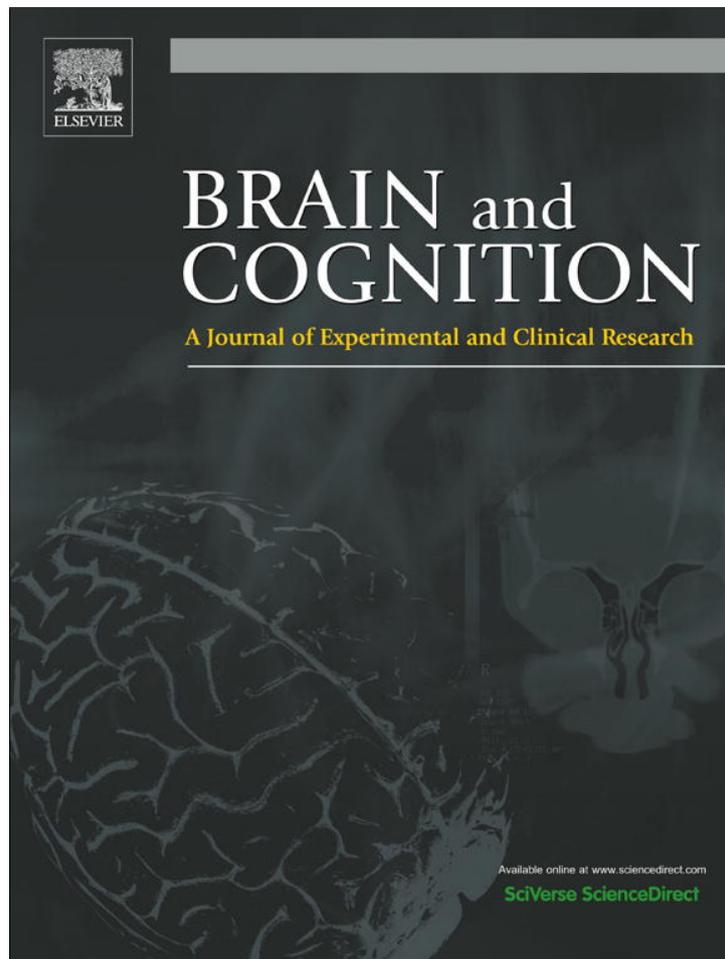


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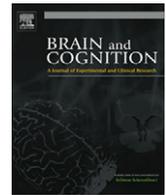
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Corticospinal excitability during the observation of social behavior

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ABSTRACT

Evidence suggests that the observation of an action induces in the observers an enhancement of motor evoked potentials (MEPs) recorded by the observer's muscles corresponding to those involved in the observed action. Although this is a well-studied phenomenon, it remains still unclear how the viewer's motor facilitation is influenced by the social content characterizing the observed scene. In the present study we investigated the facilitation of the corticospinal system during the observation of either an action that does not imply a social interaction (i.e., an actor throwing a ball against a wall), or an action which implies a social interaction (i.e., an actor passing a ball to a partner). Results indicate that MEPs amplitude is enhanced during the observation of a social rather than an individual action. We contend that the increase in MEPs activation might reflect an enhancement of the simulative activity stemming from the mirror system during the observation of social interactions. Altogether these findings show that the human corticospinal system is sensitive to social interactions and may support the role of the mirror neurons system in social cognition.

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1. Introduction

The capability to understand the meaning of others' actions is an essential characteristic for the human adaptation to social and physical environments. Insights into the neural mechanisms of action understanding comes from the discovery of neurons activated during both the execution and the observation of a given action (the so-called mirror neurons) in the monkey premotor and parietal cortices (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001). Following this discovery, neurophysiological (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Hari et al., 1998; Romani, Cesari, Facchini, & Aglioti, 2005) and neuroimaging (Buccino et al., 2001; Decety et al., 1997; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996; Turella, Pierno, Tubaldi, & Castiello, 2009) studies have uncovered a similar system in humans. In particular, it has been suggested that the action observation–execution matching system would offer a parsimonious answer to how it is possible to understand others' behavior. In this view, the observation of another's behavior elicits changes in the cortical and corticospinal activity indicating that, in the observer,

a motor representation for the same act is activated (e.g., Buccino et al., 2001; Fadiga, Craighero, & Olivier, 2005).

