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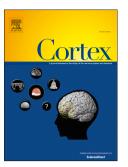
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Equal kinematics and visual context but different purposes:

Observer's moral rules modulate motor resonance

Laila Craighero¹* and Sonia Mele¹

¹Dipartimento di Scienze Biomediche e Chirurgico Specialistiche, Università di Ferrara, via Fossato di Mortara 17/19, 44100 Ferrara, Italy.

*Corresponding author:

Address: Laila Craighero, Dipartimento di Scienze Biomediche e Chirurgico Specialistiche, Università di Ferrara, via Fossato di Mortara 17/19, 44100 Ferrara, Italy.

Telephone number: +39 0532 455928;

fax number: +39 0532 455242.

E-mail address: crh@unife.it (L. Craighero).

ORCID: 0000-0002-5400-8732

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Abstract

Motor resonance is considered to be an index of the automatic under threshold motor replica of the observed action. Similar actions may be quite different in terms of long-term goals (e.g., grasp to eat vs grasp to throw) and, recently, it has been proposed that the distal goal subtle modulates movements execution, and that observers automatically use these differences in kinematics to discriminate between different intentions. This interpretation is in line with computational approaches proposing that in the agent the generative process causes that intention shapes the kinematics, and in the observer the recognition process causes that the kinematics cues the intention. Given the close entanglement between the two processes, here we investigated whether the mere knowledge of agent's intentions induces in the observer a generative process able to modulate motor resonance. We used transcranial magnetic stimulation to examine motor evoked potentials in the Opponens Pollicis muscle to verify if observer's knowledge of agent's positive, negative, or neutral intentions on a third person influences corticospinal excitability during observation of the same action performed with equal kinematics, and in the same visual context. Results showed that the observation of an action executed with the intention to induce negative effects determined a reduction of motor resonance, revealing the presence of a specific inhibition to reenact an action that results in unpleasant consequences in the other. These data suggest that the information at the intention level activates a generative process which overcomes the replica of kinematics at the goal level, and shapes motor resonance according with observer's mind and not with agent's intention, revealing the possibility of a mere cognitive influence on motor resonance based on individual's ethical values.

1. Introduction

To ring a door bell is a socially accepted action whenever the agent is a respectful person interested in meeting the house inhabitants and having as purpose a friendly interaction. However, exactly the same action on the same bell, executed by the same person, and performed with the same kinematics, may be considered unfair by most people if the agent has the purpose to make a joke and get away immediately after ringing. The question posed in the present study concerns the possibility that the knowledge of the agent's intentions can modulate motor resonance in the observer, even when the action and the visual context are maintained constant. Motor resonance is considered to be an index of the automatic motor replica of the observed action, typically measured by recording motor evoked potentials (MEPs) from a given muscle in response to single-pulse transcranial magnetic stimulation (TMS) of the primary motor cortex (M1) (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). MEPs modulation is considered to reflect changes in corticospinal (CS) excitability induced by the activity of various brain regions connected with M1 and involved in the concomitant task. Many experiments have shown that motor resonance is fine-grained and occurs according to somatotopic rules (Borroni & Baldissera, 2008; Brighina, La Bua, Oliveri, Piazza, & Fierro, 2000; Clark, Tremblay, & Ste-Marie, 2004; Gangitano, Mottaghy, & Pascual-Leone, 2001; Montagna, Cerri, Borroni, & Baldissera, 2005). Furthermore, studies indicated that the motor replica is automatic, since somatotopic specificity is present even when the individual is not aware of the use of muscles necessary to perform the action (see Fadiga et al., 1995). Embodied theories of cognition (Decety & Chaminade 2004; Gallese 2003, 2008; Keysers & Gazzola 2007), claim that this motor replica supports action perception and recognition since this automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual (Rizzolatti & Craighero, 2004). Indeed,

