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Luisa Sartori ^a, Andrea Cavallo ^b, Giulia Bucchioni ^a & Umberto Castiello ^a

^a Department of General Psychology, University of Padova, Padova, Italy

^b Department of Psychology, Centre for Cognitive Science, University of Torino, Torino, Italy

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From simulation to reciprocity: The case of complementary actions

Luisa Sartori¹, Andrea Cavallo², Giulia Bucchioni¹, and Umberto Castiello¹

¹Department of General Psychology, University of Padova, Padova, Italy

²Department of Psychology, Centre for Cognitive Science, University of Torino, Torino, Italy

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. What remains unknown is how we are to resolve the possible conflict between the automatic tendency to "mirror" and the need to perform different context-related complementary actions. By using single-pulse transcranial magnetic stimulation, we found that observation of a double-step action characterized by an implicit complementary request engendered a shift from symmetrical simulation to reciprocity in the participants' corticospinal activity. Accordingly, differential motor facilitation was revealed for the snapshots evoking imitative and complementary gestures despite the fact that the observed type of grasp was identical. Control conditions in which participants observed the same action sequence but in a context not implying a complementary request were included as well. The results provide compelling evidence that when an observed action calls for a nonidentical complementary action, an interplay between the automatic tendency to resonate with what is observed and to implicitly prepare for the complementary action does emerge. In other words, implicit complementary requests might have the ability to draw attention to specific features of the context affording nonidentical responses.

Keywords: Action observation; Transcranial magnetic stimulation; Complementary actions; Reach-to-grasp; Joint actions.

A large amount of evidence suggests that perceiving body movements of other people activates motor representations in the observer's brain (for review, see Fadiga, Craighero, & Olivier, 2005; Rizzolatti, Fabbri-Destro, & Cattaneo, 2009; Rizzolatti, Fogassi, & Gallese, 2001). A tenet emerging from these studies is that the activated motor representations appear to be imitative in nature. This would reflect an automatic resonance mechanism of motor structures in line with the observed movement.

Support for the idea of a basic neurophysiological system underlying such a motor resonance mechanism comes from different methodological approaches. First and foremost, single-cell recordings

have demonstrated the existence of neurons, termed "mirror", discharging both when a monkey grasps 3-D objects and when it observes the execution of a similar action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Subsequently, functional magnetic resonance imaging (fMRI) investigations (Buccino et al., 2001; Decety et al., 1997; Gazzola & Keysers, 2009; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Costes, & Decety, 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Turella, Erb, Grodd, & Castiello, 2009) and magnetoencephalography (MEG) (Avikainen, Forss, & Hari, 2002; Hari et al., 1998; Nishitani &

Correspondence should be addressed to: Umberto Castiello, Department of Psychology, University of Padova, via Venezia 8, 35131 Padova, Italy. E-mail: umberto.castiello@unipd.it

Hari, 2000) uncovered the existence of similar neural mechanisms within the human brain.

Furthermore, and of particular relevance for the present study, transcranial magnetic stimulation (TMS) studies report that an observer's motor system is facilitated by the mere viewing of motor actions (Aglioti, Cesari, Romani, & Urgesi, 2008; Avenanti, Bolognini, Malavita, & Aglioti, 2007; Baldissera, Cavallari, Craighero, & Fadiga, 2001; Borroni, Montagna, Cerri, & Baldissera, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Montagna, Cerri, Borroni, & Baldissera, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006a). For instance, in the pioneering study by Fadiga and colleagues (1995), single-pulse TMS was applied over the motor cortex of participants observing a model reaching and grasping for differently shaped objects. They demonstrated that observing an action induces an enhancement of the motor evoked potentials (MEPs) recorded from participants' hand muscles corresponding to those involved in the observed action.

Since then, similar paradigms have been usefully applied to further investigate the nature of the corticospinal neural activity induced by peculiar visual characteristics of an observed action (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Gangitano, Mottaghy, & Pascual-Leone, 2001; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Urgesi, Moro, Candidi, & Aglioti, 2006b). For instance, it was demonstrated that the motor facilitation contingent upon action observation strictly reflects the temporal dynamics of the observed action kinematics (Gangitano et al., 2001), it is modulated by the laterality of the observed acting effector (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002), and it is not affected by the observer-model postural congruency (Urgesi et al., 2006a). Altogether, these findings suggest that when we observe another individual acting, we "resonate" with her actions. Our motor system simulates under threshold the observed action in a strictly congruent fashion. The involved muscles are the same as those used in the observed action, and their activation is temporally strictly coupled with the dynamics of the observed action (Fadiga et al., 2005).

A question that has yet to be fully investigated is whether such automatic tendency to "mirror" is always beneficial in real-life situations. For instance, in a variety of circumstances in which two or more individuals are involved in joint actions, complementary rather than imitative actions appear to be more appropriate. For example, if someone hands us a mug by the handle, rather than imitate her action, we select a grip which is complementary to hers. In such circumstances, there would be a mismatch between the

types of grip adopted by the two agents. Mirroring the observed movement might be detrimental to successfully completing such joint action.

