

# Congruent and Incongruent Corticospinal Activations at the Level of Multiple Effectors

Luisa Sartori<sup>1</sup>, Sonia Betti<sup>1</sup>, Chiara Perrone<sup>1</sup>, and Umberto Castiello<sup>1,2</sup>

## Abstract

■ Motor resonance is defined as the subliminal activation of the motor system while observing actions performed by others. However, resonating with another person's actions is not always an appropriate response: In real life, people do not just imitate but rather respond in a suitable fashion. A growing body of neurophysiologic studies has demonstrated that motor resonance can be overridden by complementary motor responses (such as preparing a precision grip on a small object when seeing an open hand in sign of request). In this study, we investigated the relationship between congruent and incongruent corticospinal activations at the level of multiple effectors. The modulation of motor evoked potentials evoked by single-pulse TMS over the motor cortex was assessed in upper and lower limb muscles of participants observing a soccer player performing a

penalty kick straight in their direction. Study results revealed a double dissociation: Seeing the soccer player kicking the ball triggered a motor resonance in the observer's lower limb, whereas the upper limb response afforded by the object was overridden. On the other hand, seeing the ball approaching the observers elicited a complementary motor activation in upper limbs while motor resonance in lower limbs disappeared. Control conditions showing lateral kicks, mimicked kicks, and a ball in penalty area were also included to test the motor coding of object affordances. Results point to a modulation of motor responses in different limbs over the course of action and in function of their relevance in different contexts. We contend that ecologically valid paradigms are now needed to shed light on the motor system functioning in complex forms of interaction. ■

## INTRODUCTION

Findings supporting the hypothesis that there is a basic neurophysiologic system underlying the ability in an onlooker's brain to match another person's body movements with our own motor representations have been drawn from different methodological approaches. Single cell recordings demonstrated the existence of "mirror neurons," which discharged both when a monkey actually grasped 3-D objects and when it observed that action being carried out (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). In humans, single-neuron responses were likewise recorded during both action execution and observation (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010), and neuroimaging studies provided evidence that the fronto-parietal system is implicated in coupling the representations of executed and observed actions (for a review, see Molenberghs, Cunnington, & Mattingley, 2012; Turella, Tubaldi, Erb, Grodd, & Castiello, 2012; Keysers, 2009; Fabbri-Destro & Rizzolatti, 2008; Giorlino & Sinigaglia, 2007; Rizzolatti & Craighero, 2004). Motor resonance is defined as the subliminal modulation of motor pathways, which reproduces in whole or in part the activation normally utilized to execute the observed ac-

tions. In particular, a growing body of neurophysiologic studies have demonstrated that action observation selectively activates the effector muscles involved in performing that action (for a review, see Fadiga, Craighero, & Olivier, 2005). The motor potentials (MEPs) evoked by TMS during action observation appear, in fact, to be specifically attuned to the muscles involved in the action being observed (Sartori, Buccioni, & Castiello, 2012; Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Avenanti, Bolognini, Malavita, & Aglioti, 2007; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006; Strafella & Paus, 2000; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) and to its temporal pattern (Janssen, Steenbergen, & Carson, 2013; Urgesi et al., 2010; Aglioti, Cesari, Romani, & Urgesi, 2008; Borroni & Baldissera, 2008; Borroni, Montagna, Cerri, & Baldissera, 2005; Montagna, Cerri, Borroni, & Baldissera, 2005; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Gangitano, Mottaghy, & Pascual-Leone, 2001).

