

# Corticospinal excitability is specifically modulated by the social dimension of observed actions

Luisa Sartori · Andrea Cavallo · Giulia Buccioni · Umberto Castiello

Received: 21 November 2010 / Accepted: 20 March 2011 / Published online: 7 April 2011  
© Springer-Verlag 2011

**Abstract** A large body of research reports that perceiving body movements of other people activates motor representations in the observer's brain. This automatic resonance mechanism appears to be imitative in nature. However, action observation does not inevitably lead to symmetrical motor facilitation: mirroring the observed movement might be disadvantageous for successfully performing joint actions. In two experiments, we used transcranial magnetic stimulation (TMS) to investigate whether the excitability of the corticospinal system was selectively modulated by the social dimension of an observed action. We recorded motor-evoked potentials (MEPs) from right-hand muscles during the observation of an action sequence which, depending on context, might or might not elicit a complementary response. The results demonstrate a differential motor facilitation depending on action context. Specifically, when the context called for a complementary action, the excitability pattern reflected the under-threshold activation of a complementary action, whereas when the context did not imply acting in a complementary manner, the observer's corticospinal activity reflected symmetrical motor resonance. We contend that the mechanisms underlying action observation are flexible and respond to contextual factors that guide the social interaction between individuals beyond emulation.

**Keywords** Action observation · Transcranial magnetic stimulation · Complementary actions · Reach to grasp · Mirror neuron system

## Introduction

A key question for neuroscientists concerns the mechanisms that allow for skillful social interactions (Sebanz et al. 2003, 2006a; Sebanz and Frith 2004; Bekkering et al. 2009; Becchio et al. 2010). Although enormous advances in our understanding of the links between the mind, the brain, and behavior have been made in the last few decades, these have been largely based on studies in which people are considered as strictly isolated units. For example, a number of studies have typically examined how object-directed movements vary on the basis of specific object properties (e.g., fragility, size, and weight) without considering the underlying intention to use that object as to interact with other people. The challenge is to understand whether the same action performed in either individual or social contexts acquires different meanings and, therefore, evokes different responses in the observer, beyond the strictly resonant functioning of the motor system during action observation (Fadiga et al. 1995).

In this paper, we tackle this challenge by investigating the mechanisms underlying the observation of the same action carried out in different contexts. We test the possibility that corticospinal excitability varies depending on whether the same observed action is meaningless or meaningful in terms of a social request. In particular, we recorded motor-evoked potentials' (MEPs) activity from participants' hand muscles in response to either an observed action calling for a socially relevant

---

L. Sartori · G. Buccioni · U. Castiello (✉)  
Department of General Psychology, University of Padova,  
via Venezia 8, 35131 Padova, Italy  
e-mail: umberto.castiello@unipd.it

A. Cavallo  
Department of Psychology, Centre for Cognitive Science,  
University of Torino, Turin, Italy

complementary action or the same action performed in a context which did not imply a social interaction.

Available evidence indicates that different kinds of social interactions involve specific and often distinct movement parameterizations (Georgiou et al. 2007; Becchio et al. 2008a, b; Sartori et al. 2009a, b; Ocampo and Kritikos 2010) and different cortical mechanisms (e.g., Decety et al. 2004; Sebanz et al. 2006b; Newman-Nordlund et al. 2007, 2008; Kokal et al. 2009; Kokal and Keysers 2010). In first instance, differences in movement planning and execution have been demonstrated depending on whether the situation implied to manipulate an object as to cooperate with a partner, compete against an opponent, or perform an individual action (Georgiou et al. 2007; see also Becchio et al. 2008b). Further, evidence that action context plays a pivotal role in shaping joint actions has been revealed in a series of studies in which participants were explicitly requested to observe an action with the scope of either imitate it or perform a non-identical complementary action (van Schie et al. 2007, 2008; Ocampo and Kritikos 2010). The results indicate an alteration in observers' movement parameters when performing identical versus non-identical actions under imitative and complementary action context.

In neural terms, very few studies have examined the mechanisms whereby individuals coordinate their actions on line (e.g., Decety et al. 2004; Newman-Nordlund et al. 2007; Sebanz et al. 2006b; Kokal et al. 2009; Kokal and Keysers 2010). Therefore, the neural mechanisms underlying joint actions are still debated. Recently, it has been proposed that the putative human equivalent of the mirror neuron system (e.g., Di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 2001) might play a central role to this endeavor, given that such brain regions provide a close link between perception and action (Knoblich and Jordan 2002; Rizzolatti and Craighero 2004; Newman-Nordlund et al. 2007, 2008).

This possibility has been explored in a functional magnetic resonance study (fMRI), study in which the role of the human mirror neuron system for the coding of joint actions, with specific reference to imitative and complementary actions, has been investigated (Newman-Nordlund et al. 2007). Participants observed an actor grasping a manipulandum using either a precision or a power grip. In the imitative context, participants were instructed to perform the observed action, whereas in the complementary context they were requested to execute the other type of grasp. Results clearly indicate that the mirror neuron system has the ability to link non-identical observed and executed actions as long as they serve a common goal. Interestingly, key areas of the mirror neuron system were more activated for the preparation of complementary than imitative actions. This was explained in terms of different

kinds of mirror neurons. Strictly congruent mirror neurons, which respond to identical observed and executed actions, would act in a context-dependent manner. Broadly congruent mirror neurons, which respond to non-identical observed and executed actions, would be relevant for complementary actions. Although such perspective might not be fully supported by monkey data (for a discussion on this issue see Kokal et al. 2009), the appealing hypothesis is that different sets of mirror neurons might serve to integrate observed and executed actions during different kinds of social interactions.

Recently, this view has been nested within a more integrated account of the neural circuits underlying joint actions (Etzel et al. 2008; Gazzola and Keysers 2009; Kokal et al. 2009; Kokal and Keysers 2010). The suggestion is that joint actions would indirectly recruit the putative mirror neuron system ascribing it the role to transform observed and executed actions into a common code and then sending this information to an integration network specifically tailored to joint actions.

In the present study, we investigate for the first time whether the action/execution matching system has the ability to flexibly and spontaneously adapt one's own action to those of others in the social loop of joint actions. We test this by means of transcranial magnetic stimulation (TMS) applied to the primary motor cortex (M1) by capitalizing on the well-known finding that responses recorded from specific hand muscles significantly increase when participants observe another individual making similar hand movements (Fadiga et al. 1995). Such a methodological approach has provided crucial evidence for the existence of an action observation/execution matching system in humans (for review see Fadiga et al. 2005). This view has been corroborated by the revelation of a critical link between corticospinal facilitation effects contingent upon action observation and the fronto-parietal regions of the putative human mirror neurons system (Avenanti et al. 2007; Catmur et al. 2010; Koch et al. 2010). With this in mind, we implemented an action observation paradigm that might have the ability to spontaneously evoke a functional shift from simulation to the covert planning of a non-identical action in the arena of complementary contexts. We measured the effects of single-pulse TMS on the muscle specificity of motor-evoked potentials (MEP) size during action observation at different times. MEPs were recorded from the abductor digiti minimi (ADM) and the first dorsal interosseous (FDI) muscles of the participants' right hand during the observation of video-clips representing a sequence of movements which might or might not call for the covert preparation of a complementary action by the observer. As an example of the used stimuli, a model grasps either an almond with a precision grip (PG; i.e., opposition between the index finger and thumb) or an apple

with a whole-hand grasp (WHG) as to place it within a tray located nearby. Then, she stretches out her arm and unfolds her hand as to ask for a further piece of fruit (e.g., almond or apple, respectively) which is located *out of reach*. We expect that observers' MEPs recorded at the time the model initially grasps, for instance, the apple would show both ADM and FDI muscles' facilitation because of the involvement of such muscles during the performance of a WHG. Conversely, observers' MEPs recorded during the observation of a PG as to grasp the almond should show only FDI muscle facilitation. This is because of the involvement of such muscle (and not of the ADM) during the performance of a PG. We also hypothesize that observers' MEPs recorded at a later time, when the model's hand unfolds in a give-it-to-me gesture, would be modulated on the basis of the presence/absence of the out-of-reach piece of fruit. In detail, when the out-of-reach fruit is present, the act of unfolding the hand by the model might be interpreted as a request for the observer to perform a complementary action, i.e., grasp the out-of-reach piece of fruit and pass it to the model. If this is the case, then we expect both ADM and FDI muscles' activation when the out-of-reach fruit evokes a WHG and only FDI muscle activation when the out-of-reach fruit evokes a PG. This might signify that the observer is preparing under-threshold either a WHG or a PG complementary response. Lastly, we predict that such "complementary" activity would not be detected when the out-of-reach piece of fruit is not present.