studies investigating the perception of intransitive actions, such as phoneme discrimination (Ito, Tiede, & Ostry, 2009), and categorization of facial expressions (Mele, Ghirardi, & Craighero, 2017), clearly showed that the sensorimotor system is involved in action perception, given that the implementation in the observer of low-level movement details influences the discrimination of ambiguous stimuli differing for a specific involvement of those movement details. The possibility to demonstrate that the sensorimotor system is similarly involved during the perception of transitive actions is, however, more difficult, since on the same object, the same goal may be achieved by using different effectors, or by using the same effector in different ways (Borroni, Gorini, Riva, Bouchard, & Cerri, 2011; Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Cattaneo, Maule, Barchiesi, & Rizzolatti, 2013; Cavallo, Becchio, Sartori, Bucchioni, & Castiello, 2012; Cavallo, Sartori, & Castiello, 2011; Sartori, Xompero, Bucchioni, & Castiello, 2012; Sartori, Bucchioni, & Castiello, 2012). Moreover, in real life situations, the goal of the action is never restricted to "grasp an object", and grasping is usually executed to move the object from one position to another, to give it to someone, to eat it, or to do something else, and, therefore, similar actions may be quite different in terms of higher order goals. Consequently, Kilner, Friston, and Frith (2007), inspired by Hamilton and Grafton (2008), proposed that actions can be described at four levels: "(1) The intention level that defines the long-term goal of an action. (2) The goal level that describes short-term goals that are necessary to achieve the long-term intention. (3) The kinematic level that describes the shape of the hand and the movement of the arm in space and time. (4) The muscle level that describes the pattern of muscle activity required to execute the action. Therefore, to understand the intentions or goals of an observed action, the observer must be able to describe the observed movement at either the goal level or the intention level having only access to a visual representation of the kinematic level". A series of kinematic and behavioural studies has indeed proven that this possibility is feasible. In

fact, several findings showed that the distal goal of the action influences movements execution (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Naish, Reader, Houston-Price, Bremner, & Holmes, 2013; Sartori, Becchio, Bara, & Castiello, 2009), and indicated that observers are sensitive to these differences in kinematics, and use them to discriminate between movements performed with different intentions (Ansuini et al., 2016; Manera, Becchio, Cavallo, Sartori, & Castiello, 2011; Sartori, Becchio, & Castiello, 2011). Further results have also proven that, during action observation, motor resonance is modulated by the subtle differences in movement kinematics characterizing similar actions performed with different intentions (Finisguerra, Amoruso, Makris, & Urgesi, 2016; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013). It has been proposed that this kinematically consistent replica of the observed action allows the cueing of the agent's intention, prompted by the knowledge of the sensory consequences of that specific kinematics (Ansuini, Cavallo, Bertone, & Becchio, 2014). This interpretation is in accord with computational approaches to action execution and recognition (Craighero, Metta, Sandini, & Fadiga, 2007; Kilner et al., 2007; Wolpert, Doya, & Kawato, 2003; Wolpert, Ghahramani, & Flanagan, 2001) claiming that, in the recognition model, visual information "is passed by forward connections ... from lowlevel representations of the movement kinematics to high-level representations of intentions subtending the action", and that this model operates by the inversion of a generative model, where "the generative model produces a sensory representation of the kinematic level of an action given the information at the goals or intentions level" (quoted sentences from Kilner et al., 2007). Therefore, while in the agent the generative process causes that intention shapes the kinematics, in the observer the recognition process causes that the observed kinematics cues the intention. However, consistent with this close entanglement between the two processes, it is also possible that contextual cues can trigger a generative process (i.e., a

covert motor program) in the observer, consequently modulating motor resonance. This is suggested by a series of studies that showed that, during observation of the same action, different visual contexts modulate corticospinal excitability. Specifically, motor facilitation increased during observation of actions executed in a social context (Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013), while it was cancelled in the presence of a mismatch between kinematics and explicit action-related semantic cues (Senot et al., 2011), or situational contexts (Amoruso, Finisguerra & Urgesi, 2016), or intrinsic properties of the tobe-grasped object (Craighero, Zorzi, Canto, & Franca, 2014), or, in individuals with high scores in harm avoidance, during observation of static pictures where the visual context suggested the presence of immoral actions (Liuzza, Candidi, Sforza & Aglioti 2015). Furthermore, direct observation of painful stimulations delivered to the body of a stranger human model decreased MEPs amplitude in the onlooker, exactly as it happens when the same painful stimulus is applied to the observer, suggesting that observing pain in another person's hand automatically induces the covert simulation of potentially adaptive freezing and avoidance responses in the onlooker's corticospinal system (Avenanti, Paluello, Bufalari, & Aglioti, 2006; Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009). Moreover, racial cues are able to modulate this effect since a reduction of corticospinal excitability was present only when watching painful stimuli administered to the ingroup models (Avenanti, Sirigu, & Aglioti, 2010). At present, however, no studies directly investigated the possibility that a previous knowledge of agent's intention may autonomously determine a generative process influencing corticospinal excitability during observation of a neutral action (e.g., a suitable grasping of an object) in the absence of visual cues. Indeed, few results already suggested that observer's knowledge of agent's intention shapes action perception (Eshuis, Coventry, & Vulchanova, 2009; Hudson, Nicholson, Ellis, & Bach, 2016), and in the present study, for the first time, we aimed to investigate if this knowledge is also able to modulate motor resonance

during observation of the same action performed with equal kinematics, in the same visual context, but with different purposes. To this aim, we planned a TMS experiment in which we recorded MEPs from *Opponens Pollicis* (OP) muscle while participants were required to observe a video which continuously showed in a loop a hand reaching and squeezing a trumpet, during three experimental sessions differing for the consequences that the squeezing of the trumpet exerted on a third person (increasing of relief, increasing of discomfort, neutral effect).