However, in human social interactions, resonating with another person's action is not always an appropriate reaction (e.g., Hamilton, 2013; Knoblich, Butterfill, & Sebanz, 2011; Sebanz, Bekkering, & Knoblich, 2006). For instance, when we observe someone handing us a mug holding it by its handle, we will, without thinking, grab the mug with a whole-hand grasp (the most appropriate gesture to perform in this situation, although different from that observed). Along these lines, a growing amount of evidence

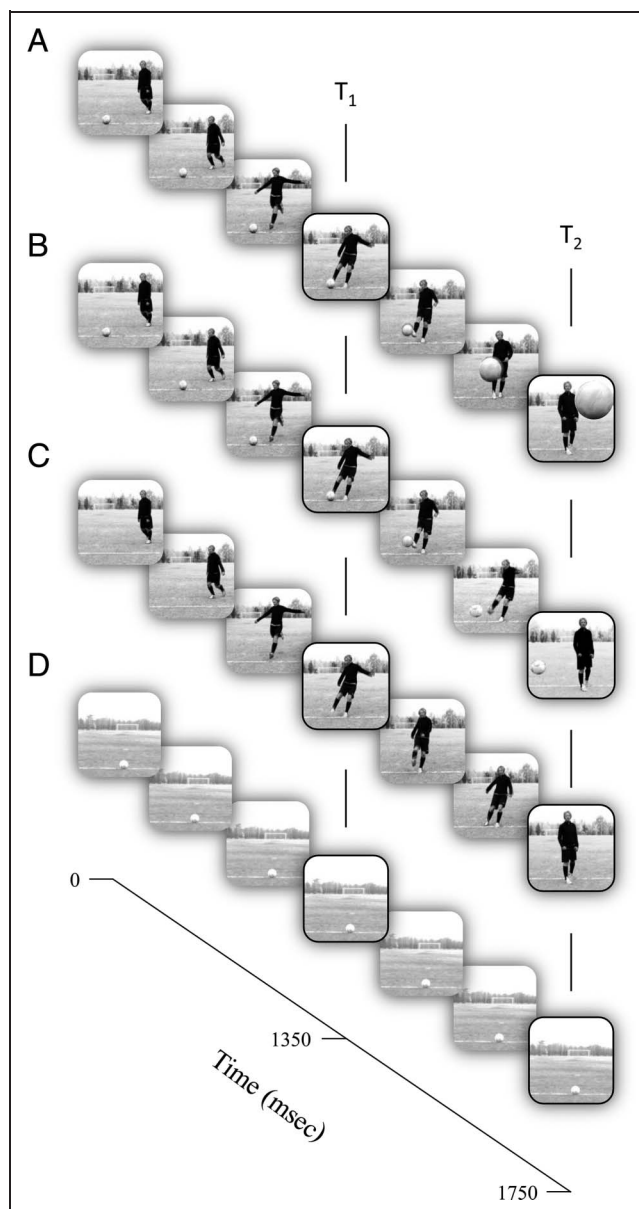
<sup>1</sup>Università di Padova, <sup>2</sup>Accademia Nazionale dei Lincei, Rome, Italy

highlights the interplay between the inflexible tendency to match observed actions onto our motor system and the request to prepare complementary responses with respect to the observed actions (Ocampo, Kritikos, & Cunnington, 2011; Sartori, Cavallo, Bucchioni, & Castiello, 2011; Flach, Press, Badet, & Heyes, 2010; Ocampo & Kritikos, 2010; Sartori, Becchio, Bulgheroni, & Castiello, 2009; van Schie, van Waterschoot, & Bekkering, 2008; Newman-Norlund, Noordzij, Meulenbroek, & Bekkering, 2007). In a series of recent psychophysiological studies, researchers assessed corticospinal (CS) facilitation while participants observed video clips evoking complementary gestures, such as an actor inviting them to pick up a cup placed in the video foreground (Sartori, Betti, & Castiello, 2013a, 2013b; Sartori, Bucchioni, & Castiello, 2013; Sartori, Cavallo, Bucchioni, & Castiello, 2012). Consistent results showed a natural switch from a motor resonant to a complementary activation in CS excitability.