## Experiment 1

### Method

#### Participants

Twenty healthy individuals (10 women and 10 men) aged 20–34 (mean 27 years) took part in the Experiment. All were right handed according to the Standard Handedness Inventory (Briggs and Nebes, 1975). They had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Wassermann 1998; Rossi et al. 2009). All participants gave their written informed consent prior to their inclusion in the study and were naïve as to its purpose. Specific information concerning the study was provided after the experimental session was terminated. The experimental procedures were approved by the Ethics Committee of the University of Padova and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. None of the individuals taking part in the experiment experienced discomfort or adverse effects during TMS.

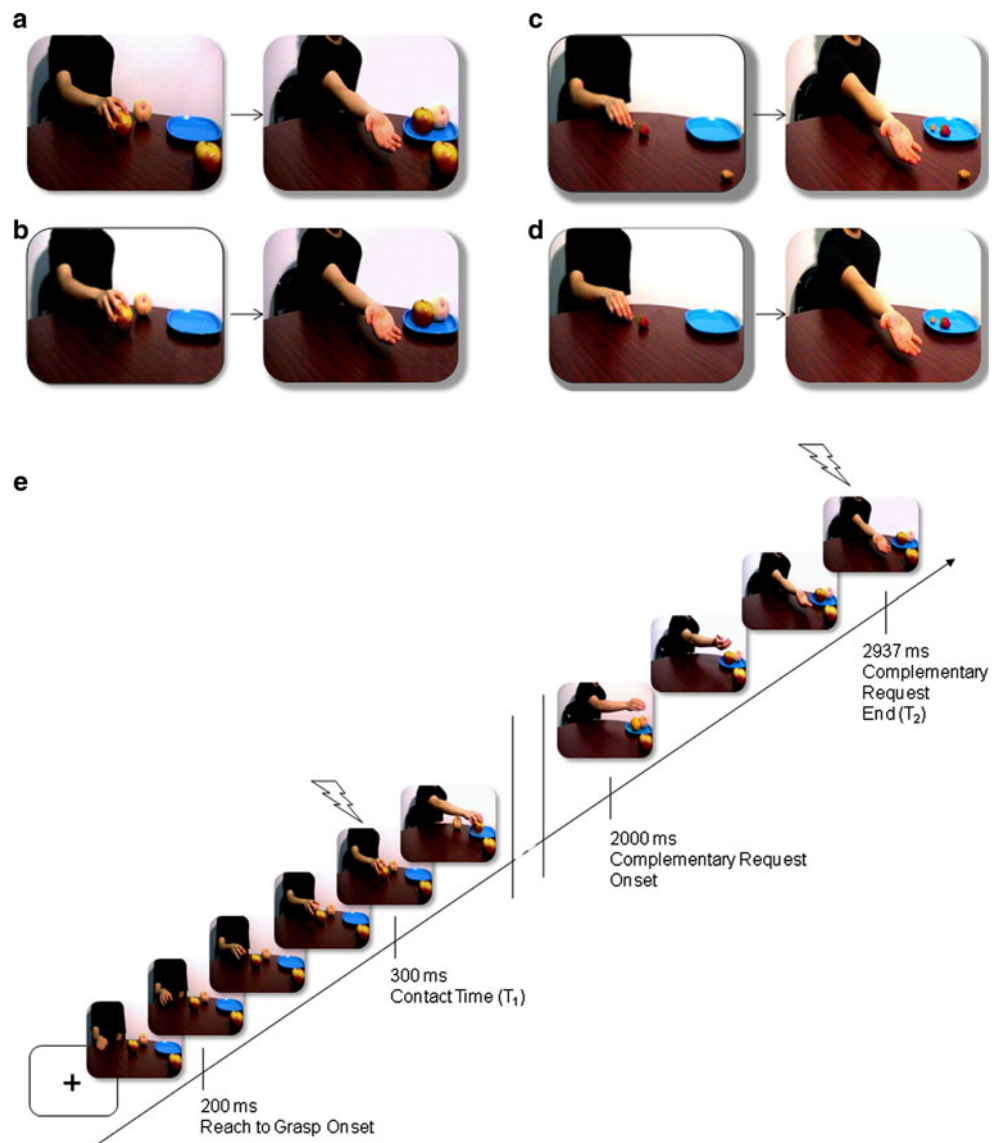
### Stimuli and experimental conditions

To create the stimulus material, we filmed four action sequences that served as experimental conditions: (1) a model reaching toward and grasping two objects eliciting a WHG movement as to place them within a tray one at the time and then stretching the arm out as to request for another object eliciting a WHG which was located *beyond-reach distance* (Fig. 1a); (2) a model reaching toward and grasping two objects eliciting a WHG movement as to place them within a tray one at the time and then simply stretching the arm out (Fig. 1b); (3) a model reaching toward and grasping two objects eliciting a PG movement as to place them within a tray one at the time and then stretching the arm out as to request for another object eliciting a PG which was located *beyond-reach distance* (Fig. 1c); (4) a model reaching toward and grasping two object eliciting a PG movement as to place them within a tray one at the time and then stretching the arm out (Fig. 1d). For the conditions in which the *beyond-reach* object was present, note that from an observer point of view this object was located on the bottom right corner of the image. A preliminary pilot investigation into a sample of subjects with similar characteristics as those participating in the experiment confirmed that the two beyond-reach objects afforded either a PG or a WHG, respectively. As outlined in Fig. 1e, at the beginning of each video-clip, the hand of the model was shown in a prone position resting on the table. Following 200 ms, the model started her reach to grasp movement (i.e., onset of the reach to grasp) and her fingers contacted the first object at around 300 ms (i.e., contact time; Fig. 1e). Following 1,700 ms, the model stretched out her arm as to require a complementary action (i.e., onset of the complementary request) that ended at 2,937 ms (Fig. 1e). The animation effect was obtained by presenting series of single frames each lasting 33 ms (resolution 720 × 576 pixels, color depth 24 bits, frame rate 30 fps) plus the first and last frames that lasted 500 and 1,000 ms, respectively.