2. Materials and Methods

2.1. Participants

Twenty-four students (13 men) of the University of Ferrara (mean age = 21.25, standard deviation = 1.53) participated in the experiment and gave their written informed consent. All were right-handed according to a standard handedness inventory (Briggs & Nebes, 1975) and reported having normal or corrected-to-normal visual acuity. Participants were unaware of the purposes of the study and were debriefed at the end of the experimental session. The procedures were approved by the local Ethics Committee and were in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. None of the participants had neurological, psychiatric, or other medical problems or any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009, 2011). No discomfort or adverse effects during TMS were reported or noticed.

2.2. Electromyography (EMG) Recording and TMS stimulation

Motor-evoked potentials (MEPs) were recorded from the *Opponens Pollicis* (OP) muscle of the right hand, a muscle which is active during grasping execution, and which,

from the seminal article by Fadiga (Fadiga et al., 1995), is commonly recorded to verify the presence of motor resonance during grasping observation in TMS studies. EMG recordings were performed through surface Ag/AgCl disposable electrodes (1-cm diameter) placed in a belly-tendon montage and connected to Aurion ZeroWire system (Aurion S.r.l, Milano, Italy) for amplification, digitization of the EMG signal (sampling rate: 2 kHz) and stored on a PC for off-line analysis. Signal Software (2.02 Version, Cambridge Electronic Design, UK) was used for TMS triggering and EMG recordings.

Focal TMS was performed by means of a 70-mm figure-of-8 stimulation coil (standard Magstim plastic-covered coil), connected to a Magstim Bistim (The Magstim Company, Carmarthenshire, Wales), producing a maximum output of 2 T at the coil surface (rise time of ~100 μs, decaying back to zero over ~0.8 ms). The coil was placed tangentially to the scalp, with the handle pointing backward and laterally 45° away from the midline, approximately perpendicular to the line of the central sulcus. 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). We chose the above coil orientation based on the finding that the lowest motor threshold is achieved when the induced electric current in the brain is flowing approximately perpendicular to the central sulcus (Brasil-Neto et al., 1992).

At the beginning of the experiment, the coil was positioned over the left motor cortex in correspondence with the optimal scalp position (OSP) for the right OP, defined as the position from which MEPs with maximal amplitude were recorded. This coil position was marked on the participants' scalp, and the coil was maintained at OSP by a coil holder with an articulated arm (Manfrotto, Italy). During data collection the experimenter continuously checked the position of the coil with respect to the marks and compensated for any small movement of the participant's head. The resting motor threshold (rMT), defined as the lowest stimulus intensity able to evoke 5 of 10 MEPs with an amplitude of at least 50 μ V, was

determined for the OSP. Stimulation intensity during the recording sessions was set at 120% of the rMT and ranged from 40% to 68% (mean = 51.08%, SD = 6.70%) of maximum stimulator output. A pre-stimulus recording of 150 ms was used to check for the presence of EMG activity before the TMS pulse; however, during MEPs recordings, the background EMG signal was continuously monitored, and when voluntary contractions of the recorded muscle were detected, participants were encouraged to fully relax their muscles. The peak-to-peak MEP amplitudes (in millivolts) were collected and stored on a computer for offline analysis.

2.3. Stimuli and Procedure

All the stimuli presented in the three experimental sessions consisted in the same video (resolution 760×576 pixels) played in a loop and showing a hand reaching and squeezing a trumpet placed at the centre of the screen (Fig. 1A). At the beginning of the video the hand was present on the table in a pinch position, then it moved towards the trumpet with a natural kinematics and speed, and, after having squeezed it, the hand released the trumpet and returned at the start position (204 frames, 25FPS. Duration of video: 8160 ms).