More recently, it has been proposed that the action observation–execution matching system is not only modulated by the physical aspects of an action, but also by the social context within which an action is embedded (Becchio et al., 2012; Iacoboni et al., 2004; Kourtis, Sebanz, & Knoblich, 2010; Oberman, Pineda, & Ramachandran, 2007). For example, in a functional magnetic resonance imaging study, Iacoboni et al. (2004) reported an increase in activation within a key 'mirror' area, namely the inferior frontal gyrus, following the observation of a scene depicting two individuals interacting, as compared to a scene depicting one individual engaging in everyday activities. Oberman et al. (2007) measured mu rhythm oscillations (an index of mirror neurons activity), during the observation of actions characterized by a different degree of social interaction. They found a correspondence between the level of mu wave suppression and the degree of social interaction to which the subject was exposed – i.e., the highest amount of mu wave suppression was recorded for the interacting condition. Similarly, Kourtis et al. (2010) by analyzing the amplitude of the contingent negative variation (CNV) and the oscillations of beta rhythm as a measure of anticipation of other's actions, have shown that the simulation of another person's action depends on the degree of social relation between the actor and the observer – i.e., motor resonance is increased when subjects perceived the other person as an interacting partner. Further support to the idea that action simulation is sensitive to the social features characterizing

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an observed action comes from a series of transcranial magnetic stimulation (TMS) studies (Sartori, Buccioni, & Castiello, 2012; Sartori, Cavallo, Buccioni, & Castiello, 2011a; Sartori, Cavallo, Buccioni, & Castiello, 2011b). This series of experiments has shown that corticospinal excitability varies depending on whether the observed action is performed in either an individual or a social context implying a complementary action by the observer.

Although the above evidence is indicative of a social sensitivity by the action observation–execution matching system, the scenarios considered in these experiments called for either an explicit or implicit involvement by the observer in terms of social interaction. What remains unclear is how the system reacts to either social or individual actions that in principle do not imply a first person involvement by the observer. Therefore the key question addressed in the present study is to highlight the role of the action observation–execution matching system in the processing of social stimuli from an external perspective. Specifically, we investigated the degree to which corticospinal excitability would be modulated based on the extent of the social content characterizing an observed action. To this end, we applied single pulse TMS on the participant's left primary motor cortex (M1) and simultaneously recorded motor evoked potentials (MEPs) from the flexor carpi ulnaris (FCU) and the abductor digiti minimi (ADM) while participants observed video-clips depicting the same action embedded in two different contexts: (i) a model passing a ball to a partner (social condition); and (ii) a model throwing a ball against a wall (individual condition). These two muscles are actually involved in the observed action. More specifically, we investigated both the degree to which corticospinal excitability would be modulated based on the social content of a given human action as well as whether the observer becomes somewhat involved by the scene.

2. Materials and methods

2.1. Participants

Twenty-three healthy volunteers (16 men and 7 women) aged 21–26 (mean 22.9 years) took part in the experiment. All were right-handed according to the Standard Handedness Inventory (Briggs & Nebes, 1975), had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998). At the beginning of each experimental session the participant, that was naïve as to the purposes of the study, signed an informed consent; information about the experimental hypothesis was given only at the end of the experiment. The procedures were approved by the ethical committee of the University of Padova and were carried out in accordance with the principles of the 1964 Declaration of Helsinki. None of the participants reported discomfort or adverse effects during TMS.