### TMS stimulation and MEP recording

TMS was delivered using a 70-mm figure-of-eight coil connected to a Magstim BiStim<sup>2</sup> stimulator (Magstim, Whitlan, Dyfed, Wales, UK). The coil was angled 45° relative to the interhemispheric fissure and perpendicularly to the central sulcus with the handle pointing laterally and caudally (Brasil-Neto et al. 1992; Mills et al. 1992). Pulses were delivered over the left primary motor cortex (M1) corresponding to the hand region. The coil was positioned in correspondence with the optimal scalp position (OSP), defined as the position at which the stimulation of a slightly suprathreshold intensity consistently produced the largest

**Fig. 1** **a–d** Depict frames extracted from the four video-clips which served as stimuli for the present experiment. Specifically, for all video-clips, the initial reach to grasp movement and the final phase of the action sequence are represented. **e** Represents the schematization of event sequence during a single trial. The continuous oblique line represents the duration of video clip presentation. The vertical lines represent the onset of the reach to grasp movement, the time at which the hand contact the object, the onset of the complementary request gesture, and the completion of the complementary request gesture, respectively. The double vertical bars indicate that there are frames in between the “object contact” and the onset of the “complementary request gesture” phase. The “light” symbol indicates the time points at which the single TMS pulse was delivered



MEP from both the abductor digiti minimi (ADM; the muscle serving little finger abduction) and the first dorsal interosseous (FDI; the muscle serving index finger flexion/extension) muscles. The coil was held by a tripod and its position was continuously checked by experimenters to maintain consistent coil positioning. The resting motor threshold (rMT) was determined for each participant as the minimum intensity that induced reliable MEPs ( $\geq 50 \mu\text{V}$  peak-to-peak amplitude) in both the relaxed muscles in five out of ten consecutive trials (Rossini et al. 1994). Stimulation intensity during the recording session was 110% of the rMT and ranged from 38 to 59% (mean 48.5%) of the maximum stimulator output intensity. Motor-evoked potentials (MEPs) were recorded simultaneously from electrodes placed over the contralateral ADM and FDI muscles. Electromyographic (EMG) recording was made through pairs of 9-mm-

diameter Ag–AgCl surface cup electrodes. The active electrodes were placed over the belly of the right ADM and FDI muscles and the reference electrodes over the ipsilateral proximal interphalangeal joints (belly-tendon technique). Electrodes were connected to an isolated portable preamplifier unit optically linked to the main EMG amplifier. The ground was placed over the participants' left wrist and connected to the common input of the preamplifier. The raw myographic signals were bandpass filtered (20 Hz–1 kHz) and amplified prior to being digitized (2-kHz sampling rate) and stored on a computer for off-line analysis. In order to prevent the contamination of MEP measurements by background EMG activity, trials in which any EMG activity greater than  $100 \mu\text{V}$  was present within the 100-ms window preceding the TMS pulse were discarded. EMG data were collected for 200 ms after the TMS pulse.

## Procedure

Each participant was tested in a single experimental session lasting approximately 40 min. Testing was carried out in a sound-attenuated Faraday room. Participants were seated in a comfortable armchair with their head positioned on a fixed head rest so that the eye–screen distance was 80 cm. The right arm was positioned on a full-arm support, while the left arm remained relaxed with the hand resting on the legs. Participants were instructed to lay their hands in prone position as still and relaxed as possible. The task was to pay attention to the visual stimuli presented on a 19" monitor (resolution 1,280 × 1,024 pixels, refresh frequency 75 Hz, background luminance of 0.5 cd/m<sup>2</sup>) set at eye level. Participants were instructed to passively watch the video-clips and to avoid any movement. In order to maintain a good level of attention, participants were told that they would be debriefed about what they had seen at the end of the experiment. Ten trials were presented for each of the four types of video-clips, for a total of 40 trials. The order of presentation of the trials was randomized across participants. Prior to video presentation, baseline corticospinal excitability was assessed by acquiring five MEPs while the participants passively watched a white-colored fixation cross on black background on the computer screen. Another series of five MEPs was recorded at the end of the experimental session. Comparisons of MEP amplitudes for the two series allowed us to check for any corticospinal excitability change related to TMS per se. The average amplitude of the two series allowed us to set the individual baseline for data normalization procedures. TMS-induced MEPs from the right ADM and the right FDI muscles were acquired once per video presentation, at one of two counterbalanced time points (Fig. 1e): (1) on the frame showing the contact of the fingers on the first object ( $T_1$ , 300 ms) and (2) on the frame showing the end of the complementary gesture ( $T_2$ , 2,937 ms). Each video presentation was followed by a 10-s rest interval. During the first 5 s of the rest period, a message informing the participants to keep their hand still and fully relaxed was presented. Such a message was replaced by a fixation cross for the remaining 5 s. Five MEPs were acquired at every time point for each video, for a total of 80 MEPs per participant. The presentation of stimuli and the timing of TMS stimulation were managed by E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC.

## Data analysis

For each condition, peak-to-peak amplitudes of the collected MEPs from the ADM and FDI muscles were measured and averaged at each time point. MEP amplitudes deviating more than 2 standard deviations from the mean for each type

of action and trials contaminated by muscular pre-activation were excluded as outliers (<2%). A paired sample  $t$  test (2-tailed) was used to compare the amplitude of MEPs recorded from the FDI and ADM muscles in the two series of baseline trials presented at the beginning and at the end of the experimental session. Ratios were then computed using individual mean amplitude of MEPs recorded in the two fixation cross periods as baseline ( $\text{MEP ratio} = \text{MEP}_{\text{obtained}} / \text{MEP}_{\text{baseline}}$ ). For the sake of clarity at analysis level, we will define the main factors included within the analysis on the basis of the presence/absence of the beyond-reach object possibly eliciting a complementary action and on the basis of the type of grasp initially performed by the model. For each muscle, a repeated-measures analysis of variance (ANOVA) was conducted on the MEP ratios with “object presence” (object, no-object), “type of grasp” (PG, WHG), and “time” ( $T_1$ ,  $T_2$ ) as within-subjects factors. Sphericity of the data was verified prior to performing statistical analysis (Mauchly’s test,  $P > 0.05$ ). Post hoc pairwise comparisons were made by using  $t$  tests, and Bonferroni correction for multiple comparisons was applied. The comparisons between normalized MEP amplitude and baseline were made by using one-sample  $t$  tests.

## Results and discussion

Mean raw MEP amplitudes during the two baseline blocks administered at the beginning and the end of the experimental session were not significantly different for either the ADM ( $t_{19} = -0.87$ ,  $P = 0.40$ ) or the FDI muscle ( $t_{19} = 0.91$ ,  $P = 0.37$ ). This suggests that TMS per se did not induce any changes in corticospinal excitability in our experimental procedures. Mean MEP ratios from the ADM and FDI muscles depending on object presence/absence, type of grasp (PG, WHG), and time ( $T_1$ ,  $T_2$ ) are reported in Table 1. Given that FDI is involved in both PG and WHG, we did not expect any MEPs modulation in terms of type of grasp. Indeed, the repeated-measure ANOVA on normalized MEPs amplitudes for the FDI muscle showed only a statistically significant interaction of object presence by time [ $F_{(1,19)} = 14.27$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.43$ ]. The repeated-measure ANOVA on normalized MEPs amplitudes for the ADM muscle yielded a statistically significant interaction of object presence by type of grasp by time [ $F_{(1,19)} = 6.14$ ,  $P < 0.05$ ,  $\eta_p^2 = 0.24$ ]. Post hoc contrasts for the FDI and the ADM muscles are reported as follows.

### MEPs are modulated in terms of complementary action

Post hoc comparisons indicated that MEPs activation is modulated by the presence/absence of the object calling for a complementary action in the observed scene.