Insert Fig.1 approximately here

Each participant sat in a comfortable armchair in a dimly lit room in front of a 19 inch monitor (resolution 1024×768 pixels; refresh frequency 60 Hz) at a distance of 100 cm. At first, OSP was identified, the coil fixed, and the rMT calculated. Therefore, participants were instructed to keep their right hand on their leg, to fully relax their muscles, and were required to carefully observe the stimulus showing the trumpet squeezing, continuously played in a loop, during three different randomized conditions differing for the positive, negative, or

neutral effects of trumpet squeezing on a third person. Each experimental condition consisted of twenty trials. To induce in the participants the knowledge of the effects of the action observed in the video, two actors were present during the experiment, and both of them naturally interacted with the participants before the starting of the experimental sessions. They simulated to be a further experimenter and a further participant involved in a parallel and associated experiment. Specifically, the actor-experimenter explained to the participants that, during the experiment, each trumpet squeezing presented on the video would determine either a constant and increasing inflation of a cuff placed around the upper arm of the actorparticipant (Dislike condition), or a constant and increasing deflation of it (Like condition). Before each TMS recording session, participants experienced the effects induced on the actor-participant by means of a sphygmomanometer applied to their left arm and manipulated by the actor-experimenter which, according to the forthcoming experimental condition, either progressively inflated or deflated the cuff in a way timed by the twenty repetitions of the action presented on the video (Effects Simulation session, ES). The progressive inflation of the cuff induced an increasing discomfort in the participants, while the progressive deflation of it induced a gradual decrease of the discomfort. After each simulation, the actorexperimenter claimed to bring the actor-participant to the nearby room and to submit him/her to a device connected to the video, which automatically inflated or deflated the cuff applied to the actor-participant's arm, in a way stepped by the repeated trumpet squeezing, with the aim to observe the influence of these effects on multiple physiological data recorded from the actor-participant. During the Neutral condition, participants were informed that the actorparticipant was disconnected from the cuff and that, therefore, the squeezing of the trumpet had no consequences on his/her arm (Fig. 2).

Insert Fig. 2 approximately here

The actor-participant gender was balanced between participants (same, other; see Fig.1C). At the end of both the Like and the Dislike ES sessions, participants were required to respectively judge on a 5 points Likert scale (1, Not at all; 2, Slightly; 3 Moderately; 4 Extremely; 5, Very Extremely) the degree of relief or discomfort perceived, respectively, during the deflation or inflation of the cuff (Self-evaluation).

At the end of each ES session, the sphygmomanometer was removed from the participant's arm, and the TMS session started. The video was shown to the participants, and they were instructed to pay particular attention to it in order to answer to some not specified questions at the end of each session (e.g., the gender of the agent, the trumpet colour, the trumpet position, etc.). TMS stimulation was delivered at frame 75 (3000 ms from the beginning of the video), corresponding to the instant when the hand touched the trumpet. Each participant was submitted to a total of 60 trials divided into three TMS sessions: 20 Like trials, 20 Dislike trials, and 20 Neutral trials. The sessions order was perfectly balanced between subjects (Fig. 1C).

At the end of both the Like and the Dislike TMS session, participants were required to respectively judge on a 5 points Likert scale (1, Not at all; 2, Slightly; 3 Moderately; 4 Extremely; 5, Very Extremely) the degree of relief or discomfort he thought was perceived by the actor-participant during, respectively, the deflation or inflation of the cuff (Otherevaluation).

As baseline, we recorded four sessions of five MEPs each while participants were observing a white-coloured fixation cross presented on a black background. Three baseline sessions were recorded before each TMS session, and the fourth was recorded at the end of the last TMS session (TMS baseline, Fig. 1B). Comparisons of MEPs amplitudes recorded during the four baseline sessions allowed us to check for any corticospinal excitability change related to TMS *per se*. Stimulus presentation timing, EMG recording, and TMS triggering,

were controlled using E-prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA) running on a PC.

2.4. Personality measures

At the end of the experiment, each participant completed two questionnaires, the Interpersonal Reactivity Index (IRI, Davis, 1980, 1983), that was designed to assess empathy, defined as "the reactions of one individual to the observed experiences of another", and the 240-item version of the Temperament and Character Inventory (TCI, Cloninger, 1994) to assess Harm Avoidance trait. Harm avoidance (HA) seems to influence motor resonance during observation of immoral actions (Liuzza et al., 2015).

2.5. Data Analysis.

Trials in which the background activity was greater than 50 μ V, or trials in which MEPs were absent, were discarded. For each participant the peak-to-peak amplitude of each MEP was calculated and the values were transformed into z-scores. Amplitudes greater or less than 2.5 SD from the mean were discarded. The total percentage of excluded MEPs (Baseline, 3.75%; Neutral, 5.41%; Dislike, 6.87%; Like, 3.75%) was not statistically different across conditions ($F_{3.69} = 1.665$, p = 0.182, $\eta_p^2 = 0.067$).