2.2. Stimuli

Two different types of colored video-clips were used as experimental stimuli: (i) a model standing in profile throwing a ball with her right arm to another actor standing in front of her (social condition; Fig. 1, left panels); and (ii) a model standing in profile throwing a ball with her right arm against a wall (individual condition; Fig. 1, right panels). At the beginning of each video-clip the actor was holding the ball only with her right hand and her left arm was out of view. After 500 ms, the model started her movement. Each video-clip lasted 3000 ms. The animation effect was obtained by presenting series of single frames each lasting 30 ms (resolution 720 × 576 pixels, with color depth of 24 bits, and frame rate of 30 fps). Only the first and the last frame lasted 500 ms and

1000 ms, respectively. In order to avoid any effect related to the interpretation of gaze we adopted a spatial occlusion procedure: the head of the models was not shown in the video clips.

2.3. Stimulation and recording

TMS pulses were administered by using the Master Magstim 200 Unit of a Magstim Bistim² stimulator (Magstim, Whitlan, Dyfed, Wales, UK) connected to a 70 mm figure-of-eight coil positioned over the left primary motor cortex (M1) corresponding to the hand region and was fixed tangentially to the scalp with the handle pointing backwards and laterally with a 45° angle to the midline. This orientation permits to achieve the lowest motor threshold, optimizing the stimulation (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). The coil was kept stable by a tripod in correspondence with the optimal scalp position (OSP), defined as the position from which MEPs with maximal amplitude were recorded simultaneously from the flexor carpi ulnaris (FCU, the muscle involved in forearm flexion) and the abductor digiti minimi (ADM, the muscle involved in little finger abduction). These two muscles have been chosen because they are involved when the observed action is performed. Activity at the level of the ADM and FCU muscles might differ across conditions because of the need to maximize the level of accuracy by the ADM muscle in handling the ball and by the FCU muscle in determining a precise direction to the ball when the task implies a precise pass to another person (i.e., social condition) rather when the task implies to throw a ball against a wall (i.e., individual condition).

The OSP was found for each subject moving the coil in steps of 1 cm around M1. Then the individual resting motor threshold (rMT) was determined as the lowest stimulus intensity that induced at least five MEPs (no less than 50 μV of pick-to-pick amplitude) out of ten consecutive TMS pulses in both the considered muscles (Rossini et al., 1994). During the recording session stimulation intensity was 110% of the rMT and it ranged from 47% to 67% (mean 59.3%) of the maximum stimulation intensity.

MEPs were recorded simultaneously from the FCU and the ADM muscles of the right limb. For recording the electromyographic (EMG) signal from both muscles two couples of surface Ag–AgCl electrodes (9 mm diameter) were used. The belly–tendon technique was applied for the electrode montage: one electrode of the couple was placed over the muscle belly, the second one was placed over the joint or tendon. Electrodes were connected to an isolated portable ExG input box linked to the main EMG amplifier for signal transmission via twin fiber optic cable (Professional BrainAmp ExG MR; Brain Products, Munich, Germany). The ground was placed over the participants' left wrist and connected to the common input of the ExG input box. In the recording session EMG signals were sampled, amplified, band-pass filtered (20 Hz–2 kHz), and stored on a PC for off-line analysis. In order to prevent contaminations of MEPs by background EMG activity, a window of 100 ms before TMS pulse was used to check for trials with any background activity greater than 100 μV. EMG data were collected for 200 ms after the TMS pulse and trials contaminated were excluded from MEP analysis.

2.4. Procedure

Participants were tested in a single experimental session lasting 40 min approximately. Experimentation was carried out in a dimly illuminated room in which each subject sat in a comfortable armchair in front of a 19-in. monitor (resolution 1280 × 1024 pixels, refresh frequency 75 Hz, background luminance of 0.5 cd/m²) set at the eye–screen distance of 80 cm. The right arm was positioned on a pillow and the head was positioned on a fixed head rest. Participants were instructed to fully relax their muscles and to pay

