; a message asking participants to keep their hand still and fully relaxed was presented during the first 7 s and then replaced by a fixation cross for the remaining 2 s. The stimulus-presentation timing, EMG recording and TMS triggering, as well as randomisation of stimuli, were controlled by E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC.

Data analysis

Data were analysed offline using Brain Vision Analizer software (Brain Products GmbH, Munich, Germany) and SPSS 17.0.1 (SPSS Inc., Chicago, IL, USA). The background EMG level prior to TMS was calculated for each trial. Individual mean peak-to-peak amplitudes of MEPs recorded from the FDI and ADM muscles were calculated separately for each type of action sequence (PG_constrained,

PG_unconstrained and WHG) and TMS pulse delay (start and contact). MEP amplitudes and onset latencies deviating more than 2 SDs from the mean of each experimental condition and single trials contaminated by muscular pre-activation were excluded as outliers and pre-contracted trials, respectively. The resulting average number of MEPs in any cell for each participant was 7.29 ± 0.50. The individual mean amplitude of MEPs recorded from both muscles during fixation cross trials (10 out of 74 trials) served as the baseline for MEPs of trials where movements were shown, so that MEP amplitudes were converted into a proportion of the baseline value. From the converted data, the MEP ratio was calculated for each trial by dividing the ADM data point by the FDI data point. The resulting MEP ratio was then normalised using log10 transformation to address non-normality resulting from positive skew (Osborne, 2002). The MEP ratio is considered to reflect the effectiveness of muscle-specific mapping of the observed movement onto the motor system (Catmur *et al.*, 2011). Values of this index greater than zero indicate that the ADM was more strongly involved than the FDI, as expected during whole hand prehension; values lower than zero indicate that the FDI was more strongly involved than the ADM, as expected during precision grip.

Normalised data were submitted to a 3 × 2 repeated-measures ANOVA with type of action sequence (PG_constrained, PG_unconstrained, WHG) and TMS pulse delay (start, contact) as within-subjects factors. A paired sample t-test (two-tailed) was used to compare the amplitude of MEPs collected from the two muscles in the baseline trials. Finally, to control for differences in MEP onset latencies across conditions, onset latencies were submitted to a 3 × 2 × 2 repeated-measures ANOVA with type of observed movement (PG_constrained, PG_unconstrained, WHG), TMS pulse delay (start, contact), and muscle (FDI, ADM) as within-subjects factors. A significance threshold of $P < 0.05$ was set for all statistical tests.

Results

Mean raw MEP amplitudes during the two baseline blocks run at the beginning and end of the experimental session were not significantly different for either the FDI ($t_{21} = 0.970$, $P = 0.343$) or the ADM ($t_{21} = 1.417$, $P = 0.171$) muscle. This indicates that, in our experimental procedure, TMS *per se* did not induce any changes in cortico-spinal excitability. The 3 × 2 ANOVA on normalised MEP ratios yielded a statistically significant main effect of type of action sequence ($F_{1,21} = 10.832$, $P < 0.01$) indicating a linear trend in the pattern of modulation. In particular, MEP ratios were greater for the WHG condition ($M = 0.062$), lower for the PG_unconstrained condition ($M = 0.001$), and lowest for the PG_constrained condition ($M = -0.019$). *Post-hoc* comparisons confirmed that MEP ratios were greater for the WHG than for the PG_constrained condition ($P = 0.003$). In contrast, no statistical difference was found between the WHG and PG_unconstrained ($P = 0.110$) and the PG_constrained and PG_unconstrained ($P = 0.544$) condition. This may reflect different mechanisms. First, it is possible that sensitivity to situational constraints modulated muscle-specific mapping during movement observation. Second, it might be that, in line with our experimental hypothesis, the mapping of the observed movement onto the observer's motor system differed depending on the processing stage, such that goal-related modulation to situational constraints at movement onset turns into movement-related modulation during movement observation. To explore this possibility we compared MEP ratios at the start and contact for each type of action sequence.