The experimental design required to show the repetition of the same video during all the experimental conditions, and we were aware of the possibility that this requirement could induce a habituation effect (Thompson, 2009) in motor resonance. Furthermore, the effects of trumpet squeezing for the Like condition were more evident at the beginning of the experimental session (i.e., the high pressure exerted by the cuff began to diminish), while for the Dislike condition they were more evident towards the end of the experimental session (i.e., the pressure exerted by the cuff began to be close to the maximum).

To verify the effects of habituation, we firstly tested the presence of motor resonance during condition Neutral (N), verifying if action observation, in the absence of any indication of action intention, determined greater MEPs amplitude with respect to baseline (i.e., observation of a cross). We ran a preliminary analysis in which, for each participant, we calculated the difference between the average of MEPs recorded during condition N (20 MEPs) and the average of MEPs recorded during the four baseline recording sessions (4 x 5 MEPs), and we compared the results against 0 with one-sample t-test (two-tailed). The result of the t-test was not significant (t_{24} = 1.020, p = 0.318), indicating an absence of motor resonance probably due to the habituation effect. To check for this possibility, we verified the presence of motor resonance separately in the first and in the second half of the trials recorded during the condition N. Consequently, for each participant, the 20 MEPs recorded during condition N were divided into two temporal bins of 10 MEPs each. For each bin we calculated the Motor Resonance Index (MRI), according to the formula MRI = Condition – Baseline. We considered as baseline values the mean of the total 10 MEPs collected during the baseline session recorded just before (5 MEPs) and just after (5 MEPs) condition N. Thus, we obtained Nbin1, the MRI value relative to condition N in the first bin, and Nbin2, the MRI value relative to condition N in the second bin. We compared Nbin1 and Nbin2 against 0 with two separate one-sample t-tests (two-tailed). The results showed that Nbin1 was greater than 0 (t_{24} = 2.316, p = 0.029), and that Nbin2 was not different from 0 (t_{24} = -0.736, p = 0.468), showing that motor resonance was present at the beginning of the recording of session N and it disappeared at the end of it, a result in favour of the video habituation hypothesis.

To control if the sessions order influenced the MRI of condition N, we ran a two-way 3×2 mixed-model Analysis of Variance (ANOVA) with session N order (first, second, third) as between-subject variable and with Bin (bin1, bin2) as within-subject variable. The 2-way interaction Order × Bin ($F_{2,21} = 0.737$, p = 0.49, $\eta_p^2 = 0.065$) was not significant, showing that

the relative order of session N with respect to sessions Dislike (D) and Like (L) did not affect the results.

Given the presence of the habituation effect, and given the hypothesis that the effects of trumpet squeezing could be different during the first and the second part of the experimental sessions characterized by a specific agent's intention, we separately calculated for bin 1 and for bin 2, the MRI for both the Like (Lbin1, Lbin2) and the Dislike (Dbin1, Dbin2) conditions: positive values indicated that MEPs amplitude was greater during action observation than during the observation of a cross, suggesting the presence of an automatic motor replica of the observed action; on the contrary, negative values indicated that MEPs amplitude was smaller during action observation than during the observation of the cross, suggesting an inhibition to reenact the action. To calculate the MRI for condition L we considered as baseline values the mean of the total 10 MEPs collected during the baseline sessions recorded just before (5 MEPs) and just after (5 MEPs) session L, and for condition D those recorded just before (5 MEPs) and just after (5 MEPs) session D. The data were entered into a two-way 3×2 ANOVA with Condition (N, D, L), and Bin (bin1, bin2) as within-subject variables. All pairwise comparisons were calculated with the Newman-Keuls post-hoc test. A significance threshold of p < 0.05 was set for all statistical analyses. Effect sizes were estimated using the partial eta square measure (η_p^2) . The data are reported as the mean \pm standard error of the mean (sem).

Finally, to correlate TMS data with Personality measures (P), we subtracted the baseline motor resonance in condition N from the motor resonance in the conditions characterized by a specific agent's intention. For each participant, and for each bin, we calculated the difference in MEPs amplitude between condition D and N (DPbin1, DPbin2), and the difference in MEPs amplitude between condition L and N (LPbin1, LPbin2). The data obtained were used to compute the Pearson correlation coefficients with the five scores of the

Interpersonal Reactivity Index (Perspective-Taking scale, Fantasy scale, Empathic Concern scale, Personal Distress scale, and Sum score), and with the Harm avoidance score of TCI. The significance level for the first correlation analysis was set at p = 0.01 (Bonferroni correction, 5 correlations) and for the second one was set at p = 0.05 (1 correlation).