Capitalizing on this literature, here, we asked participants to observe meaningful action sequences, and we avoided imparting instructions to uncover spontaneous congruent and incongruent CS modulations in different limb muscles. In particular, we adopted a paradigm involving videos of penalty kicks in view of the well-established association between observing someone in frontal view kicking a ball far above the ground—straight in our direction—and the spontaneous reaction (i.e., parrying the ball). The effectiveness of this manipulation in priming an upper limb reaction has been confirmed in different studies (Sartori, Betti, Chinellato, & Castiello, 2015; Tomeo, Cesari, Aglioti, & Urgesi, 2013). We thus filmed penalty kicks performed by a soccer player who ran up to a ball and then kicked it straight in the direction of the goal—the place from which the action was filmed and thus the perspective of the person who was watching the video clip (Figure 1A).

Three additional control conditions were also included: Participants were asked to observe the video of a penalty kick that was not directed toward them (Figure 1B) and another kick that was only mimicked, without the ball (Figure 1C). Finally, the image of a soccer ball was shown alone in the penalty area (Figure 1D) to control for the motor coding of object affordances (Tucker & Ellis, 1998; Gibson, 1979). It is well known, indeed, that visual information linked to an object is transformed into appropriate motor commands even in the absence of an explicit intention to act (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Tucker & Ellis, 1998; Jeannerod, 1994). Crucially, soccer balls offer a unique control for our purposes in that they elicit both hand and leg muscles (i.e., contrary to basketballs or baseballs, we not only use our hands for throws but also kick them).

Single-pulse TMS was used to assess CS excitability of participants' hand and leg muscles as they watched the videos. Because participants remained at rest throughout the task, the degree to which the motor system was activated provides an index of activity elicited by action observation.



**Figure 1.** Sequence of events for each condition: (A) Central kick, (B) lateral kick, (C) mimicked kick, and (D) ball. The vertical lines denote the time points when single TMS pulses were delivered: at  $T_1$  (when the player's foot made contact with the ball) and at  $T_2$  (the end of the video clip).

We hypothesize that facing a central penalty kick might prime a complementary motor activation, depending on the action progression. In particular, we expected a motor resonant response in participants' leg muscles during the first part of the video showing a soccer player running and kicking the ball, along with the suppression of upper limb motor responses afforded by the object, and vice versa during the second part of the video. An activation in participants' upper limb muscles was expected along with the suppression of lower limb muscles. We also predict that presenting a simple mimicked kick without the ball would only produce motor resonance in lower limbs, whereas observing a ball in the penalty area should

elicit activation in both limbs because of the motor coding of object affordance. To better control for affordance effects linked to the ball, we included a lateral kick condition, in which the ball was shown disappearing to the left after the kick. We expected that this action would produce motor resonance in the observers' lower limbs, associated with the suppression of upper limb responses. We specifically selected an extensor leg muscle and an abductor hand muscle to rigorously test our predictions because they are typically recruited during kick and parry actions. This allowed us to avoid possible alternative explanations in terms of generalized unspecific activations.

## METHODS

### Participants

Thirty individuals (19 women;  $M_{\text{age}} = 23$  years,  $SD = 2$  years) participated in the experiment. All the participants were right-handed (Briggs & Nebes, 1975), reported right-foot dominance, and had normal or corrected-to-normal visual acuity. As their greater action simulation abilities could have biased the results, individuals with any motor expertise in playing soccer were excluded from the experiment by means of a prescreening procedure. Athletes, in fact, present superior abilities in predicting and anticipating other players' actions (Makris & Urgesi, 2014; Tomeo et al., 2013; Urgesi, Savonitto, Fabbro, & Aglioti, 2012; Abernethy, Zawi, & Jackson, 2008; Aglioti et al., 2008; Weissensteiner, Abernethy, Farrow, & Müller, 2008). Notably, observational practice may contribute to action prediction abilities (Urgesi et al., 2012), and soccer is a quite familiar sport. However, in this case, we presented an action sequence observed from the goal post, and this is quite an uncommon view. None of the participants had any neurological, psychiatric, or other medical problems, nor did they have any contraindication to TMS (Rossi, Hallett, Rossini, Pascual-Leone, & Safety of TMS Consensus Group, 2009; Wassermann, 1998). None was aware of the experiment's purpose, and all gave their written informed consent at the time they were recruited. The study protocol was approved by the ethics committee of the University of Padova and was carried out in accordance with the principles of the Declaration of Helsinki. None of the participants reported experiencing discomfort or adverse effects during the experiment.