Paired *t*-tests performed separately for each type of action confirmed the hypothesis of a stage-specific modulation. As illustrated in Fig. 2, the comparison between the start and the contact time yielded a statistically significant effect for the PG_unconstrained condition ($t_{21} = 2.258$, $P = 0.035$), suggesting a reversal in MEP responses. As predicted, the difference between time pulse delays (start, contact) for the PG_constrained and WHG conditions was not significant ($t_{21} = -0.369$, $P = 0.716$; $t_{21} = -0.662$, $P = 0.515$, respectively). A 3 × 2 × 2 ANOVA on MEP onset latencies revealed no significant difference (*P*-values ranging from 0.153 to 0.993).

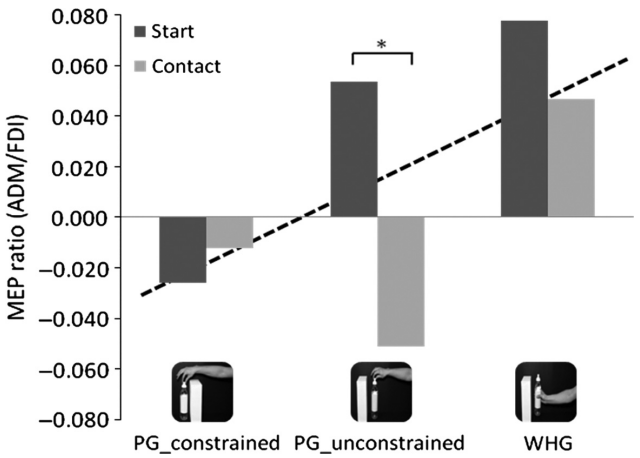

FIG. 2. Peak-to-peak amplitude scores recorded during the observation of different types of movement. MEP amplitudes are expressed as a ratio calculated for each trial by dividing the ADM data point by the FDI data point. The resulting MEP ratio is normalised using log10 transformation. The dashed line indicates a significant linear trend in the pattern of modulation with MEP ratios being greater for the WHG condition, lower for the PG_unconstrained condition, and lowest for the PG_constrained condition. *Significant paired t-test comparisons ($P < 0.05$).

Discussion

Motor facilitation during action observation requires that the observed action is mapped, at some level of the action hierarchy, onto the observer's motor system. In the present TMS study we sought to investigate the level at which this visuo-motor mapping occurs within the M1. Participants observed a hand reach towards and grasp a bottle. To test for alternative coding levels (goal vs. movement), three relevant aspects were varied: the type of observed movement (precision grip or whole hand grasping), situational context (bottle positioned in front of or behind a wall-like barrier), and processing stage (TMS pulse delivered at the onset of the movement or at the moment of contact between the fingers and the object).

The main result of our experiment was the demonstration of a transition from goal-related modulation towards movement-related modulation when the observed movement did not correspond to the motor program that was initially facilitated (PG_unconstrained condition). At movement onset, MEP responses in the PG_unconstrained condition were similar to the WHG condition. This suggests that, at movement start, facilitatory modulation reflected the program necessary to achieve the action goal within the situational context. When no physical constraint barred a direct reach of the bottle (PG_unconstrained and WHG conditions), observers displayed a muscle facilitation pattern compatible with a WHG. When the bottle was placed behind the barrier and a direct reach of the bottle was therefore prevented (PG_constrained condition), observer displayed a facilitation pattern compatible with a precision grip.

In the WHG and PG_constrained conditions, the action unfolded in accordance with the initially facilitated motor program. Consistently,

no significant difference was observed in MEP ratios between the start and the contact phase. In the PG_unconstrained condition, in contrast, although no physical constraint prevented a direct reach of the bottle, the model's hand grasped the bottle with a precision grip. As predicted, this unexpected unfolding determined a reversal in MEP responses at the time that the hand entered into contact with the object, suggesting that the initial motor program (WHG) was substituted by a new plan taking into account the specific features of the observed movement (precision grip).

Motor facilitation during action observation has been proposed to result from the comprehensive loading of a motor plan at the beginning of action observation (Gangitano *et al.*, 2004). Our findings extend this literature by suggesting that the goal-related motor plan loaded before movement onset can be substituted by a new plan so as to match the specific properties of the observed movement. In this manner, the expectation of a predictable ensuing movement may be integrated with the modulation triggered by the observation of the actual movement.