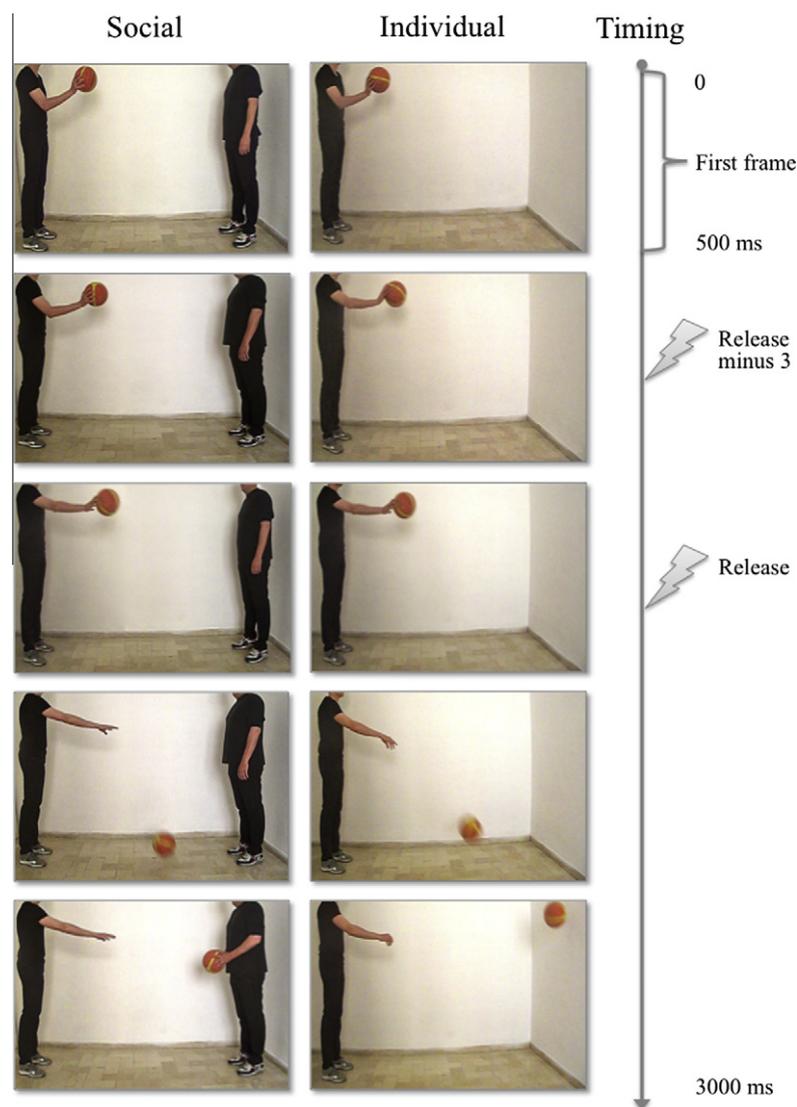


Fig. 1. Schematization of the event sequencing during a single trial for the social (left panels) and individual conditions (right panels). The “light” symbols along the timeline represent the two trigger delays at which the single TMS pulse was delivered: three frames before the detachment of fingers from the ball (release-minus-three, $R - 3$) and the frame that shows the detachment of fingers from the ball (release, R).

attention to the visual stimuli. As a control for attention, they were told they would be questioned at the end of the experiment about what they had seen. Baseline corticospinal excitability was assessed at the beginning and at the end of each experimental session recording two series of ten MEPs while participants passively observed a white-colored fixation cross presented on a black background on the computer screen. Comparisons of MEP amplitudes for the two series allowed us to check for any corticospinal excitability change related to TMS per se.