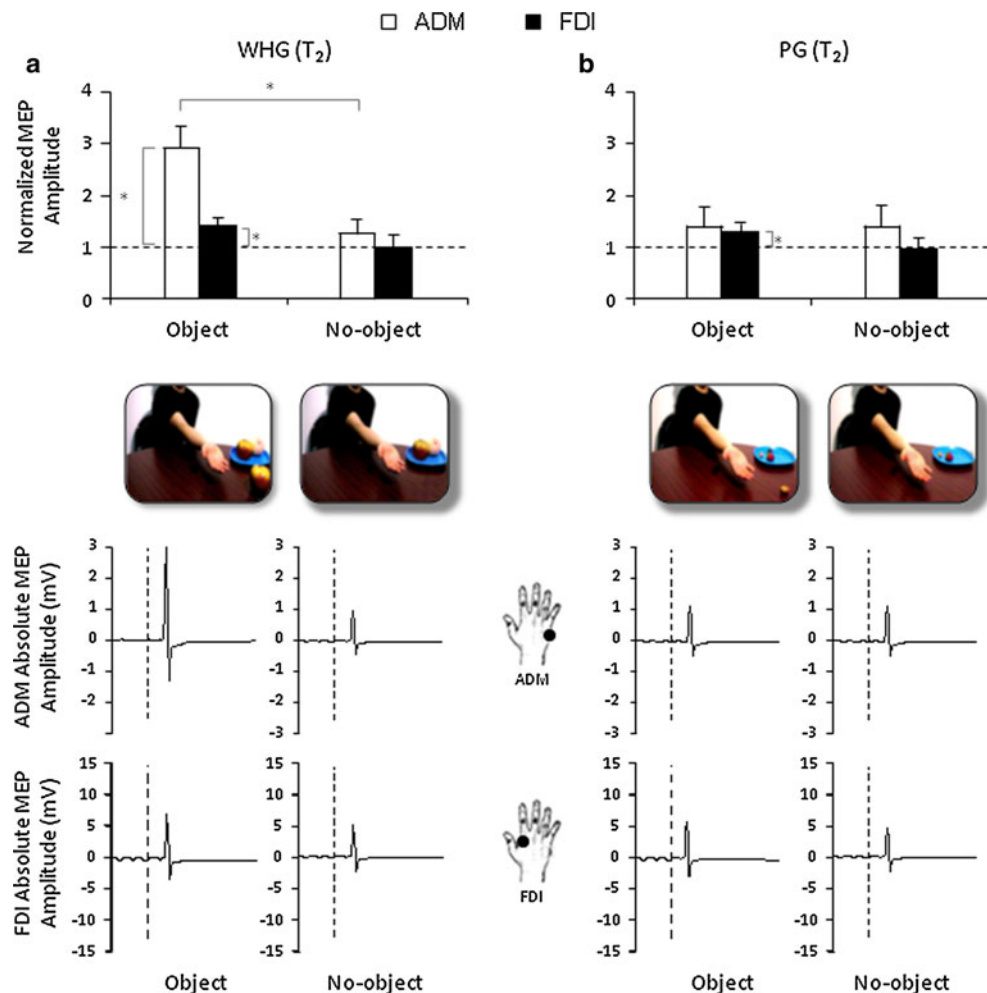
**Table 1** Normalized mean ( $\pm$ SEM) peak-to-peak amplitude of MEPs recorded from the FDI and the ADM muscles during the two observation conditions for each type of observed grasp at each trigger delay

	Normalized peak-to-peak mean amplitude							
	WHG				PG			
	Object condition ( $T_1$ )	Object condition ( $T_2$ )	No-object condition ( $T_1$ )	No-object condition ( $T_2$ )	Object condition ( $T_1$ )	Object condition ( $T_2$ )	No-object condition ( $T_1$ )	No-object condition ( $T_2$ )
FDI	1.05 ( $\pm$ 0.11)	1.40 ( $\pm$ 0.15)	1.26 ( $\pm$ 0.15)	1.00 ( $\pm$ 0.15)	1.19 ( $\pm$ 0.17)	1.27 ( $\pm$ 0.16)	1.26 ( $\pm$ 0.13)	0.97 ( $\pm$ 0.14)
ADM	2.13 ( $\pm$ 0.39)	2.98 ( $\pm$ 0.32)	2.03 ( $\pm$ 0.31)	1.27 ( $\pm$ 0.17)	1.44 ( $\pm$ 0.26)	1.42 ( $\pm$ 0.22)	1.38 ( $\pm$ 0.14)	1.42 ( $\pm$ 0.24)

Specifically, normalized MEP amplitude for the FDI muscle at  $T_2$  was greater for the object than for the no-object condition (1.34 vs. 0.98,  $P < 0.001$ ). As shown in Fig. 2, when contrasting normalized MEP amplitude at  $T_2$  in the object condition against baseline, we found significant FDI activation for both the precision and the whole-hand types of grasp ( $P < 0.05$ ). Similarly, normalized MEP amplitude for the ADM muscle at  $T_2$  was greater ( $P < 0.05$ ) when participants observed the model stretching out the arm as to ask for the *large* object (i.e., object

condition) than when participants observed the model simply stretching out the arm (i.e., no-object condition; Fig. 2a). Conversely, no difference in normalized MEP amplitude for the ADM muscle at  $T_2$  was noticed ( $P > 0.05$ ) when participants observed the model stretching out the arm as to ask for the *small* object and when they observed the model simply stretching out the arm (Fig. 2b). That is, there was ADM activation when the object calling for a complementary action required a whole-hand grasp, but not when it entailed a precision grip action.

**Fig. 2** The *upper panels* represent the means of the normalized MEP amplitudes across conditions (object, no-object) following the observation of either a WHG (a) or a PG (b) at  $T_2$ . Bars represent the standard error of means. The *horizontal dotted line* indicates MEP baseline. The *lower panels* represent a typical MEP recording from the ADM and the FDI muscles for one participant across conditions (object, no-object) following the observation of either a WHG (a) or a PG (b)