### Stimuli

The stimuli were four digitally recorded video clips showing penalty kicks by a professional soccer player (Figure 1A–D): (a) In the first, the player kicked the ball into the goal straight toward the observer; (b) in the second, the player kicked the ball clearly to the left of the camera; (c) in the third, the player mimicked kicking a ball; and (d) in the fourth and last, a static soccer ball was shown. All of the videos were taken from a frontal

view. A 1800-msec sequence was extracted from each of the four videos, which included the player's initial run and the ball's trajectory until it disappeared. The player's foot made contact with the ball approximately 1350 msec after the video began, and the ball trajectory reached its highest peak approximately 400 msec later (1750 msec after onset of the video). The ball was traveling at a velocity of approximately 10 m/sec during its trajectory. An animation effect was obtained by presenting a series of single frames each lasting 25 msec (resolution =  $720 \times 576$  pixels, color depth = 24 bits, frame rate = 30 fps) after the first frame, which lasted 500 msec. A preliminary pilot investigation, carried out with a questionnaire and the assistance of a group of participants with characteristics that were similar to those participating in the study experiment, confirmed that only the central kick (straight toward the observer) led in the onlooker an impulse to react with the hands (98% of positive responses).

### Procedure

The participants were tested individually in a sound-attenuated Faraday room during a single experimental session lasting approximately 40 min and consisting of two blocks (upper limb, lower limb). Each participant was directed to sit in a slightly raised armchair with his or her legs comfortably stretched, the right hand positioned on an arm support, and the head positioned on a fixed head rest. Each was instructed to remain as still and relaxed as possible and to watch the four video clips that were presented on a 19-in. monitor (resolution =  $1280 \times 1024$  pixels, refresh frequency = 75 Hz, background luminance of  $0.5 \text{ cd/m}^2$ ) set at eye level (the eye-screen distance was 80 cm). To ensure that the participants paid attention to the contents of the video clips, they were told that they would be questioned at the end of the session about the visual stimuli presented. TMS-induced MEPs were acquired from the participant's right opponens pollicis (OP) and quadriceps femoris (QF) muscles. Upper and lower limb activity was recorded in separate blocks to precisely identify the optimal scalp locations (OSP) for stimulating each muscle and avoid loss of modulation involving the less stimulated muscle. The order in which the two blocks were presented was counterbalanced across the participants. A single TMS pulse was released during each video presentation at one of two specific time points: (i) during the frame showing the player's foot making contact with the ball ( $T_1$ , 1350 msec) and (ii) during the frame showing the highest peak of the ball's trajectory ( $T_2$ , 1750 msec). The same timing was applied to all of the control conditions. The first time point ( $T_1$ ) was chosen to evaluate the motor resonant response. As recently demonstrated by Lago and Fernandez-del-Olmo (2011), an unspecific motor activation was found in the hand muscles of participants observing an effector before it made contact with an object. When the effector-object interaction was