For each video-clip a single MEP from the right FCU and the right ADM muscles was acquired. For each condition (social and individual) the magnetic pulse was randomly delivered at two different delays: (i) on the frame showing the detachment of fingers from the ball (release, R); (ii) three frames before the frame showing the detachment of fingers from the ball (release minus three, $R - 3$). These different trigger delays were set just to control for simulation effects occurring before the start of the action and that could affect MEP size. Twelve trials were presented for each of the two types of video-clips for the two delays, for a total of 48 trials. The order of presentation of the trials was randomized across participants. The inter trial interval ranged from 13–14 s: during

the first 5 s a message was presented on the PC screen informing participants to keep their limbs still and fully relaxed, than this was replaced by a fixation cross for the remaining 5 s. This inter-pulse interval, based on the research by Chen et al. (1997), ensures that none experimental effect may be caused to TMS per se. In fact, it was shown that even 1 h of repetitive TMS at 0.1 Hz did not induce any change in corticospinal excitability (ibid). Stimulus-presentation timing, randomization of stimuli and TMS triggering were controlled by using E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA) running on a PC. Another PC was equipped with Brain Vision Recorder software for the EMG recording (Brain Products GmbH, Munich, Germany).

2.5. Data analysis

Data were analyzed off-line using Brain Vision Analyzer software (Brain Products GmbH, Munich, Germany) and SPSS 17.0.1 (SPSS Inc., Chicago, IL, USA). MEP amplitudes that fell two standard deviations above or below each individual mean for the two experimental conditions and single trials contaminated by muscular pre-activation were excluded respectively as outliers (1%) and

Table 1

MEPs amplitudes recorded during baseline blocks together with the mean for normalized and log-transformed MEPs data at the two trigger delays for the two experimental conditions.

	Baseline		Social condition			Individual condition		
	B1	B2	R – 3	R	Mean	R – 3	R	Mean
FCU raw (μ V)	282	255						
Normalized			1.29	1.30	1.29	1.15	1.13	1.14
Log transformed			0.33	0.34	0.35	0.32	0.32	0.32
ADM raw (μ V)	410	374						
Normalized			1.39	1.30	1.34	1.14	1.00	1.07
Log transformed			0.37	0.35	0.36	0.33	0.29	0.31

Note: FCU: from the flexor carpi ulnaris. ADM: abductor digiti minimi. B1: baseline block recorded at the start of the experimental session. B2: baseline block recorded at the end of the experimental session. R – 3: release-minus-three. R: release).

precontracted trials (<1% of total). Individual mean peak-to-peak amplitudes of the collected MEPs recorded from the FCU and ADM muscles were separately measured and averaged for the two baseline blocks, the two experimental conditions (social, individual) and the two different trigger delays (R , $R - 3$). The individual mean amplitude of MEPs recorded from the FCU and ADM muscles in the two series of trials presented at the beginning and at the end of the experimental session served as baseline. A paired sample t -test (2-tailed) was used to compare the amplitude of MEPs collected from the two muscles in the baseline trials. For both participants' muscles, MEP amplitudes were converted into a proportion of the baseline value and a logarithmic transformation was applied to the mean MEP size in order to normalize data distribution. In particular, to address non-normality resulting from positive skew, \log_{10} and constant value of 1 were chosen while maintaining as closely as possible the order and spacing of the original distribution (Osborne, 2002). The log-transformed data, calculated for each muscle separately, were embedded into a $2 \times 2 \times 2$ repeated-measures ANOVAs with muscle (FCU, ADM), type of action (social, individual) and trigger delay (R , $R - 3$) as within-subjects factors. Before performing statistical analysis all data were inspected for adherence to the assumptions of ANOVA and in particular it was checked the Sphericity of the data with the Mauchly's test ($P > 0.05$). Post hoc pairwise comparisons were carried out by using t -tests, and Bonferroni corrections were applied. Differences were considered statistically significant when the probability P of a type I error was < 0.05 .