At this stage, the natural question is how are we to resolve the possible conflict between the automatic tendency to "mirror" and the need to perform different context-related complementary actions. Preliminary answers to this question come from recent studies in which this issue has been investigated by means of TMS and fMRI techniques (Catmur, Walsh, & Heyes, 2007; Catmur et al., 2008; Kokal, Gazzola, & Keysers, 2009; Newman-Nordlund, van Schie, van Zuijlen, & Bekkering, 2007; see also Ocampo & Kritikos, 2010; van Schie, van Waterschoot, & Bekkering, 2008). In the first instance, a TMS study demonstrated that the properties of the mirror system are not fixed but may vary by a process of sensorimotor learning (Catmur et al., 2007, 2008; see also Heyes, Bird, Johnson, & Haggard, 2005). Training participants to perform index finger actions when they observe little finger actions, and vice versa, results in activation of primary motor cortical representations of the index finger when passively observing little finger actions, and activation of representations of the little finger when observing index finger actions. Therefore, nonidentical responses were facilitated when associated with the observed stimuli. In the second instance, the role of the human mirror neuron system for the coding of imitative and complementary actions has been recently investigated by asking participants to prepare and execute imitative or complementary actions (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 requested to perform the observed action, whereas in the complementary context they were requested to execute the other type of grasp. The data relative to the behavioral part of this fMRI experiment indicated that, for the imitative context, reaction times (RTs) were faster for identical than nonidentical actions. In the complementary context, RTs were faster for nonidentical than for identical actions. This suggests that the action context is critical for movement preparation. In neural terms, results clearly indicate that the mirror neuron system has the ability to link nonidentical observed and executed actions as long as they serve a common goal. Key areas of the mirror neuron system were more activated for the preparation of complementary than imitative actions. This has been explained in terms of different kinds of mirror neurons. Strictly congruent mirror neurons, which respond to identical observed and executed actions, may act in a context-dependent manner. Broadly congruent mirror neurons, which respond to nonidentical observed and

executed actions upon the same object, might be relevant to complementary actions. However, the question of whether mirror neurons play a role in social interactions, implying different actions on different objects, has yet to be fully investigated.

In sum, these data indicate that action observation does not inevitably lead to an imitative kind of motor facilitation. Merely changing the context in which an action is embedded can modulate the biasing effect of action observation (Catmur et al., 2007, 2008; Newman-Nordlund et al., 2007). In this view, the potential conflict emerging between observed and nonidentical complementary actions might be resolved flexibly in a double-step fashion by the same system; that is, a step in which the observed action has to be experienced and understood in order to predict its goal, and a subsequent step in which associations between observed and nonidentical movements are formed in order to eventually act in a complementary manner. To date, no one has investigated whether such a double-step process exists and how it unfolds.

Here we test the existence of a functional shift from symmetrical simulation to reciprocity in the arena of complementary actions. We measured the effects of single-pulse TMS on the muscle specificity of MEP size during action observation at different times. MEPs were recorded from the abductor digiti minimi (ADM) and the first dorsal interosseus (FDI) muscles of the right hand during the observation of video clips representing a sequence of movements which might or might not elicit a spontaneous complementary action by the observer. As an example of the considered complementary actions, a model grasps a thermos filled with coffee in a whole-hand grasp (WHG), that is, opposition of the thumb with the other fingers, and pours coffee into three cups located nearby. Then she stretches out her arm as if to pour coffee into a fourth cup which is out of her reach. Note that from the observer's point of view this cup was located on the bottom right corner of the image and would require a precision grip (PG), that is, opposition between the index finger and thumb by the handle, in order to be reached. It is well known that the mere sight of an object activates the representation of the action that can be performed on it, even in the absence of explicit intentions to act (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Jeannerod, 1994; Tucker & Ellis, 1998). Moreover, the results of a recent TMS study show that MEP facilitation was observed only when the handle of an object was located contralaterally with respect to the site stimulated (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009).

Along these lines, we expect that MEPs recorded at the time the observer initially perceives the model

grasping the thermos might elicit both ADM and FDI muscle facilitation because such muscles are usually recruited for a WHG. Conversely, the model's move to pour coffee into an out-of-reach cup might be able to elicit a nonidentical complementary gesture (i.e., PG) in the observer. At this stage, only MEPs recorded from the FDI muscle should reveal a pronounced increase in activation. This is because the PG does not imply the recruitment of the ADM muscle. Furthermore, we predict that when the object possibly eliciting a complementary action is not present, symmetrical facilitation effects should emerge both at the time the first manipulative action (i.e., WHG) is perceived and when observing the model simply stretching her arm out holding the thermos (i.e., WHG).

MATERIALS AND METHODS

Participants

Twenty healthy individuals (15 women and 5 men) aged 20–34 (mean 27 years) took part in the experiment. All were right-handed according to the Standard Handedness Inventory (Briggs & Nebes, 1975). They had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998). All participants gave their written, informed consent prior to their inclusion on the study and were naive 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.