instead shown, the motor program activated via action observation was muscle specific. The second time point ( $T_2$ ) was set at the highest peak of the ball's trajectory before it disappeared as we intended to maximize the complementary reaction to the stimulus. The order of the videos and the two different TMS delays were randomized within each of the two blocks. One hundred sixty MEPs (2 muscles  $\times$  4 conditions  $\times$  10 repetitions  $\times$  2 time points) were recorded for each participant. Before presenting the videos, each participant's baseline was assessed by acquiring 10 MEPs per block while they passively watched a white-colored fixation cross (10  $\times$  10 mm) on a black background on the computer screen. Ten more MEPs were recorded at the end of each block. By comparing MEP amplitudes recorded during the two baseline series, it was possible to check for any CS excitability changes related to TMS per se in each block. The average amplitude of the two series was then utilized to set each participant's individual baseline for data normalization procedure. An interpulse interval lasting 10 sec was presented between trials to minimize the potential risk of carryover effect of a TMS pulse on the subsequent one. During the first 5 sec of the rest period, a message reminding the participants to keep their hands and legs still and fully relaxed appeared on the screen. Stimuli presentation, EMG recordings, and timing of TMS stimulation were managed by E-Prime V2.0 software (Psychology Software Tools, Pittsburgh, PA) running on a PC.

## Data Recording

### TMS

Single-pulse TMS (pulse characteristics: 100- $\mu$ sec rise time, 1-msec duration) was delivered using a 70-mm figure-of-eight coil (Magstim polyurethane-coated coil) connected to a Magstim BiStim<sup>2</sup> stimulator (The Magstim Company, Carmarthenshire, UK). Pulses were delivered to the left M1 corresponding to the hand and leg regions during the "upper limb" and "lower limb" blocks, respectively. The coil was placed tangentially on the scalp, with the handle pointing laterally and caudally (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). The OSP was determined by moving the intersection of the coil in approximately 0.5-cm steps around the target area until a position was reached at which a maximal MEP amplitude was produced in each target muscle with a minimal stimulation intensity. This position was marked on a tight-fitting cap that each participant was asked to wear. During the experimental sessions, the coil was held by a tripod with an articulated arm. The position and orientation of the coil over the OSP was recorded and loaded into theBrainsight 2.0 neuronavigation system (Rogue Research, Montreal, QC, Canada) to maintain accurate placement of the coil throughout the experiment. Defined as the minimum stimulation intensity on the OSP that induced reliable MEPs

( $\geq 50$ - $\mu$ V peak-to-peak amplitude) in a relaxed muscle in 5 of 10 consecutive trials, the resting motor threshold (rMT) was determined for each participant. rMT ranged from 30% to 62% (mean = 49.2%,  $SD$  = 6%) of the maximum stimulator output in the upper limb block and from 54% to 78% (mean = 64.7%,  $SD$  = 7.2%) in the lower limb one. Stimulation intensity was set at 120% of the rMT to record a clear and stable EMG signal.

### Electromyography

MEPs were recorded from the OP muscle of the right hand and from the QF of the right leg. EMG activity was recorded through pairs of surface Ag-AgCl cup electrodes (9-mm diameter) placed in a belly-tendon montage. The ground electrode was placed over the dorsal part of the wrist during the upper limb block and over the patella of the leg during the lower limb block. The skin impedance condition, evaluated at rest before beginning the experimental session, was considered of good quality when below the threshold level (5 k $\Omega$ ). Electrodes were connected to an isolable portable ExG input box linked to the main EMG digital amplifier for signal transmission via a twin fiber optic cable (Professional BrainAmp ExG MR). The raw myographic signals were band-pass filtered (20 Hz–1 kHz), amplified before being digitalized (5-KHz sampling rate), and stored on a computer for off-line analysis. EMG data were recorded for a 300-msec interval. The interval was time locked to the delivery of the magnetic stimulation pulse and began 100 msec before the onset of stimulation and ended 200 msec after stimulation. Trials in which any EMG activity was present in the time window preceding the TMS pulse were discarded to prevent contamination of MEP measurements by background EMG activity.