3. Results

Mean raw MEP amplitudes during the two baseline blocks run at the beginning and at the end of the experimental session were not significantly different for either the FCU ($t_{22} = 1.713$, $P = 0.101$) or the ADM muscle ($t_{22} = 1.046$, $P = 0.307$). This suggests that TMS per se did not induce any changes in corticospinal excitability in our experimental procedures. Table 1 shows mean raw MEP amplitudes recorded from the FCU and ADM muscles during the two baseline blocks, the two conditions (social and individual) and the two different trigger delays ($R - 3$, R). The $2 \times 2 \times 2$ ANOVA on normalized MEP amplitudes yielded a statistically significant main effect of type of action [$F_{(1,22)} = 9.528$, $P < 0.01$]. This indicates that MEPs activation is modulated by the social nature of the action independently from the type of muscle and trigger delay (Fig. 2). Specifically, MEP amplitude for both FCU and ADM muscles were greater for the social than for the individual condition (Fig. 2). The main effects of muscle [$F_{(1,22)} = 0.083$, $P = 0.776$] and trigger delay [$F_{(1,22)} = 1.725$, $P = 0.203$], as well as all the interactions, were not significant.

4. Discussion

Understanding the relations between others is a crucial unique component of human social cognition that we can easily recognize

in a variety of everyday life situations. Predicting the behavior of others as well as planning one's own action in a social context presupposes this ability. Discriminating whether they act on one's own or are engaged in interaction may be regarded as a first, basic step in representing social relations. In our experiment participants were requested to observe social or individual actions. We showed that corticospinal excitability was greater during the observation of social interactions as compared to individual actions.

Previous understanding of the role played by the action observation execution matching system in coding social interaction has been confined to on-line interactions or situations implying an implicit request to socially interact. Here we demonstrate that corticospinal excitability is sensitive to the observation of social interaction between agents that, in principle, should not involve the observer. Crucially, MEPs activity seems to be substantially increased by the social content of an observed action. A results which is in line with previous evidence of a role played by the action observation/execution matching mechanism in social cognition (Becchio et al., 2012; Kourti et al., 2010; Oberman et al., 2007; Sartori et al., 2011a,b; 2012). A mechanism that has typically being interpreted in the terms of the "mirror system".

In this connection, the present findings are in line with the idea that the mirror system may play a pivotal role in social understanding even when, as in our study, the top-down bias due to face perception (for a review see Brown & Brüne, 2012) is controlled by showing headless bodies. Support to the social understanding contention comes from research demonstrating a link between the action observation–execution matching system and social cognition (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Kaplan & Iacoboni, 2006; Sebanz, Rebbelch, Knoblich, Prinz, & Frith, 2007; Theoret et al., 2005). Of relevance, it has been posited that the action observation–execution matching system is more attuned to social than individual behavior. In other words, mirror system activation could be enhanced for the observation of motor behaviors that occur within a social context (Iacoboni et al., 2004; Kourti et al., 2010; Oberman et al., 2007). For instance, using fMRI, Iacoboni et al. (2004) observed increased inferior frontal gyrus (IFG) activation when viewing everyday activities in which two people interacted compared with individual activity. In a similar vein, Oberman et al. (2007) found increased "mu suppression" while viewing cooperative behaviors when compared with individual behavior, and further increased mu suppression when viewing behavior that suggested an interaction between the actor and the observer. The present study extends this literature by revealing that our social stimuli appear to produce an increase in corticospinal excitability. And it suggests that this system is also sensitive to the degree of sociality, as evidenced by the modulation in the degree of MEPs activity between the two experimental conditions. This characteristic might provide a link between simple action observation and more complex social skills.

Continuing on this analysis, other recent studies have found increased activation of regions implicated in mirror system during