Experimental stimuli

To create the stimulus material, we filmed a model performing four types of action sequences: (1) reaching and grasping a thermos, pouring coffee into three cups and then stretching the arm out as to pour coffee into a fourth cup which was beyond reach distance (Figure 1, panel a); (2) reaching and grasping a thermos, pouring coffee into three cups, and then simply stretching the arm out holding the thermos (Figure 1, panel b); (3) reaching and grasping a sugar shaker, pouring sugar into three cups, and then stretching the arm out to pour



Figure 1. Frames extracted from the four video clips which served as stimuli for the present experiment. Specifically, for all video clips, the onset of the reach-to-grasp movement and the final phase of the action sequence are represented.

sugar into a fourth cup which was beyond reach distance (Figure 1, panel c); (4) reaching and grasping a sugar shaker, pouring sugar into three cups, and then simply stretching the arm out holding the sugar shaker (Figure 1, panel d). The model naturally grasped the

thermos with a WHG, that is, the opposition of the thumb with the other fingers, and the sugar shaker with a PG, that is, the opposition of the thumb with the index finger. As outlined in Figure 2, at the beginning of each video clip, the hand of the model was shown

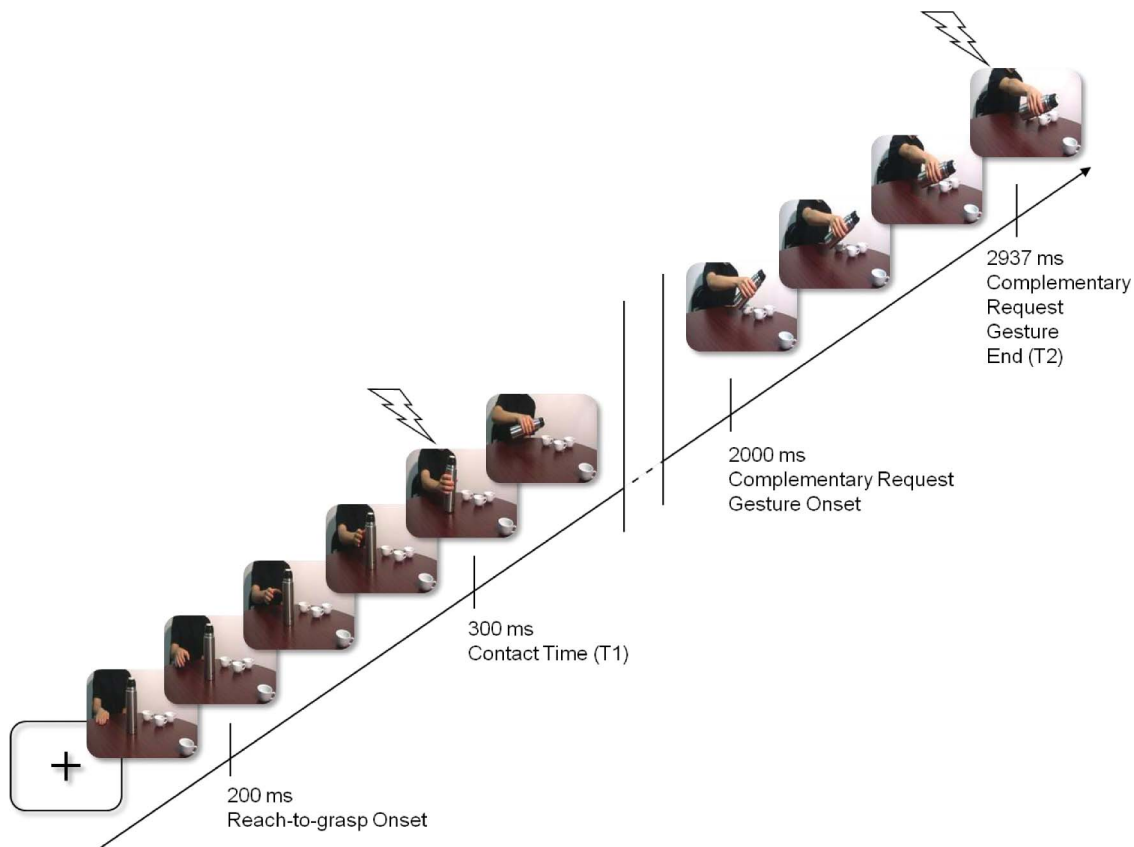


Figure 2. Schematization of events sequence during a single trial is shown. The continuous oblique line represents the duration of video-clip presentation. The vertical lines represent the onset of the reach-to-grasp movement, the time at which the hand contacts the object, the onset of the complementary request gesture, and the completion of the complementary request gesture, respectively. The double vertical bars indicate that there are frames 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.

in a prone position resting on the table. After 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) (Figure 2). After 1700 ms, the model stretched out her arm as if to require a complementary action (i.e., onset of the complementary request), which ended at 2937 ms (Figure 2). The animation effect was obtained by presenting a series of single frames, each lasting 33 ms (resolution 720×576 pixels, with color depth of 24 bits, and frame rate of 30 fps), plus the first and last frames, which lasted 500 and 1000 ms, respectively.

TMS stimulation and MEP recording

TMS was delivered with a 70-mm, figure-of-eight coil connected to a Magstim BiStim² 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, Boniface, & Schubert, 1992). This orientation induced a posterior-anterior current in the brain, which tends to activate corticospinal neurons indirectly via excitatory synaptic inputs (Di Lazzaro et al., 1998). 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 MEP from both the ADM, the muscle serving little finger abduction, and the 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 keep it consistent. 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 the relaxed muscle in 5 out of 10 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. MEPs were recorded simultaneously from electrodes placed over the contralateral ADM and FDI muscles. Electromyographic (EMG) recording was performed through pairs of 9-mm diameter Ag-AgCl surface 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 joint (belly-tendon technique). Electrodes were connected to an isolated portable ExG input box linked to the main

EMG amplifier for signal transmission via twin fiber-optic cables (Professional BrainAmp ExG MR, Brain Products, Munich, Germany). The ground was placed over the participants' left wrist and connected to the common input of the ExG input box. The raw myographic signals were band-pass filtered (20 Hz–1 kHz) and amplified prior to being digitized (5 kHz sampling rate), and stored on a computer for off-line analysis. In order to prevent contamination of MEP measurements by background EMG activity, trials in which any EMG activity greater than $100 \mu\text{V}$ was present in 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-inch monitor (resolution 1280×1024 pixels, refresh frequency 75 Hz, background luminance of 0.5 cd/m^2) 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. For each of the four types of video clips, 10 trials were presented 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 5 MEPs while the participants passively watched a white-colored fixation cross on black background on the computer screen. Another series of 5 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: (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 request gesture (T_2 , 2937 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. This message was replaced by a fixation cross for the remaining 5 s. Five MEPs per muscle 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. Participants underwent the following four experimental conditions.