3. Results

3.1. Self-evaluation and Other-evaluation of action effects.

To firstly verify if indeed in the participant the inflation of the cuff produced discomfort, and the deflation of it produced relief, and to control if similar effects were hypothesized to be present in the actor-participant, we compared against 1 (i.e., the "Not at all" judgement) the scores individuated on the Likert scale as Self-evaluation and as Otherevaluation, relative to both relief (L condition: Self-evaluation 3,08 \pm 0,63; Other-evaluation $3,17 \pm 0,65$) and discomfort (D condition: Self-evaluation $2,83 \pm 0,58$; Other-evaluation 3,17 \pm 0,65), with four separate one-sample t-tests (two-tailed). The results showed that all the four scores were greater than 1 (L condition: Self-evaluation $t_{(24)} = 1.100$, p < 0.0001; Otherevaluation $t_{(24)} = 1.090$, p < 0.0001; D condition: Self-evaluation $t_{(24)} = 1.129$, p < 0.0001; Other-evaluation $t_{(24)} = 1.090$, p < 0.0001), indicating that our experimental manipulation produced the expected effects. To further control if the Other-evaluation was different from the Self-evaluation, we submitted the relative judgements for both relief and discomfort to two separate paired-sample t-tests. The results showed that the scores individuated on the Likert scale relative to both relief (t (24) = -0.526, p = 0.603), and discomfort (t (24) = -0.526), and discomfort (t (24) = -0.526). 0.526, p = 0.603) were not statistically different between Self-evaluation and Otherevaluation.

3.2. TMS results.

To verify the presence of any corticospinal excitability change related to TMS *per se*, the MEPs recorded during each of the four baseline sessions were entered into a one-way ANOVA with session (1, 2, 3, 4) as within-subject variable. The main effect of session was not significant ($F_{3,69} = 0.435$, p = 0.72, $\eta_p^2 = 0.018$), indicating that our results did not relate to TMS *per se*.

The two-way 3×2 ANOVA performed on MRI with Condition (N, D, L), and Bin (bin1, bin2) as within-subject variables, revealed that Condition main effect was not significant ($F_{2,46} = 2.314$, p = 0.110, $\eta_p^2 = 0.091$), and Bin main effect was significant ($F_{1,23} = 9.715$, p = 0.004, $\eta_p^2 = 0.296$), showing greater MRI value in the first bin (0.07 ± 0.06) than in the second bin (-0.12 ± 0.07). The 2-way interaction Condition × Bin ($F_{2,46} = 3.598$, p = 0.035, $\eta_p^2 = 0.135$) was significant. The post-hoc analysis indicated that Nbin1 was statistically significant greater than all other MRI values, and that Dbin2 was smaller than all other MRI values. Specifically, for condition N, MRI value was positive in the first bin (Nbin1, 0.26 ± 0.11) and close to zero in the second bin (Nbin2, -0.07 ± 0.10). This result confirmed the one obtained in the preliminary analysis in favour of the video habituation hypothesis. For condition D, MRI was close to zero in the first bin (Dbin1, -0.02 ± 0.08) and very negative in the second bin (Dbin2, -0.26 ± 0.10). For condition L, MRI was close to zero in both bins (Lbin1, -0.03 ± 0.10; Lbin2, -0.03 ± 0.10) (see Fig. 3).

Insert Fig. 3 approximately here

3.3. Correlation analysis.

All the correlation analyses between TMS data and the five scores of the Interpersonal Reactivity Index (Perspective-Taking scale, Fantasy scale, Empathic Concern scale, Personal

Distress scale, and Sum score), and between TMS data and the Harm avoidance score of TCI showed no significant effects. In Table 1, for each correlation, r coefficient and p are reported.

Insert Table 1 approximately here



4. Discussion

In the present study we verified the presence of a motor resonance modulation induced by the knowledge of agent's intentions during the observation of the same action, executed with the same kinematics parameters, in the same visual context, but for different purposes. To this aim we recorded motor potentials from Opponens Pollicis muscle, evoked by single pulse TMS over the primary motor cortex, while participants were required to observe a video which continuously showed in a loop a hand reaching and squeezing a trumpet, during three experimental sessions differing for the positive, negative or neutral effects that the squeezing of the trumpet exerted on a third person. The results showed that, independently of the personality traits of the participants, the observation of an action executed to induce effects in the other determined a decrease of motor resonance with respect to action observation in the absence of any indication of agent's intention. Furthermore, the observation of an action executed with the intention to induce negative effects, specifically during the second half of the recording session when the effects were more intense, determined a further reduction of motor resonance, suggesting the presence of a specific inhibition to reenact an action that results in unpleasant consequences in the other. Present results imply the possibility that, during action observation, the information at the intention level suggesting the long-term goal of the action, produces a sensory representation of the kinematic level of the action, which shapes motor resonance according with observer's mind and not with agent's intention, overcoming the replica of kinematics at the goal level automatically evoked in the absence of any indication of action intention (Kilner et al., 2007). In support of this are results indicating that when the observed kinematics (e.g., a free basket shot that causes the ball landing outside the basket) differ from the kinematics of the observer's intended action (e.g., a free basket shot that causes the ball landing in the basket), motor facilitation is congruent with the observer's intention (Aglioti, Cesari, Romani, &