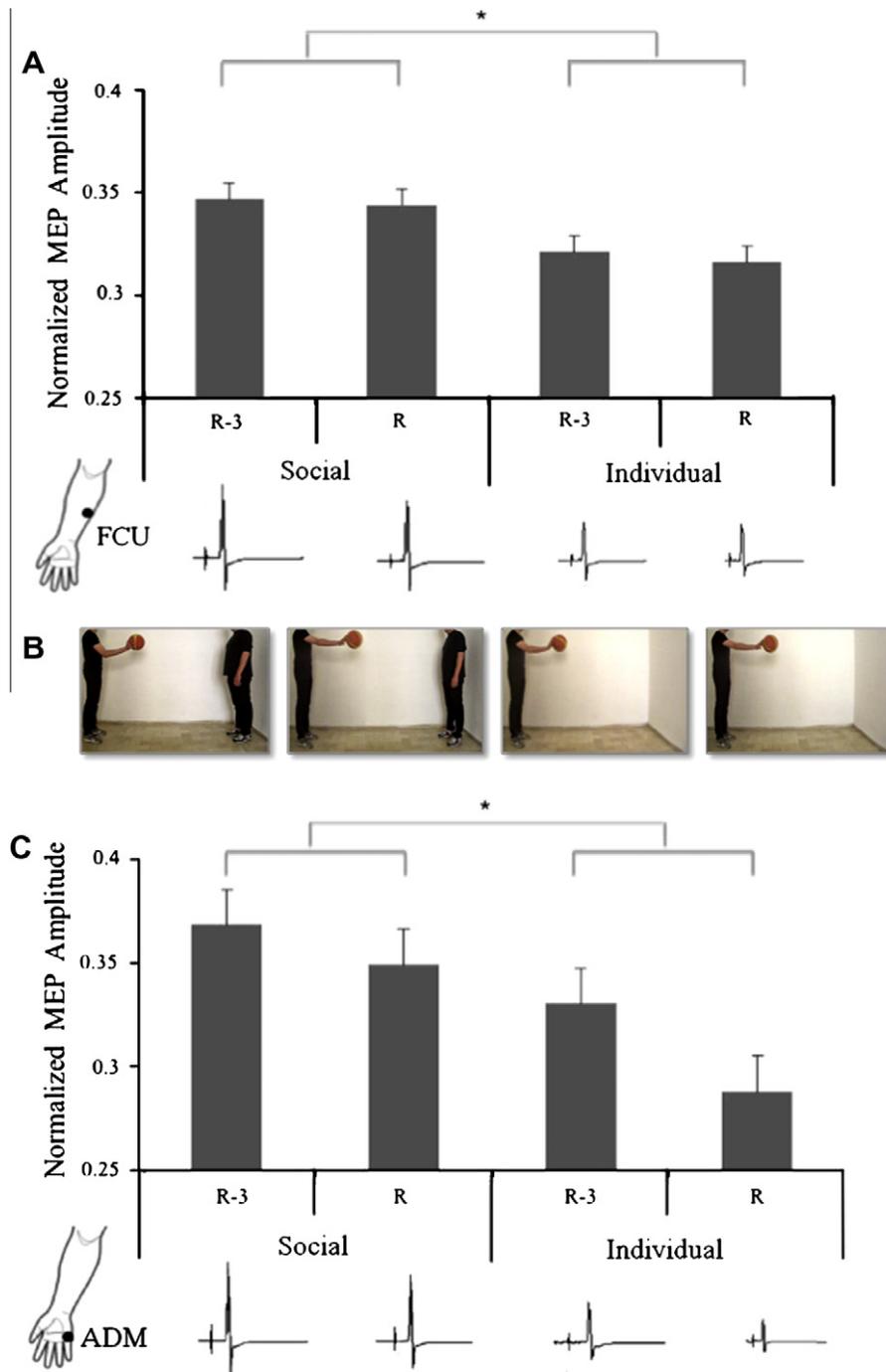


Fig. 2. Panel A and Panel C: Means of the normalized peak-to-peak amplitude scores from the FCU (A) and the ADM (C) muscles recorded during the observation of the two conditions (social, individual) with two different trigger delays (release-minus-three, R – 3 and release, R). Vertical bars represent the standard error of means. Asterisks indicate significant post hoc comparisons ($P < 0.05$). Beneath each graph the typical FCU (A) and ADM (C) MEPs for social and individual actions and for the two moments at which the magnetic pulse was delivered are represented. Black dots on the limbs figures indicate to which muscle MEPs data refer to. Panel B: Graphical representation of the frames presented to participants for the two experimental conditions.