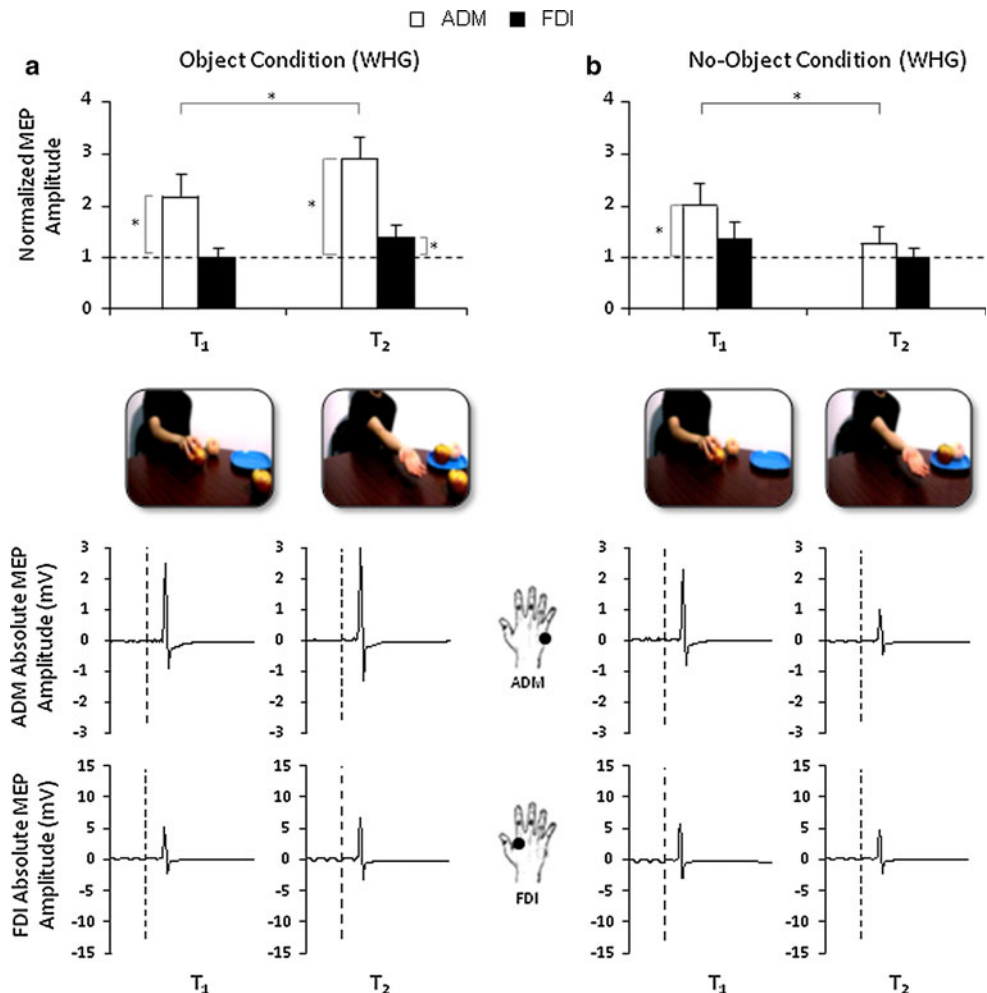


*The time course of complementary activations*

In terms of temporal delay ( $T_1$ ,  $T_2$ ), for the object condition, normalized MEP amplitude for the FDI muscle was greater at  $T_2$ , when participants observed the model stretching out the arm and unfolding the hand as to ask for the object than at  $T_1$ , when observing a grasping action on the same object (1.34 vs. 1.12,  $P < 0.05$ ). With respect to the no-object conditions, the normalized MEP amplitude evoked for the FDI muscle at  $T_1$  by the observation of a grasping action was greater than that evoked at  $T_2$  by the observation of an unfolded hand (1.26 vs. 0.98,  $P < 0.05$ ). As shown in Fig. 3, when contrasting MEPs at  $T_2$  against baseline for the whole-hand type of grasp, we found FDI activation when the object was present ( $P < 0.05$ ) but not when the model's hand calling for a complementary action was shown without the object ( $P > 0.05$ ). Similarly, normalized MEP amplitude for the ADM muscle was smaller ( $P < 0.05$ ) when participants observed a grasping action on the large object ( $T_1$ ) than when they observed the model stretching out the arm and

unfolding the hand as to ask for the same object ( $T_2$ ; Fig. 3a). As concerned with the no-object condition, the MEP amplitude evoked for the ADM muscle at  $T_1$  by the observation of a WHG was greater ( $P < 0.05$ ) than that evoked by the observation of an unfolded hand at  $T_2$  (Fig. 3b). As regards the condition in which a PG was observed, no statistically significant difference resulted in terms of time. When contrasting MEPs for the condition characterized by a WHG against baseline, we found ADM activation across all time delays ( $p_s < 0.05$ ) except when the model's hand calling for a complementary action was shown without the object at  $T_2$  ( $P > 0.05$ ; Fig. 3b). The fact that we found a statistically significant difference between  $T_1$  and  $T_2$  for the no-object condition seems to suggest that the presence of the model's unfolded hand was not leading to any effect per se. This should rule out the possibility that differences across conditions (object vs. no-object) at  $T_2$  may simply depend on the presence of the model's gesture. Altogether, these results indicate that a greater activation of both the ADM and the FDI muscles is elicited during the observation of an object calling

**Fig. 3** The upper panels represent the means of the normalized MEP amplitudes for the object (a) and the no-object (b) conditions at  $T_1$  and  $T_2$  for the video-clips characterized by a WHG. Bars represent the standard error of means. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM and the FDI muscles for one participant for the object and the no-object conditions across the time at which TMS was delivered ( $T_1$  and  $T_2$ )



for a complementary action than during the observation of a grasping action upon the same object.

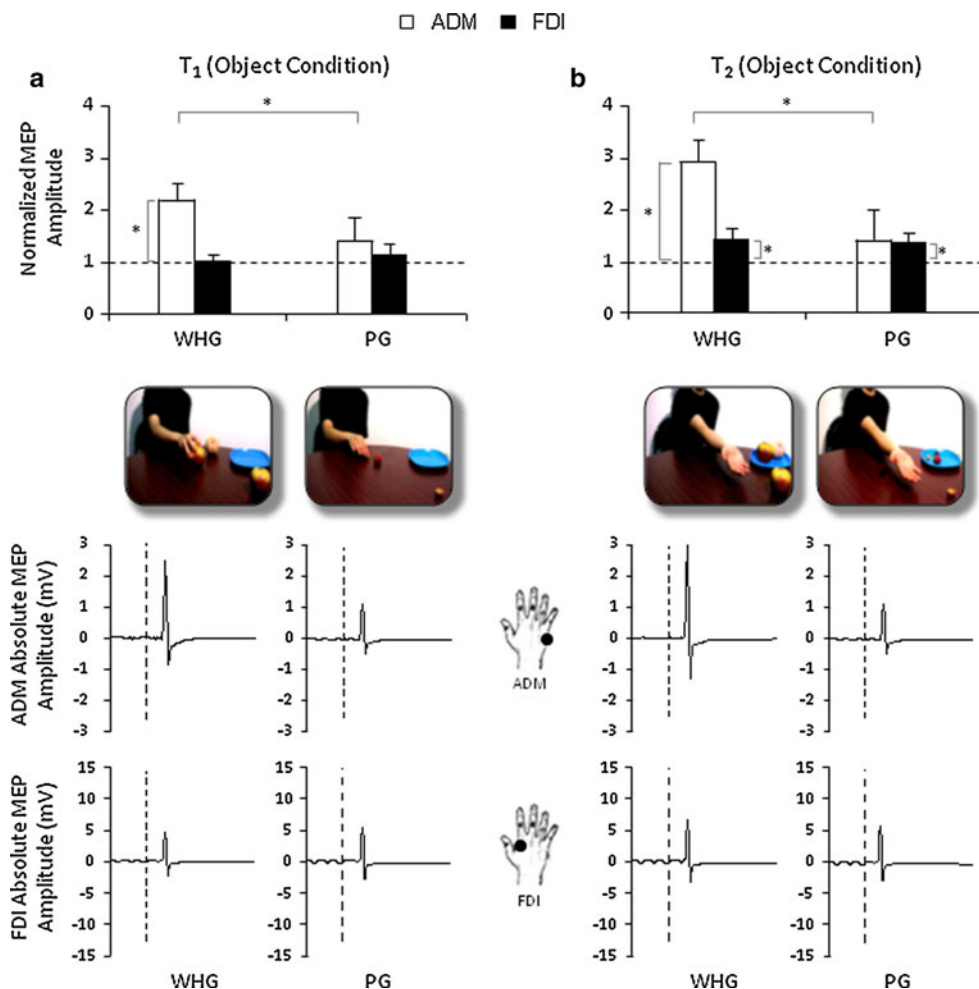
#### MEPs are modulated in terms of type of grasp

As expected, only the MEPs amplitude for the ADM muscle was modulated in terms of type of grasp. Post hoc comparisons for the ADM muscle revealed that for the object condition, MEP amplitude at  $T_1$  was greater when observing the model performing a WHG on a *large* object than PG on a *small* object (Fig. 4a). This occurred for both conditions, regardless of the presence/absence of the out-of-reach object ( $p_s < 0.05$ ). Accordingly, for the object condition at  $T_2$ , MEP amplitude was greater ( $P < 0.05$ ) when participants observed the model stretching out the arm as to ask for the *large* than for the *small* object (Fig. 4b). As expected, when contrasting normalized MEP amplitude at  $T_2$  for the FDI muscle against baseline, we found that such contrast was significant for both types of grasp ( $p_s < 0.05$ ; Fig. 4b).