### Data Analysis

The CS excitability of OP and QF muscles was quantified at each stimulation point during each experimental condition by the MEP peak-to-peak amplitude (mV). Those amplitudes deviating more than 3  $SD$ s from the mean and the trials contaminated by muscular preactivation were excluded as outliers (<5%). A paired-sample  $t$  test (two-tailed) was used to compare the amplitude of MEPs recorded during the two baseline trials carried out at the beginning and end of each block. Ratios were computed using the participants' individual mean MEP amplitude recorded during the two fixation-cross periods as baseline (MEP ratio = MEP obtained / MEP baseline). We entered the MEP ratios in a repeated-measures ANOVA with Muscle (OP, QF), Type of action (central kick, lateral kick, mimicked kick, ball), and Stimulation time ( $T_1$ ,  $T_2$ ) as within-subject factors. The sphericity of the data was verified before performing statistical analysis (Mauchly's test,  $p > .05$ ). Post hoc pairwise comparisons were carried out using  $t$  tests, and Bonferroni correction was applied to



control  $p$  values for multiple comparisons. A significance threshold of  $p < .05$  was set for all statistical analyses run in IBM SPSS Statistics 21.0 (Armonk, NY).

## RESULTS

The mean raw MEP amplitudes recorded for each participant during the preexperimental and postexperimental sessions were not significantly different for the OP ( $1.127 \pm 0.716$  vs.  $1.013 \pm 0.589$  mV, respectively;  $t(29) = 1.42, p = .17$ ) or QF ( $0.185 \pm 0.092$  vs.  $0.186 \pm 0.089$  mV, respectively;  $t(29) = 0.04, p = .97$ ) muscles. It can be concluded, therefore, that TMS per se induced no changes in CS excitability during the experiment and that modulation of EMG activity was linked exclusively to the different experimental conditions. The ANOVA on normalized MEP amplitudes showed a statistically significant main effect of Time ( $F(1, 29) = 7.21, p < .01, \eta^2_p = 0.20$ ), a two-way interaction of Muscle  $\times$  Time ( $F(1, 29) = 4.26, p < .05, \eta^2_p = 0.13$ ), and a three-way interaction of Muscle  $\times$  Type of action  $\times$  Time ( $F(3, 87) = 7.27, p < .01, \eta^2_p = 0.20$ ). The results obtained from the post hoc contrasts exploring the source of the significant three-way interaction are outlined as follows.

### Motor Resonance in Lower Limb Muscles

In terms of congruent motor activation, watching the player making contact with the ball elicited a higher activity in the participants' lower limbs at the beginning of the video ( $T_1$ ) with respect to the end ( $T_2$ ) in the "central," "lateral," and "mimicked" kick conditions ( $ps < .05$ ; Figure 2A). This decrease did not occur for the "ball" condition ( $p > .05$ ), in which a stable activity was found across time points. Notably, the statistically significant decrease in the central, lateral, and mimicked kick conditions at  $T_2$  was confirmed when compared with the ball condition ( $ps < .05$ , Figure 2A), thus suggesting an in-

hibitory process leading to a dynamic reduction in CS excitability.