Complementary PG action

In this condition, participants observed the video clips representing a model performing a WHG as if to handle a thermos filled with coffee and then pouring the coffee into three cups located near her left side. After the coffee was poured into the third cup, the model stretched out her arm as if to pour the coffee into a fourth cup which was located out of reach. From an observer's point of view, this cup was situated on the bottom right corner of the image (Figure 1, panel a). Crucially, this cup afforded a PG movement in order to be handled. Therefore, in this condition, there was a mismatch between the observed model's initial action (i.e., WHG) and the movement the observer would eventually perform as to complete the observed action (i.e., PG). A preliminary pilot investigation on a sample of subjects with similar characteristics to those participating in the experiment indicated that the "fourth" cup strongly afforded a PG by the handle.

Control PG action

In this condition, participants observed the video clips of the model performing the same action sequence as for the "complementary PG action" condition except that the fourth cup was not present (Figure 1, panel b). Therefore, in this condition, the final part of the action sequence was not implying the performance of any complementary action by the observer.

Complementary WHG action

In this condition, participants observed the video clips of a model performing a PG as if to handle a

sugar shaker and then pouring its content into three cups located nearby to her left. After the sugar was poured into the third cup, the model stretched out her arm as if to pour the sugar into a fourth cup which was located out of reach (Figure 1, panel c). Crucially, this cup afforded a WHG movement in order to be handled. Therefore, in this condition, there was a mismatch between the observed model's action (i.e., PG) and the action the observer would eventually perform so as to complete the observed movement (i.e., WHG).

Control WHG action

In this condition, participants observed the video clips of the model performing the same action sequence as for the "complementary WHG action" condition except that the fourth cup was not present (Figure 1, panel d). Therefore, in this condition, the action sequence was not implying the performance of any complementary action by the observer.

Data analysis

For each condition, peak-to-peak amplitudes of the collected MEPs from both the ADM and FDI muscles were measured and averaged at each time point. MEP amplitudes deviating more than 2 *SDs* from the mean for each type of action and trials contaminated by muscular preactivation were excluded as outliers (<2%). A paired-sample *t*-test (two-tailed) was used to compare the amplitude of MEPs recorded from the ADM and FDI 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 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. A repeated-measures analysis of variance (ANOVA) was conducted on the MEP ratios with "condition" (object, no-object), "type of observed 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, $p > .05$). Post hoc, pairwise comparisons were carried out by using *t*-tests, and the Bonferroni correction for multiple comparisons was applied. The comparisons between normalized MEP amplitude and baseline were performed by using one-sample *t*-tests.

RESULTS

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 muscle—235 vs. 297 μV , respectively— $t(19) = -0.87$, $p = .40$, or the FDI muscle—692 vs. 585 μV , respectively— $t(19) = 0.91$, $p = .37$. This suggests that TMS *per se* did not induce any changes in corticospinal excitability in our experimental procedure. Mean MEP ratios from the ADM and the FDI muscles for each “type of condition” (object, no-object), “type of observed grasp” (PG, WHG), and “time” (T_1 , T_2) are reported in Table 1. Given that FDI is recruited for both PG and WHG, we did not expect any MEP modulation in terms of type of observed grasp. Indeed, the repeated-measure ANOVA on normalized MEP amplitude for the FDI muscle showed only a significant main effect of time, $F(1, 19) = 4.65$, $p < .05$, $\eta^2_p = .20$. The repeated-measure ANOVA on normalized MEP amplitudes for the ADM muscle yielded a statistically significant interaction of “condition by type of grasp by time,” $F(1, 19) = 28.81$, $p < .001$, $\eta^2_p = .60$. Normalized mean amplitude for the FDI and the ADM muscles are reported in Table 1.

MEPs are modulated in terms of complementary action

Post hoc comparisons indicated that MEP activation is modulated by the presence/absence of the object calling for a complementary action. Specifically, normalized MEP amplitude for the ADM muscle at T_2 was smaller ($p < .05$) when participants observed the model holding the thermos as if to approach the beyond-reach cup affording a PG (i.e., object condition; Figure 3, panel a) than when participants observed the model simply holding the same thermos with a WHG (i.e., no-object condition; Figure 3, panel a). Conversely, MEP amplitude at T_2 was greater ($p <$

.05) when participants observed the model holding the sugar shaker as if to approach the fourth cup affording a WHG (i.e., object condition; Figure 3, panel b) than when participants observed the model simply holding the same sugar shaker with a PG (i.e., no-object condition; Figure 3, panel b). In contrasting MEPs at T_2 against baseline, there was no ADM muscle activation when the object calling for a complementary action required a PG action, $t(19) = 0.7$, $p = .49$. Similarly, there was no ADM activation when participants observed the model simply holding the sugar shaker with a PG, $t(19) = 0.64$, $p = .53$. The very fact that we did not find any statistically significant difference ($p_s > .05$) between the object and the no-object conditions at T_1 seems to suggest that the mere presence of the fourth cup affording either a PG or a WHG at the early stage of the action sequence was not leading to any priming effect. This should rule out the possibility that differences across conditions may simply depend on the presence/absence of the beyond-reach cup *per se*.