The present results confirm the known effects of motor excitability during observation of grasping actions by

revealing MEP activity in muscles of the hand that directly match with the behavior that is observed. In addition, they greatly extend previous TMS findings by revealing motor excitability in response to the observation of a gesture requesting a complementary action. This result is only found when the gesture is referring to an object that is located just out of reach of the actor, but not when there is no object present. Furthermore, the specific muscles that are found activated in response to this social request indicate that the observer is triggered to grasp the object (using a precision grip for a small object or a whole-hand grip for a large object). These findings support the idea that the mechanisms underlying action observation and execution are highly flexible and sensitive to the social context in which actions are observed. However, before any firm conclusion can be drawn, two issues need to be addressed. First, we need to ascertain whether it is the object per se to determine the reported effect. Second, whether such effect is intrinsically social or it might be also be elicited by non-social cues. The following experiment has been designed to disentangle these matters.

**Fig. 4** The upper panels represent the means of the normalized MEP amplitudes across types of observed grasp (WHG, PG) recorded at either  $T_1$  (a) or  $T_2$  (b) for the object condition. Bars represent the standard error of means. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM and the FDI muscles at either  $T_1$  (a) or  $T_2$  (b) for one participant for the object condition following the observation of either a WHG or a PG





## Experiment 2

The current experiment considers two new conditions in addition to the critical “request” condition included within “Experiment 1”. Specifically, we compared corticospinal excitability during the observation of a scene including either only an object, an arrow cue pointing toward an object, or a request gesture toward an object. If the mere presence of an object or an arrow cue replacing the arm gesture would not determine the kind of facilitation found for the “request” gesture, then the “social context” hypothesis should be confirmed. Conversely, if the mere presence of an object or an arrow cue replacing the arm gesture would determine the same kind of facilitation as for the “request” gesture, then such hypothesis should be rejected.

### Method

#### Participants

Ten healthy individuals (6 women and 4 men) aged 20–32 (mean 23 years) with the same characteristics as those who took part in “Experiment 1” participated in the study.

#### Data recording, procedures, stimuli, and data analysis

These were exactly the same as for “Experiment 1” except that we considered two novel conditions. A condition in which only an object (i.e., an apple) was present in the scene (Fig. 5; “object” condition) and a condition in which there was an arrow pointing to the object (Fig. 5; “object-arrow” condition). For the sake of comparison, we also included the critical condition in which there was a model stretching out the arm as to request for an object located beyond-reach distance (Fig. 5; “object-hand” condition). Note that in order to create the “object-arrow” condition, we have edited the video-clips used for the “object-hand” condition by substituting frame-by-frame model with a moving arrow of a similar length as the model’s arm. Video-clips for all conditions were of the same length and they were presented in a randomized order. For each muscle, a repeated-measures analysis of variance (ANOVA) was conducted on the MEP ratios with “condition” (object, arrow-object, hand-object) and “time” ( $T_1$ ,  $T_2$ ) as within-subjects factors.

### Results and discussion

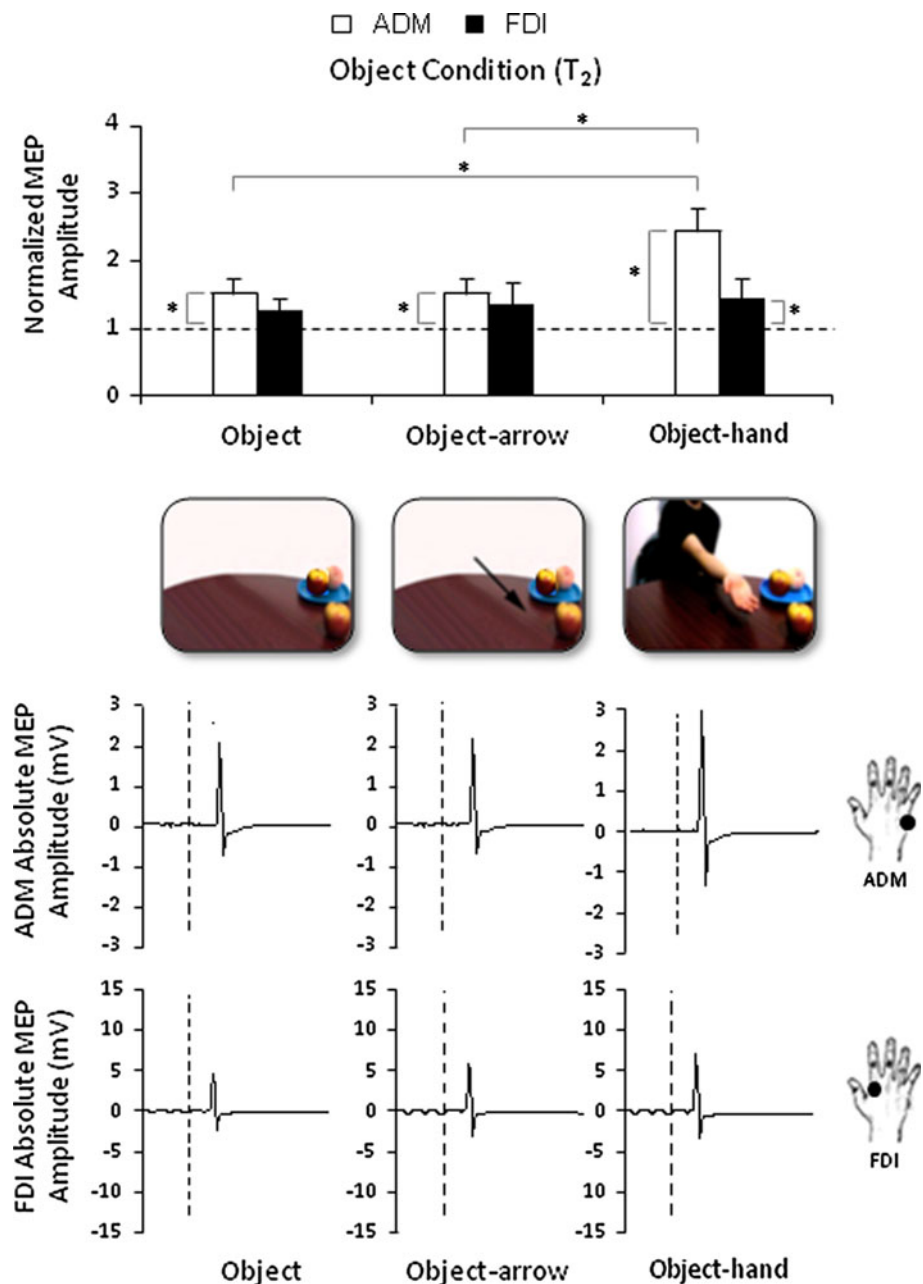
Mean raw MEP amplitudes during the two baseline blocks administered at the beginning and the end of the experimental session were not significantly different for either the FDI ( $t_9 = -1.71$ ,  $P = 0.12$ ) or the ADM ( $t_9 = -1.84$ ,