Urgesi, 2008; Craighero et al., 2014). Furthermore, studies in which observed actions have the clear purpose to cue a complementary response (e.g., someone holding a mug by its handle and handing it towards the observer) explicitly revealed that the observer's motor system is not involved in the automatic imitation of the goal level of the action (e.g., holding a mug by its handle), but in the planning of observer's complementary action (e.g., grasping the mug with a whole hand prehension) (for review see Sartori & Betti, 2015). A further suggestion specifying the importance of observer's predisposition to act in the shaping of motor resonance, even at the goal level, is given by a study showing that corticospinal excitability modulation was present only when the observer received the information necessary to reveal the movement dynamics of an unrecognizable moving hand (Alaerts, Van Aggelpoel, Swinnen, & Wenderoth, 2009). This interpretation of the data is in line with the dual-route model for action observation proposed by Cattaneo (Barchiesi & Cattaneo, 2013; Ubaldi, Barchiesi, & Cattaneo, 2015), according to which a fast bottom-up process (150 ms from onset of visual stimuli) would be followed by a slower top-down process (300 ms). The authors suggested that the early process is a stimulus-driven process mediated by the dorsal visual stream, and the later one is a goal-driven process, mediated by the prefrontal cortex. Therefore, according to the Kilner, Friston, and Frith (2007) model, during the early process the available muscle/kinematic information automatically activates the motor system (pure "mirror" response, Ubaldi et al., 2015), allowing the cueing of the goal and, possibly, the intention of the action. Subsequently, the recognized intention prompts the later process ("executive" response, Ubaldi et al., 2015) which consists in the elaboration of a generative process (i.e., a covert motor program) shaping motor resonance. We propose that this later process may implement not only the observer's explicitly defined intended goal (e.g., the correct kinematics, a complementary action, an arbitrary rule), but also the observer's implicit moral rules. Consequently, during observation of neutral actions with no indication

of agent's intention, the generative process in the agent and in the observer do coincide, and the resulting motor resonance consists in the fine-grained, somatotopic, automatic replica of the observed kinematics (Fig. 4, panel A). On the contrary, when the agent's intention is in conflict with observer's moral rules, the generative process may determine a specific inhibition to reenact the observed action (Fig. 4, panel B).

Insert Fig.4 approximately here

Therefore, in the present study, the inhibition of motor resonance during observation of actions inducing the most negative effects in the other can be interpreted as an observer's intention to refrain from pursuing the agent's aim, a restraint that was not present when the action determined positive effects. It is to note that these findings were independent of the personality traits of the participants which seem to modulate corticospinal excitability during observation of static pictures of hands grasping objects, presented in a visual context which informed that the purpose of the action was immoral (Liuzza, et al., 2015)..

The results of this study have also shown that in the first bin, where the video habituation effect was not present, a non-specific reduction of motor resonance characterized conditions in which the action exerted some consequence in another person, both positive (i.e., Like condition) and negative (i.e., Dislike condition), with respect to the condition in which only the goal level of the action was present (i.e., Neutral condition). A possible interpretation of this effect could be that the social content of the experimental conditions has a role in inhibiting the involvement of the observer's motor system. However, this hypothesis is in contrast with results of a study showing that MEPs amplitude was enhanced during the observation of a social rather than an individual action (Bucchioni et al., 2013), though the visual context differed between the two conditions (i.e., the presence or the absence of a

partner in the scene informed about the type of action), and this difference could have influenced the results. An alternative possibility is that the cognitive evaluation prompted by the knowledge of the long-term goal of the action reduces the recruitment of the motor system, an effect present in situations in which the features of the presented action are at odds with its automatically evoked sensorimotor representation (D'Ausilio, Jarmolowska, Busan, Bufalari, & Craighero, 2011; Gangitano et al., 2001).