One limitation of the present design is that it does not allow characterisation of the time-course of the MEP transition from goal coding to movement coding, i.e. at what point during action unfolding MEP modulation ceases to reflect the goal of the action to reproduce the actual observed movement. Gangitano *et al.* (2004) found that unpredictable unnatural features (sudden closure movement of the hand) inserted 1200 ms after grasping onset exerted no corticospinal modulation in the motor system of the observer. This may indicate that the substitution of the initially facilitated motor plan can take place immediately after the observed movement onset, but not during movement unfolding. However, it is also possible that integration is limited to features matching a 'natural motor template' (Gangitano *et al.*, 2004). The resonant plan evoked at the beginning of the movement may be substituted by a new plan during movement unfolding, but only when the unexpected features match the motor plans resident in the observer motor system. Future investigations could use additional stimulation time-points between action onset and completion to clarify whether plan substitution can take place in flight in response to natural changes in the observed movement and to characterise the exact time-course of this substitution.

It may be argued that the reversal in MEP responses for the PG_unconstrained condition reflects the decay of the initial activation rather than the loading of a new motor plan. According to this alternative explanation, the initial motor plan neither takes into account the unexpected features of the observed movement nor is substituted by a new plan. Once activated, it loads the features of the predictable ensuing movement and is discarded when these features cease to match the visual properties of the observed movement (Gangitano *et al.*, 2004). In such a case, however, finger closure in the PG_unconstrained condition should not exert any modulatory effect. Moreover, a significant difference should be expected between the MEP ratios for the PG_unconstrained condition and the PG_constrained condition at contact. This was not the case ($t_{21} = 0.744$, $P = 0.448$). These findings suggest that the unexpected unfolding was substituted by a new plan rather than by a slow decay of the initial modulation. Future research employing additional stimulation time-points delivered at the time of appearance of specific kinematic features (e.g. finger opening) may help to examine this alternative hypothesis more closely. If motor output modulation is the result of deployment of the original plan, then there should be a disparity between MEP modulation and kinematic profiles (Gangitano *et al.*, 2004). If, on the contrary, reversal in MEP responses results from the loading of a new plan, then the pattern of cortico-spinal excitability should follow the dynamics of the observed movements.

To date, the action level relevant for visuo-motor mapping in the M1 is still debated (Cattaneo *et al.*, 2009; Borroni *et al.*, 2011; Cavallo *et al.*, 2012; Sartori *et al.*, 2012a,b). The present findings provide a means to integrate a contrasting perspective on goal and movement coding. In particular, they suggest that, rather being mutually exclusive alternatives, modulation to goal and movement may relate to different processing stages. Goal coding may take place at movement onset. At this stage, motor excitability is modulated according to situational constraints and, regardless of the observed effector, reflects the muscle facilitation pattern necessary to achieve the goal of the action (Lago & Fernandez-del-Olmo, 2011). During movement observation, however, the type of movement and the effector are taken into account and a transition towards movement-related modulation is observed (Fadiga *et al.*, 1995; Strafella & Paus, 2000; Gangitano *et al.*, 2001; Aziz-Zadeh *et al.*, 2002; Maeda *et al.*, 2002; Montagna *et al.*, 2005; Urgesi *et al.*, 2006, 2010; Alaerts *et al.*, 2009). The goal-directed program initially facilitated by the observation of a static effector is in this way translated into a program representing the specific features of the observed movement.

Acknowledgements

This work was supported by a grant from the Regione Piemonte, bando Scienze Umane e Sociali 2008, L.R. n.4/2006 to CB.

Abbreviations

ADM, abductor digiti minimi; EMG, electromyographic; FDI, first dorsal interosseous; M1, primary motor cortex; MEP, motor evoked potential; OSP, optimal scalp position; PG_constrained, precision grip constrained; PG_unconstrained, precision grip unconstrained; TMS, transcranial magnetic stimulation; WHG, whole hand grasp.

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