the coordination of joint and complementary actions (Newman-Nordlund, Bosga, Meulenbroek, & Bekkering, 2008; Newman-Nordlund, van Schie, van Zuijlen, & Bekkering, 2007; Sartori et al., 2011a,b; 2012). As an example, Newman-Nordlund et al. (2008, 2007) reported greater mirror system activity as participants prepared for complementary rather than imitative actions, and during partnered rather than solitary virtual tasks. These findings have been substantiated by a series of TMS studies reporting that observing a two-step action characterized by an implicit,

complementary request by the observer determined a greater motor facilitation than when actions not implying a complementary request were being observed (Sartori et al., 2011a,b; 2012).

An alternative possibility is that, compared to the observation of a single agent, observing an action involving two agents might determine an higher level of perceived goal-directness for that specific action (Donne, Enticott, Rinehart, & Fitzgerald, 2011). In this perspective, the increase in CSE could be due to an enhancement of goal processing rather than to the social nature of the observed

action. Therefore it might well be that in the present study the processing of the goal underlying the very same action, that is throwing the ball, become more prominent when there were two agents interacting. Along these lines, it should be noticed that the enhancement in CSE due to the observation of interacting agents might also be due to emotional elements (Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2011). To elaborate, Enticott et al. (2011) claimed that the inclusion of an interactive context might not be sufficient to modulate CSE without an interpersonal understanding facilitation driven by stronger emotional elements. Unfortunately this is an aspect that our experimental design as well as that by Donne et al. (2011) does not allow to address.

Finally, we cannot exclude that the observer's corticospinal excitability was not only driven by the observation of the passing action, but attuned to the complementary response that the receiving agent performed. Indeed, in order to take hold of the ball properly a similar muscular mobilization should have been put in place by a receiving agent. In this view, the brain's ability to mirror motor integration processes while observing social actions might help an onlooker to perceive what people are doing and to predict their motor alternatives. Tracking the behavior of conspecifics in real time to generate predictions of the unfolding action would allow the perceiver to rapidly interpret the perceptual signal, to react quickly, and to disambiguate what is observed (Wilson & Knoblich, 2005).

Furthermore, given the complementary nature of the observed action, what might have occurred is that the observer herself prepared for the complementary action. And the pattern of muscular activity reflected the inclination to prepare for the complementary gesture. Thus, associations would be made between the observed action and the movement needed to accomplish a complementary goal. This idea might imply that MEPs are greater when the stimulus is social because of the level of personal involvement (Decety & Sommerville, 2003; Schilbach et al., 2006). Although in our study participants were not personally involved, but simply observed a triadic interaction between two agents (off-line triadic interaction), it might well be that the complementary "call" is so powerful as to inevitably determine a personal involvement by the observer.

5. Conclusions

Here we propose three main possibilities for explaining the reported increase in corticospinal excitability for the social rather than the individual condition. First, a generalized enhancement of the mirror system activity for observed actions occurring within a social context. Second, a greater simulation of the muscular pattern evidenced by the passing agent. Third, a simulation of the complementary response that the receiver (or the observer herself) should perform. Unfortunately, limitations in the experimental design do not allow espousing one idea with respect to the others. What remains to be investigated is whether the level of perceived sociality of the showed stimuli as well as the observation of two interacting agents are able to determine a better comprehension of other's behavior. Emotional elements driven by the presence of an interaction between two agents, together with a better awareness of the goal of the action might have also generated an enhancement of CSE. Further research considering separate measures of social cognition and action comprehension is needed. Another aspect that future studies should consider is the recording of MEPs from muscles that are differently involved in terms of the action performed by the interacting agents at different time points during observation. This might allow to dissociate between the proposed hypotheses and confirm at what stage the information regarding social content is processed. Nevertheless the present study corroborates an implication of the mirror systems in social

cognition. It supports the contention that observation of behavior that occurs within a social interactive context yields greater activation in the primary motor cortex.

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