The time-course of complementary activations

In terms of normalized MEP amplitude for the ADM muscle, no difference was noticed across delays (T_1 , T_2) for the no-object conditions ($p_s > .05$). The MEP amplitude evoked at T_1 by the observation of a grasp movement (e.g., PG) was similar to that elicited by the observation of a PG not implying any complementary request at T_2 (Table 1). As expected, statistical differences arose for both the conditions in which the beyond-reach object was present. Specifically, normalized MEP amplitude was larger ($p < .05$) when the TMS pulse was delivered at T_1 during the observation of a WHG on the thermos than at T_2 when participants observed the model holding the same thermos as if to approach the cup affording a PG (Figure 4, panel a). One could argue that inferences about the motor facilitation elicited by a PG relies on null results. However, the lack of differences from baseline was confined to the ADM muscle. As revealed by the analysis on the

TABLE 1

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

| | Implicit complementary action sequences | | | | | | | |
|-----|---|----------------------------|-------------------------------|-------------------------------|----------------------------|----------------------------|-------------------------------|-------------------------------|
| | 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 | 1.31 (± 0.15) | 1.54 (± 0.19) | 1.15 (± 0.16) | 1.4 (± 0.24) | 1.13 (± 0.11) | 1.34 (± 0.16) | 1.15 (± 0.13) | 1.25 (± 0.16) |
| ADM | 1.64 (± 0.28) | 1.07 (± 0.10) | 1.25 (± 0.19) | 1.64 (± 0.23) | 1.10 (± 0.15) | 1.83 (± 0.29) | .29 (± 0.19) | 1.09 (± 0.14) |

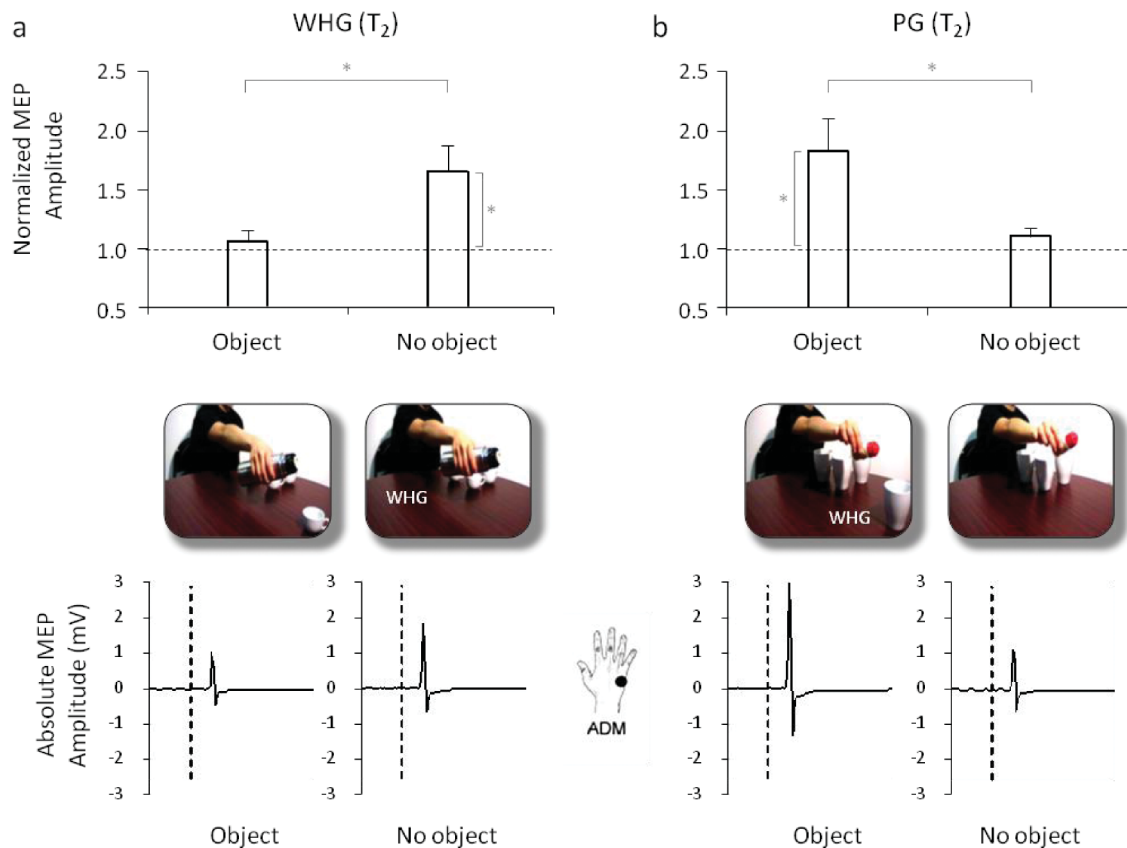


Figure 3. The upper panels represent the means of the normalized MEP amplitudes across conditions (object, no-object) following the observation of either a WHG (a) or a PG (b) at T_2 . Bars represent the *SEM*. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM muscle for one participant across conditions (object, no-object) following the observation of either a WHG (a) or a PG (b).