### Complementary Motor Activation in Upper Limb Muscles

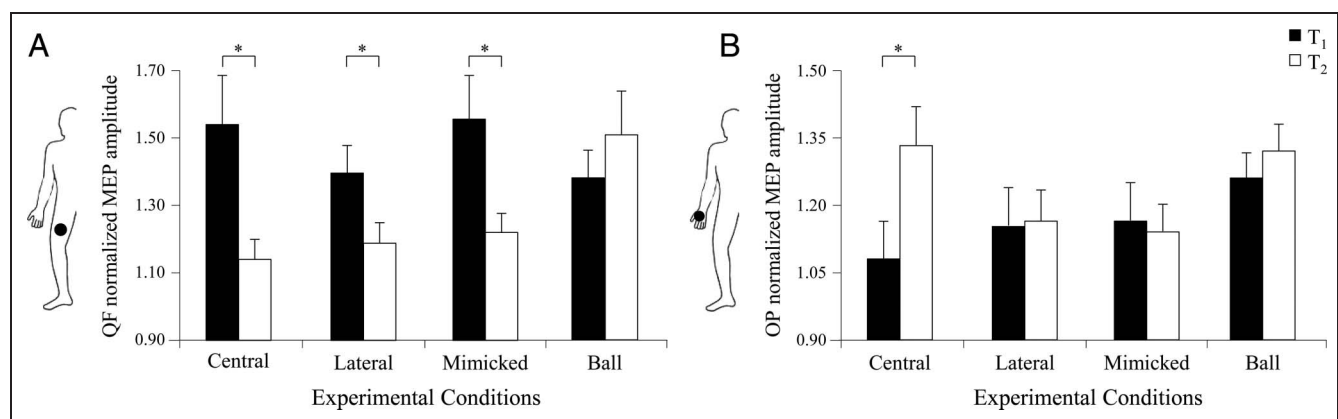
The mean MEP amplitude of the OP muscle was higher at  $T_2$  than at  $T_1$  only for the central kick condition ( $p < .05$ ; Figure 2B). Post hoc comparisons at  $T_2$  confirmed this increased activation with respect to the lateral and mimicked conditions ( $ps < .05$ ; Figure 2B). A significant motor activation in the observer's hand muscle was also found when observing the soccer ball alone in penalty area with respect to the lateral and mimicked conditions ( $p < .05$ ; Figure 2B). This seems to suggest that complementary motor activations are likely linked to object affordance and suitable actions, rather than being a simple by-product of motor imagery (as it might have occurred in the mimicked condition).

### Interaction between Motor Resonance and Complementary Motor Activation

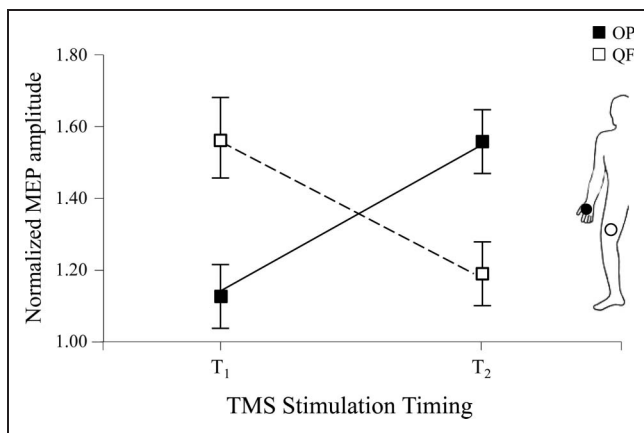
Interestingly, post hoc analyses for the central kick condition showed a statistically significant increase in the leg muscle at the time of contact ( $T_1$ ) compared with the hand muscle ( $p < .05$ ; Figure 3), followed by a larger increase in the hand muscle when the ball approached the viewer ( $T_2$ ) compared with the leg muscle ( $p < .05$ ; Figure 3).

## DISCUSSION

This study examined the modulation of CS excitability during action observation priming for both congruent and incongruent motor responses at the level of multiple effectors. Our experimental findings show an interesting dissociation: an increase in the leg muscle at the time of



**Figure 2.** CS activation during observation of a central, lateral, and mimicked kick and of a ball in penalty area. The graph represents the means of the normalized MEP amplitudes recorded from the QF (A) and OP (B) at  $T_1$  and  $T_2$ . Error bars indicate SEMs. Asterisks indicate statistically significant comparisons across TMS time points ( $p < .05$ ).



**Figure 3.** Interplay between normalized MEP amplitudes recorded from the OP and QF at T<sub>1</sub> and T<sub>2</sub> for the “central” kick condition. Error bars indicate SEMs. Notably, seeing the soccer player kicking the ball at T<sub>1</sub> triggered a statistically significant motor facilitation in the observer’s lower limb muscles (QF) as compared with the upper limb (OP) muscles, whereas seeing the ball approaching the observer at T<sub>2</sub> elicited a statistically significant motor facilitation in the upper limb muscle (OP) as compared with the lower limb (QF) muscle.

contact, followed by an increase in the hand muscle when the ball approaches the viewer.