To summarize present results we may consider the Dr. Jekyll and Mr Hyde thoughtexperiment described in Jacob and Jeannerod (Jacob & Jeannerod, 2005). The authors claimed that it is unlikely that what enables Dr Watson to represent Jekyll-Hyde's intention when taking hold of a scalpel and applying it to a human body is his ability to match the perceived movements onto his own motor repertoire, as the observed movement is identical in both cases. However, as we already discussed in the Introduction, recent results have shown that motor resonance is modulated by the subtle differences in observed kinematics characterizing similar actions performed with different intentions (Finisguerra et al., 2016; Tidoni et al., 2013). Therefore, it is possible that the kinematics of Dr Jekyll when is using the scalpel to cure a patient differs from the kinematics of Mr Hyde when his aim is to inflict pain in the person. Consequently, Dr Watson's motor resonance may be differently modulated by the different kinematics, allowing him to identify the long-term intention of the actions, and thus to discriminate Dr Jekyll from Mr Hyde (Ansuini, Cavallo, Bertone, & Becchio, 2015). However, present data suggest that if Dr Watson knows from the beginning that the agent is Mr Hyde, and that his intention is to inflict pain, Dr Watson's motor system results strongly inhibited since Hyde's intention is not consistent with Watson's one.

In other words, present results indicate that, during action observation, the simple information at the intention level activates a generative process which interferes with the sensorimotor effects induced by the concomitant recognition process, overcoming the replica

of kinematics at the goal level automatically evoked in the absence of any indication of action intention. In turn, the generative process produces a sensorimotor representation of the kinematic level of the action, which shapes motor resonance according with observer's mind and not with agent's intention, revealing the possibility of a cognitive influence on motor resonance based on individual's ethical values.

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Figures and Table legends

- **Fig. 1**: **Observed action and experimental design**. A) Stimulus: Six frames extracted from the video continuously showed in a loop during the three experimental conditions. TMS pulse was delivered at frame 75 (3000 ms from the beginning of the video), corresponding to the instant when the hand touched the trumpet; B) General procedure: a schema representing the sequence of events during the three experimental sessions; C) Participants and Session order: Tables showing participants gender, actor-participants gender with respect to participants gender, and sessions order with number of repetitions. D, dislike condition; L, like condition; N, neutral condition.
- **Fig. 2**: **Instructions about agent's intention**. The figure shows a cartoon describing the instructions given by the actor-experimenter to the participants during the three different Effects Simulation (ES) sessions. On the left, ES preceding the Like TMS experimental session (L). At the centre, ES preceding the Dislike TMS experimental session (D). On the right, ES preceding the Neutral TMS experimental session (N) (for details refer to the text).
- **Fig. 3 Results.** Motor resonance index in each condition separated by bin. Asterisks indicate statistically significant effects.
- **Table1. Correlation matrix.** Correlation matrix between TMS data recorded during the first and the second bin of the Dislike condition (DEbin1, DEbin2) and of the Like condition (LEbin1, LEbin2), and the five scores of the Interpersonal Reactivity Index (Perspective-Taking scale, Fantasy scale, Empathic Concern scale, Personal Distress scale, and Sum score), and the Harm avoidance score of TCI.
- **Fig. 4: Cartoon showing the proposed relationship between the recognition and the generative process during action observation.** Panel A refers to observation of neutral actions with no indication of agent's intention. In this case, in the observer the recognition process activates a generative process which coincides with agent's one, and the resulting motor resonance consists in the fine-grained, somatotopic, automatic replica of the observed kinematics. Panel B refers to observation of actions with indication of agent's intentions when they are in contrast with observer's ones. In this case, the generative process in the agent and in the observer do not coincide, and the replica of the observed kinematics is absent. See the text for details.

	IRI Perspective – Taking Scale	IRI Fantasy Scale	IRI Empathic Concern Scale	IRI Personal Distress Scale	IRI Sum Score	TCI Harm Avoidance
DEbin1	r = 0.28 p = 0.18	r = 0.13 p = 0.56	r = 0.32 p = 0.13	r = -0.10 p = 0.64	r = 0.23 p = 0.28	r = -0.19 p = 0.38
DEbin2	r = 0.10 $p = 0.65$	r = -0.16 p = 0.45	r = 0.38 p = 0.07	r = 0.23 $p = 0.92$	r = 0.13 $p = 0.56$	r = 0.22 $p = 0.29$
LEbin1	r = 0.03	r = -0.16	r = 0.16	r = -0.19	r = -0.05	r = 0.39
LEbin2	p = 0.88 r = 0.14 p = 0.52	p = 0.46 r = -0.34 p = 0.10	p = 0.45 r = 0.56 p = 0.79	p = 0.37 r = -0.40 p = 0.05	p = 0.82 r = -0.19 p = 0.36	p = 0.86 $r = 0.21$ $p = 0.92$