FDI muscle activity, the normalized MEP amplitude was greater at T_2 than at T_1 (Table 1). In particular, when participants observed the model holding the thermos as if to approach the cup affording a PG, MEP amplitude for the FDI muscle was significantly greater than the baseline, $t(19) = 2.75$, $p = .01$. Coming back to ADM muscle activation, normalized MEP amplitude was smaller during the observation of a PG on the sugar shaker ($p < .05$) at T_1 than at T_2 when participants observed the model holding the same sugar shaker as if to approach the beyond-reach cup affording a WHG (Figure 4, panel b). Altogether, these results indicate a switch from a symmetrical motor resonance to a complementary activation of the ADM muscle during the observation of an action sequence.

MEPs are modulated in terms of the observed type of grasp

In terms of type of grasp, post-hoc comparisons for the ADM muscle revealed statistically significant

differences for both the object and the no-object conditions. In particular, MEP amplitude at T_1 was greater when observing a WHG on the thermos than a PG on the sugar shaker (Figure 5, panel a). This occurred for both conditions at T_1 ($p_s < .05$) (Table 1) despite the presence/absence of the fourth object. This might signify that at the early stage of the action sequence participants were resonating with the model's action and ignoring the action-irrelevant fourth object. And it corroborates the idea that the mere presence of the fourth object affording either a PG or a WHG at the early stage of the action sequence (T_1) was not leading to any priming effect. Therefore, the possibility that the differences observed between the two object conditions might simply depend on the mere presence of the object can be rejected. Regarding T_2 , for the no-object condition, MEP amplitude was greater ($p < .05$) when participants observed the model holding a thermos (i.e., WHG) than when they observed the model holding a sugar shaker (i.e., PG) (Table 1). Conversely, for the object condition, MEP amplitude at T_2 was smaller ($p < .05$) when participants observed

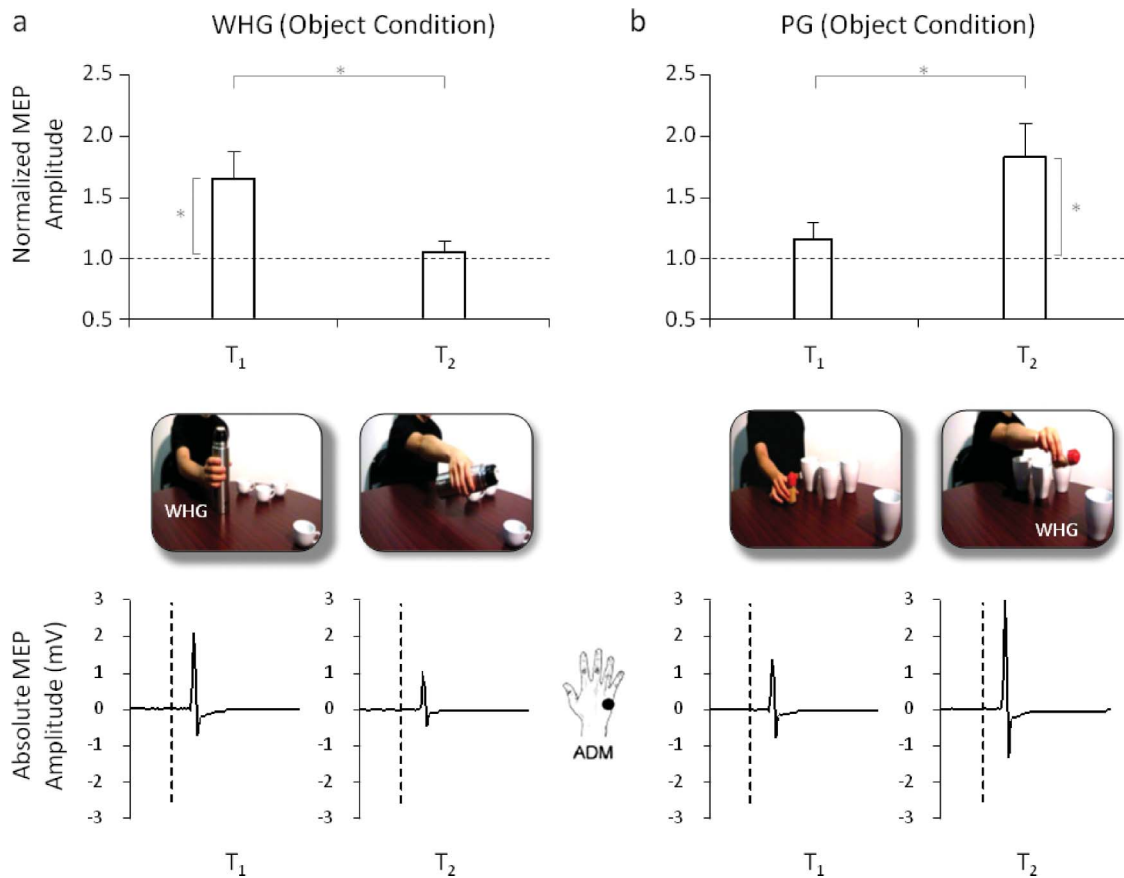


Figure 4. The upper panels represent the means of the normalized MEP amplitudes across the time at which TMS was delivered (T_1 , T_2) following the observation of either a WHG or a PG for the object condition. Bars represent the *SEM*. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM muscle for one participant across the time at which TMS was delivered (T_1 and T_2) following the observation of either a WHG or a PG for the object condition.

the model holding a thermos with a WHG while trying to pour coffee into the fourth cup eliciting a PG than when participants observed the model performing a PG on the sugar shaker as if to approach the fourth cup affording a WHG (Figure 5, panel b).