The study’s findings seem to delineate a sophisticated mechanism that is able to dynamically modulate the observer’s motor reactions at the level of different limbs over the course of the action and as a function of their relevance given different contexts. Producing an internal replica of the observed action is only useful during the first part of the action sequence, while the observed action unfolds. On the other hand, activating the upper limbs is only useful at T<sub>2</sub>, when preparing for a potential interaction. According to the theoretical framework proposed by Chinellato and colleagues (2013), a two-level competition is at the basis of the mechanism for choosing the most suitable responses to an observed action. In the present paradigm, it is necessary not only to activate the motor pattern that matches the observed action (e.g., kicking the ball) and the one that constitutes the appropriate complementary response (e.g., blocking the ball) but also to decide whether either or both should be simultaneously executed (in the above example, kicking should be inhibited to avoid affecting the quality of the blocking response). As the complexity of movement increases, greater CS modulation may be required to uncouple the two limbs, to prevent unwanted mirror movements (Verstynen & Ivry, 2011).

Notably, in the ball condition, a stable motor activation was present across time points. The presence of the ball in the penalty area and the salient affordances about what one could do in this situation (i.e., kick it, but also use our hands for throw-ins) likely evoked a readiness to enact them, which is a disposition to engage in meaningful situations (Di Paolo & De Jaegher, 2012).

In neural terms, this pattern of results might be because of an activation of the canonical neuron networks.

This type of neuron responds not only during the execution of a specific type of action but also during the perception of the objects that are related to this particular action (Rizzolatti & Craighero, 2004). For instance, canonical motor neurons that become active during precision grip movements become also active upon presentation of a small object graspable by a precision grip (Murata et al., 1997). On the contrary, it might well be that the modulation of motor pathways excitability found in participant’s lower limbs while observing a mimicked kick was the product of the activation of classical mirror neurons. The role of the human mirror neuron system has long been debated in the light of different interpretations focusing on its comprehension purposes (i.e., extracting the goals underlying observed actions; Rizzolatti & Sinigaglia, 2010) or on its predictive aspects (Kilner, 2011).

In a recent stimulating review, Hamilton (2013) suggests a third perspective: the social responding hypothesis. In her view, the main purpose of the mirror neuron system would be “to respond, in real-time and in a socially appropriate fashion, to the actions of others” (Hamilton, 2013). Alternatively, the idea of an associative memory able to implement mirroring behavior and adapt through experience to generate complementary responses would also explain our results: The existence of counter-mirror effects might support this hypothesis (Barchiesi & Cattaneo, 2013; Cavallo, Heyes, Becchio, Bird, & Catmur, 2013; Catmur, Walsh, & Heyes, 2007).

In conclusion, the findings presented here take research on the action observation system a step further by showing that the observation of a pure biological movement (i.e., “mimicked” kick condition) is sufficient to produce motor resonance and that an interplay of congruent and incongruent CS activations at the level of multiple effectors might occur, depending on the context.

An aspect that must be emphasized is that the participants in our experiments were not given instructions, which could have created a bias to mentally matching (or not) the observed action, or asked to perform tasks not associated with meaningful behavior in real life. We firmly support the adoption of paradigms that are likely to uncover spontaneous tendencies rather than dispositions formed during the execution of the experimental task itself. Future studies in ecological contexts are needed to assess whether the complementary motor response is generated as a product of a parallel, visually derived associative process.

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Reprint requests should be sent to Luisa Sartori, Dipartimento di Psicologia Generale, Università di Padova, Via Venezia 8, 35131, Padova, Italy, or via e-mail: luisa.sartori@unipd.it.

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