$P = 0.08$ ) muscle. This suggests that TMS per se did not induce any changes in corticospinal excitability in our experimental procedures. The repeated-measure ANOVA on normalized MEPs amplitudes for the FDI muscle showed a statistically significant effect of time [ $F_{(1,9)} = 5.07$ ,  $P < 0.05$ ,  $\eta_p^2 = 0.36$ ]. MEPs amplitude at  $T_1$  was lower than at  $T_2$  (1.41 vs. 1.79). In particular, only when contrasting normalized MEP amplitude for the FDI muscle at  $T_2$  in the object-hand condition against baseline, a significant activation was found ( $P < 0.05$ ; Fig. 5). The repeated-measure ANOVA on normalized MEPs amplitudes for the ADM muscle yielded a statistically significant effect of condition [ $F_{(2,18)} = 5.98$ ,  $P < 0.05$ ,  $\eta_p^2 = 0.40$ ] and of time [ $F_{(1,9)} = 18.48$ ,  $P < 0.05$ ,  $\eta_p^2 = 0.67$ ] and a significant interaction of condition by time [ $F_{(2,18)} = 9.62$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.52$ ]. As found for the FDI muscle, post hoc contrasts indicated that only for the object-hand condition, normalized MEP amplitude was greater at  $T_2$  than at  $T_1$  (2.37 vs. 1.42;  $P < 0.001$ ). No significant differences depending upon the time at which the TMS stimulus was delivered were noticed for the remaining conditions ( $p_s > 0.05$ ). Furthermore, normalized MEP amplitude at  $T_2$  was greater for the object-hand condition than that for the object and the object-arrow conditions ( $p_s < 0.001$ ; Fig. 5). Normalized MEP amplitude for the object and the object-arrow conditions was not statistically different ( $P > 0.05$ ). When contrasting normalized MEP amplitude against baseline, we found ADM activation for all conditions ( $p_s < 0.05$ ). These latter results suggest that the mere presence of an object or of an arrow pointing toward the object has the ability to determine MEP activation, but to a lesser extent than that when the context is characterized by a request gesture toward the object. Altogether, these findings corroborate those obtained for “Experiment 1”, supporting the idea that it is the social nature of the observed gesture, along with the presence of the object, to determine the observed effect.

### General discussion

The aim of the present study was to investigate whether the automatic effects of action observation on corticospinal excitability are modulated on the basis of the contextual factors characterizing the observed action. Specifically, we recorded MEPs activity at different times following the observation of an action sequence performed in a context which could imply or not imply a complementary gesture. The results indicate that MEPs activity recorded at the beginning of the observed action sequence ( $T_1$ ) was suggestive of an imitative mechanism. However, MEPs activity recorded at the end of the action sequence ( $T_2$ ) was

**Fig. 5** The upper panels represent the means of the normalized MEP amplitudes across conditions (object, object-arrow, object-hand) recorded at  $T_2$ . Bars represent the standard error of means. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM and the FDI muscles at  $T_2$  for one participant across conditions (object, object-arrow, object-hand)



suggestive of a covert preparation for a non-imitative complementary action.

Much previous research on the effects of action observation on corticospinal excitability has provided evidence for an automatic resonance mechanism of motor structures in line with the observed movement. According to this tenet, observed actions would be directly matched onto the observer's own motor system regardless of the context within which the observed action is performed. This issue becomes particularly relevant in the domain of complementary actions in which performed actions often differ from those observed. The present results shed some light on this topic. We demonstrate that a context calling for a

complementary action has the ability to modulate the pattern of MEP activity. MEPs recorded at the time participants observed the model grasping an object revealed a strict "mirror" mechanism, whereas MEPs recorded at the time the model unfolded the hand toward the observers in a request kind of gesture reflected the complementary intended-but-not-performed action, which was related (in grasp terms) to the size of the out-of-reach object. Moreover, the pattern of MEP activity related to the request gesture was distinct depending on the presence/absence of the out-of-reach object. This allows us to conclude that it was not the observation of that particular hand movement to elicit the observed pattern of MEP activity per se, but

that it was the combination of the unfolded hand and the out-of-reach object which determined a complementary type of effect.

How can these results be explained? Recent fMRI experiments have been aimed at uncovering the neural basis of complementary actions (Newman-Nordlund et al. 2007, 2008; Etzel et al. 2008; Gazzola and Keysers 2009; Kokal et al. 2009; Kokal and Keysers 2010). Data from these experiments suggest that such kind of actions might be subserved by an integration network that includes areas belonging to the putative mirror neuron system. In one experiment, the response of the human putative mirror neuron system was compared between an imitative and a complementary action task (Newman-Nordlund et al. 2007). The results indicate that complementary actions determined larger BOLD signal than imitative actions in key areas of the putative human mirror neuron system. Similarly, Kokal et al. (2009) found an increase in activation in the regions of the human putative mirror system when participants were engaged in joint actions with a human agent than with a computer that did not respond to their actions. Here, we found an increase in MEP activity recorded at the time the complementary request became evident in the presence of the out-of-reach object. Although we are aware that we cannot say anything definite regarding the neural chain which brought about an increase in MEP activation for the complementary condition, the present TMS data might provide further evidence that complementary actions require a more robust and/or more extensive simulation process, possibly because of the more intrinsic difficulty in simulating responses that are non-identical to the observed action (Brass et al. 2001, 2005; Bekkering et al. 2009). This would imply that the participant has in her brain actions which are both similar and complementary to those observed. The process of selecting the appropriate action, therefore, might become more demanding.

The present findings might also be explained in terms of motor imagery. According to previous observations, motor imagery influences the corticospinal excitability (Bonnet et al. 1997; Kasai et al. 1997; Fadiga et al. 1999). Furthermore, there is agreement that mental simulation of movements involves the same neural substrate that is addressed during action execution and during the observation of actions performed by other individuals (Fadiga et al. 1995; Jeannerod and Frak, 1999). In the present study, the reported differential MEP activity for the complementary context might be due to the mental inference the observer is making regarding the observed actions. When the context calls for a complementary action, the observer might mentally prepare for performing such action. Therefore, our data might suggest that in humans the observation/execution matching system may constitute the cortical substrate not only for thinking about the observed movements, but also for

thinking regarding how to respond to observed movements in a complementary manner. Seeing the hand unfolding in a request fashion might trigger in the observer the need to “fill-in” the elicited social loop. Because no explicit instructions to participants in terms of contextual factors were given, the reported effects might be an example of a spontaneous tendency to fulfill the request embedded in a potential social kind of interaction. This possibility might be confirmed by the fact that when debriefed at the end of the experimental session, all participants spontaneously reported that they felt to imagine handling the object to the model.

It might be said that the reported effects can be ascribed to the mere presence of the object in terms of motor coding of object affordances (Tucker and Ellis 1998; Buccino et al. 2009) or to a possible attentional shift dictated by whatever non-social cue. On the contrary, our data demonstrate that there is a shift from a symmetrical action simulation to the covert planning for a non-identical action at  $T_2$  only when both the object and the social request gesture are present.

As a final point, the reported effects might relate to different aspects of the simulation process. For instance, the reported MEP modulation might reflect an automatic action anticipation process (Kilner et al. 2004; Urgesi et al. 2010) or a spontaneous form of motor imagery in either first-person or third-person perspective (Fourkas et al. 2006). In light of the present findings, we cannot determine which exact process is taking place. Nevertheless, these are all examples of simulative processing beyond emulation.

In conclusion, our results suggest that the notion of an action observation system which yields an automatic match in the observer is not as strict as previously thought. The present findings support the idea that the mechanisms underlying action observation are flexible and highly responsive to the complex requests embedded in contexts characterized by a social dimension.