DISCUSSION

The overarching aim of the present study was to investigate the effect of action observation in complementary contexts. The results suggest that when an observed action calls for a nonidentical complementary action, an interplay between the automatic tendency to resonate with what is observed and to implicitly prepare for the complementary action does emerge. In other words, observed actions embedding an implicit complementary request might have the ability to prime nonidentical responses.

Little is known regarding how the inflexible tendency to match observed actions onto our motor

system can be reconciled with the request to prepare nonidentical responses. In this respect, some investigations have focused on imitation and action observation conditions. For instance, Heyes and colleagues (Catmur et al., 2007; Heyes et al., 2005) showed that the automatic effects of imitation can be abolished following incompatible training. In the same vein, Gowen and colleagues (Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff, 2010) have recently demonstrated that automatic imitation is not as “automatic” as previously thought, but can be influenced by context. In order for visuomotor priming to occur, attention must be directed specifically to the action being performed. Other studies which have begun to consider task context, in the sense of the relation between model and observer, have compared imitation and complementary action tasks (Newman-Nordlund et al., 2007; Ocampo & Kritikos, 2010; van Schie et al., 2008). In behavioral terms, these studies agree that there are differences in preparing and executing complementary actions with respect to imitative actions (Ocampo & Kritikos, 2010;

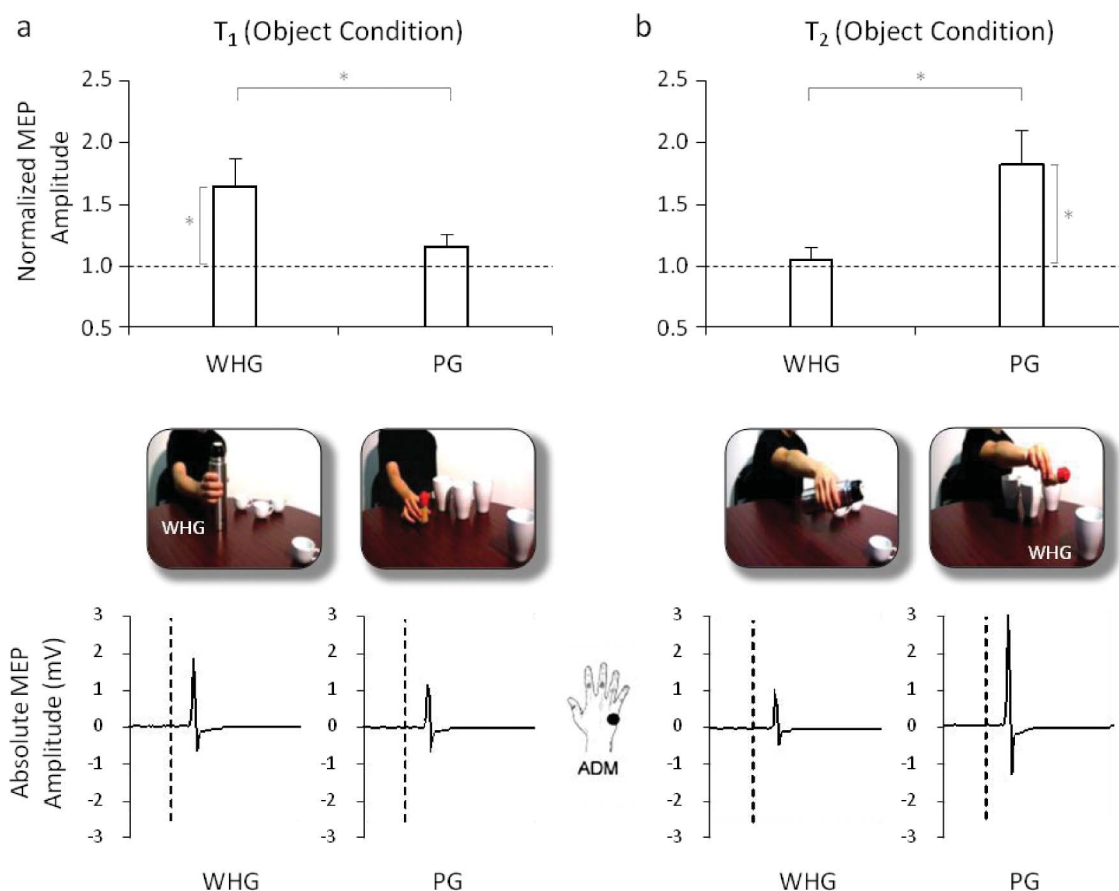


Figure 5. The upper panels represent the means of the normalized MEP amplitudes across types of observed grasp (WHG, PG) recorded at either T₁ (a) or T₂ (b) for the object conditions. Bars represent the SEM. The horizontal dotted line indicates MEP baseline. The lower panels represent a typical MEP recording from the ADM muscle at either T₁ (a) or T₂ (b) for one participant for the object condition following the observation of either a WHG or a PG.

van Schie et al., 2008). In neural terms, greater activation during the preparation of complementary than imitative actions has been found within key areas of the mirror system, namely the inferior frontal gyrus and the inferior parietal lobe (Newman-Nordlund et al., 2007). Our results extend this literature by demonstrating for the first time that corticospinal activation resulting from action observation does not necessarily introduce an imitative bias, but can as well prime motor activation for complementary actions depending on contextual factors. They provide evidence of flexible stimulus-response adjustments, which are a prerequisite when people need to cooperate with and respond to others in a different manner. Interestingly, in contrast to previous studies (e.g., Catmur et al., 2007), here we managed to reveal either symmetrical or complementary *spontaneous* corticospinal activation by avoiding the use of instructions to participants that might have created a bias to mentally matching or complementing the observed action. Our stimuli

had the ability to elicit a switch between the changes in MEP activity classically found following action observation and changes in MEP activity related to the implicit complementary request embedded in the observed stimulus.

Along these lines, a recent fMRI study has revealed that the mirror neuron system is relevant to the planning of both imitative and complementary actions (Newman-Nordlund et al., 2007). The basic idea is that the properties of a specific class of mirror neurons, namely the broadly congruent mirror neurons (Gallese et al., 1996), might have the ability to support the performance of complementary actions. This is because broadly congruent mirror neurons generalize the goal of an action across many types of instances, such as performing a grasping movement with a PG or a WHG (Fogassi & Gallese, 2002; Gallese et al. 1996). Rather, in the present experiment, participants observed an object-related movement which draw attention to an additional object eliciting a different movement. This

might have determined an interplay between “mirror” and “canonical” neurons. This latter type of neuron responds not only during the execution of behaviors, but also during the perception of the objects that are related to these behaviors (Rizzolatti & Craighero, 2004). For instance, canonical motor neurons, which become active during PG movements, also become active upon presentation of a small object graspable by a PG. Conversely, canonical neurons that become active during a WHG are selectively activated when a large object is shown (Murata et al., 1997). In this perspective, the need to perform a complementary action involving a different object might imply a combination of mirror and canonical neurons, coding for different types of actions at different times. Indeed, we found MEP activity strongly indicative of a pure “matching” mechanism at the start of the action sequence and a “complementary” type of MEP activity at the time the request for a complementary action, dictated by contextual factors, became evident. This points to a mechanism for recognizing object affordances (Gibson, 1979) and to the possible existence of a specific type of intentional affordances; that is, “social affordances.” Intentional affordances are produced by the establishment of a shared intentional space (Tomasello, 1999). Indeed, the present results suggest how social affordances might be critical in order to automatically facilitate a complementary motoric response. The crucial aspects of our experiment which favored a readiness to engage in joint action are various. First, there is the presence of objects that are necessary for the action to occur (i.e., a cup that can be held by the perceiver and a thermos/shaker that can be poured by the actor). Second, there is the ability of the observer to virtually take up the object which is facing her. Third, we have the implicit request by the actor that opens up the affordance to engage in joint action. Finally, we have an appropriate relational orientation between actor and perceiver that allows for joint action (i.e., facing rather than behind or to the side; within rather than outside the personal space). In light of this, the present results seem to suggest that automatic responses to another person’s action have to do with the salient affordances about what one could do in this situation. In other words, making affordances salient evokes a readiness to enact them. This is in line with previous demonstrations that visual objects potentiate actions that might be performed on them, even in the absence of explicit intention to act (Buccino et al., 2009; Craighero et al., 1998; Jeannerod, 1994; Tucker & Ellis, 1998).

We are aware that our data cannot provide a detailed description of the time at which the proposed

functional shift occurs. This is because MEPs have only been recorded at two different stages of the action sequence, namely during the first observed action and during the unfolding of the implicit complementary request. Nevertheless, such an approach might be valuable for our understanding of how specific neural networks flexibly adapt when contextual factors dictate a mismatch between observed and performed actions.

Another aspect which particularly depicts the novelty of the present findings is concerned with the use of stimuli which implicitly ask for a complementary action. It might well be that the “complementary” MEP activity recorded at the end of the action sequence stemmed from inferring the intentions behind the observed action. That is, in a manner which is congruent to the intentions of the observer rather than with what the model actually performed. Therefore, with a certain degree of caution, our findings indicate that different intentions might be assigned to a model’s action depending on context (i.e., object presence/absence). Specifically, the context calling for a complementary action induces an enhancement of MEPs, an idea which is in line with the overarching intention to fulfill a specific outcome rather than with the tendency to resonate with the model’s action. This result is not evident when the context within which the model’s action is performed does not subtend a “complementary” intention. This issue might be particularly relevant to understanding how humans coordinate their actions in social situations in which the task at hand does not require simulating the actions of another person (Sebanz, Bekkering, & Knoblich, 2006; Sebanz & Frith, 2004; Sebanz, Knoblich, & Prinz, 2003).

In conclusion, the present findings reconcile the notion that action observation mechanisms inevitably yield to the simulation of what is observed, and therefore might not subserve the performance of non-identical complementary actions, with a more flexible context-dependent view of action observation. Such a perspective entails an interplay between an initial simulation process, which might allow one to experience what is observed, and a process which elaborates the consequences of the initially observed actions in terms of context and intentions.

Although recent studies have impressively extended our view of the motor system and its cognitive functions, the role of the motor system in semantics is largely unexplored and the study of complementary actions is still in its infancy. Many questions remain to be addressed, but future studies might benefit from the present findings for the determination

of the neural mechanisms underlying complex social situations characterized by complementary behaviors.

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