## References

- Avenanti A, Bolognini N, Maravita A, Aglioti SM (2007) Somatic and motor components of action simulation. *Curr Biol* 17:2129–2135
- Becchio C, Sartori L, Bulgheroni M, Castiello U (2008a) The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. *Conscious Cogn* 17:557–564
- Becchio C, Sartori L, Bulgheroni M, Castiello U (2008b) Both your intention and mine are reflected in the kinematics of my reach to grasp movement. *Cognition* 106:894–912
- Becchio C, Sartori L, Castiello U (2010) Toward you: the social side of actions. *Curr Dir Psychol Sci* 19:183–188
- Bekkering H, de Bruijn ERA, Cuijpers RH, Newman-Nordlund R, van Schie HT, Meulenbroek R (2009) Joint action: neurocognitive mechanisms supporting human interaction. *Topics Cogn Sci* 1:340–352

- Bonnet M, Decety J, Requin J, Jeannerod M (1997) Mental simulation of an action modulates the excitability of spinal reflex pathways in the man. *Cogn Brain Res* 5:221–228
- Brasil-Neto JP, Cohen LG, Panizza M, Nilsson J, Roth BJ, Hallett M (1992) Optimal focal transcranial magnetic activation of the human motor cortex: effects of coil orientation, shape of the induced current pulse, and stimulus intensity. *J Clin Neurophysiol* 9:132–136
- Brass M, Derrfuss J, von Cramon DY (2001) The inhibition of imitative and overlearned responses: a functional double dissociation. *Neuropsychologia* 43:89–98
- Brass M, Zysset S, von Cramon DY (2005) The inhibition of imitative response tendencies. *Neuroimage* 14:1416–1423
- Briggs GG, Nebes RD (1975) Patterns of hand preference in a student population. *Cortex* 11:230–238
- Buccino G, Sato M, Cattaneo L, Rodà F, Riggio L (2009) Broken affordances, broken objects: a TMS study. *Neuropsychologia* 47:3074–3078
- Decety J, Jackson PL, Sommerville JA, Chaminade T, Meltzoff AN (2004) The neural bases of cooperation and competition: an fMRI study. *NeuroImage* 23:744–751
- di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992) Understanding motor events: a neurophysiological study. *Exp Brain Res* 91:176–180
- Etzel JA, Gazzola V, Keysers C (2008) Testing simulation theory with cross-modal multivariate classification of fMRI data. *PLoS ONE* 3:e3690
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 73:2608–2611
- Fadiga L, Buccino G, Craighero L, Fogassi L, Gallese V, Pavesi G (1999) Corticospinal excitability is specifically modulated by motor imagery. A magnetic stimulation study. *Neuropsychologia* 37:147–158
- Fadiga L, Craighero L, Olivier E (2005) Human motor cortex excitability during the perception of others' actions. *Curr Opin Neurobiol* 15:213–218
- Fourkas A, Avenanti A, Urgesi C, Aglioti SM (2006) Corticospinal facilitation during first and third person imagery. *Exp Brain Res* 168:143–151
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593–609
- Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI Data. *Cereb Cortex* 19:1239–1255
- Georgiou J, Becchio C, Glover S, Castiello U (2007) Different action patterns for cooperative and competitive behaviour. *Cognition* 102:415–433
- Jeannerod M, Frak V (1999) Mental imaging of motor activity in humans. *Curr Opin Neurobiol* 9:735–739
- Kasai T, Kawai S, Kawanishi M, Yahagi S (1997) Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. *Brain Res* 744:147–150
- Kilner J, Vargas C, Duval S, Blakemore SJ, Sirigu A (2004) Motor activation prior to observation of a predicted movement. *Nat Neurosci* 7:1299–1301
- Knoblich G, Jordan S (2002) The mirror system and joint action. In: Samenov M, Gallese V (eds) *Mirror neurons and the evolution of brain and language*. John Benjamins, Amsterdam, pp 115–124
- Koch G, Versace V, Bonni S, Lupo F, Lo Gerfo E, Oliveri M, Caltagirone C (2010) Resonance of cortico-cortical connections of the motor system with the observation of goal directed grasping movements. *Neuropsychologia* 48:3513–3520
- Kokal I, Keysers C (2010) Granger causality mapping during joint actions reveals evidence for forward models that could overcome sensory-motor delays. *PLoS One* 5:e13507
- Kokal I, Gazzola V, Keysers C (2009) Acting together in and beyond the mirror neuron system. *Neuroimage* 47:2046–2056
- Mills KR, Boniface SJ, Schubert M (1992) Magnetic brain stimulation with a double coil: the importance of coil orientation. *Electroencephal Clin Neurophysiol* 85:17–21
- Newman-Nordlund RD, van Schie HT, van Zuijlen AM, Bekkering H (2007) The mirror neuron system is more activated during complementary compared with imitative action. *Nat Neurosci* 10:817–818
- Newman-Nordlund RD, Bosga J, Meulenbroek RG, Bekkering H (2008) Anatomical substrates of cooperative joint-action in a continuous motor task: virtual lifting and balancing. *Neuroimage* 41:169–177
- Ocampo B, Kritikos A (2010) Placing actions in context: motor facilitation following observation of identical and non-identical manual acts. *Exp Brain Res* 201:743–751
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. *Annu Rev Neurosci* 27:169–192
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2:661–670
- Rossi S, Hallett M, Rossini PM, Pascual-Leone A (2009) Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clin Neurophysiol* 120:2008–2039
- Rossini PM, Barker AT, Berardelli A, Caramia MD, Caruso G, Cracco RQ et al (1994) Noninvasive electrical and magnetic stimulation of the brain, spinal-cord and roots-basic principles and procedures for routine clinical application. *Electroencephal Clin Neurophysiol* 91:79–82
- Sartori L, Becchio C, Bara BG, Castiello U (2009a) Does the intention to communicate affect action kinematics? *Conscious Cogn* 8:766–772
- Sartori L, Becchio C, Castiello U (2009b) Modulation of the action control system by social intention: unexpected social requests override preplanned action. *J Exp Psychol Hum Percept Perf* 35:1490–1500
- Sebanz N, Frith C (2004) Beyond simulation? Neural mechanisms for predicting the actions of others. *Nat Neurosci* 7:5–6
- Sebanz N, Knoblich G, Prinz W (2003) Representing other's actions: just like one's own? *Cognition* 88:B11–B12
- Sebanz N, Bekkering H, Knoblich G (2006a) Joint action: bodies and minds moving together. *Trends Cogn Sci* 10:70–76
- Sebanz N, Knoblich G, Prinz W, Wascher E (2006b) Twin peaks: an ERP study of action planning and control in co-acting individuals. *J Cogn Neurosci* 18:859–870
- Tucker M, Ellis R (1998) On the relations between seen objects and components of potential actions. *J Exp Psychol Hum Percept Perf* 24:830–846
- Urgesi C, Maieron M, Avenanti A, Tidoni E, Fabbro F, Aglioti SM (2010) Simulating the future of actions in the human corticospinal system. *Cereb Cortex* 20:2511–2521
- van Schie HT, Bekkering H (2007) Neural mechanisms underlying immediate and final action goals in object use reflected by slow wave brain potentials. *Brain Res* 1148:183–197
- van Schie HT, van Waterschoot BM, Bekkering H (2008) Understanding action beyond imitation: reversed compatibility effects of action observation in imitation and joint action. *J Exp Psychol Hum Percept Perform* 34:1493–1500
- Wassermann EM (1998) Risk and safety of repetitive transcranial magnetic stimulation: report and suggested guidelines from the international workshop on the safety of repetitive transcranial magnetic stimulation, June 5–7, 1996. *Electroencephal Clin Neurophysiol* 108:1–16