Visual Cognition

Same kinematics but different objects during action observation: Detection times and motor evoked potentials

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Same kinematics but different objects during action observation: Detection times and motor evoked potentials

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Motor resonance refers to the fact that an observed action is online subliminally reenacted. The aim of the present paper was to verify if, on equal terms of kinematics, the to-be-grasped object's intrinsic properties are influencing the observers' motor behaviour. A detection time and a single pulse transcranial magnetic stimulation experiment were performed to verify the effects of a change of object's intrinsic properties artificially made on a video showing a grasping action. In particular, the object substituting the original one was not graspable by the showed movement. Results indicated an influence of object's intrinsic properties: Detection times were delayed and motor evoked potentials were reduced when the movement shown was not suitable to grasp the object. These results are interpreted as an evidence that during grasping action observation the motor system of the observer is influenced not only by the seen movements but also by the to-be-grasped object.

Many experimental evidences have been collected to prove the presence of a representational sharing between action observation and action execution. In

humans, the clearest proof of this sharing is represented by the presence of motor activity during action observation (Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, … & Freund, 2001; Buccino, Binkofski, & Riggio, 2004; Fadiga, Craighero, & Olivier, 2005). This phenomenon, named motor resonance, has been mainly investigated by transcranial magnetic stimulation studies (TMS). In fact, among the different electrophysiological techniques only TMS is characterized by a sufficiently high temporal resolution to verify if the observer's motor system is dynamically (online) replicating the observed movements. In their seminal work Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) applied TMS to the area of motor cortex that represents the hand and motor evoked potentials (MEPs) were recorded from contralateral hand muscles during observation of transitive (grasping of different objects) and intransitive (arm elevation) arm–hand movements. The results showed that the pattern of MEPs elicited by TMS during action observation exactly replicated the pattern of EMG activation recorded during the execution of the same action. These results have been successfully confirmed and extended by other groups (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) and they indicate that, during the observation of a specific action, the same muscles used by the observer when performing the observed action are activated, and, furthermore, that muscles modulation has the same temporal dynamics present during the execution of that action. Therefore, motor resonance is characterized by high temporal fidelity and somatotopic specificity and refers to the fact that an observed action is subliminally reenacted.

All the studies present in literature interpreted the presence of motor activity during the observation of a grasping as an influence of the kinematics of the seen movement on corticospinal excitability, without considering the possible role of the soon to-be-grasped object (see de Vignemont & Haggard, 2008).

However, it is very well known that, during a reach and grasp, the arm, hand, and digits move towards the desired object in a highly structured behavioural pattern, with kinematic features reflecting the object's size, shape, orientation, and position (Jeannerod, 1981, 1984, 1986). Furthermore, numerous experiments demonstrated that the representational sharing between perception and action is present also during the mere viewing of an object. Grafton, Fadiga, Arbib, and Rizzolatti (1997), in a study using positron emission tomography (PET), showed for the first time that passive object viewing activated the left dorsal premotor cortex in a sector where arm/hand movements are represented (Deiber et al., 1991; Matsumura, Kawashima, Naito, Satoh, Takahashi, Yanagisawa, & Fukuda, 1996). Similar results have been shown by other neuroimaging studies (Chao & Martin, 2000; Grabowski, Damasio, & Damasio, 1998; Grèzes & Decety, 2002; Martin, Wiggs, Ungerleider, & Haxby, 1996). These findings suggest that the simple viewing of an object can indeed stimulate the human motor cortex into producing plans for action. However, neuroimaging technique, for its intrinsic methodological

limitations, do not allow to verify the specificity of the motor plan with respect to the intrinsic properties of the observed objects. A series of experimental psychology studies addressed this issue and showed that objects specifically potentiate only the actions they afford (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998, 1999; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Ellis & Tucker, 2000; Symes, Ellis, & Tucker, 2007; Tucker & Ellis, 1998), confirming that a sharing of sensorimotor representations is present between not only action observation and action execution but also graspable object observation and grasping execution. Recent TMS studies (Franca, Turella, Canto, Brunelli, Allione, Andreasi, … & Fadiga, 2012; Makris, Hadar, & Yarrow, 2011) showed that the vision of everyday-life graspable objects determined a rapid and short-lived automatic facilitation of the motor system, largely limited to the muscles mostly involved in the actual manipulation of the object. Furthermore, Proverbio (2012) provided evidence that tool perception is associated with a μ desynchronization over centroparietal sites which shares several similarities with the rolandic cortical μ rhythm that is suppressed during action execution and observation over the primary motor and somatosensory cortex (Hari, 2006; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006).

Thus, considering the neuronal and behavioural effects that the vision of a graspable object determines on the observer, the attribution of the corticospinal modulation found during observation of others' transitive actions exclusively to the influence of the seen movements, probably should be reconsidered. This is also necessary in the light of the results showing that the presence of proactive gaze behaviour during observation of a block stacking task (Flanagan & Johansson, 2003) indicates that observers' gaze, and therefore their attention, is not following the hand's trajectory but it is focused onto the goal of the action well before the arrival of the actor's hand.

To verify if motor resonance mainly reflects the observed movement kinematics or if it is also modulated by the to-be-acted-upon object's intrinsic properties, we compared results obtained during observation of one video showing a natural grasping movement with those obtained during observation of another video in which the movement kinematics were kept constant but the object's intrinsic properties changed to create an "impossible" grasping movement (see Craighero et al., 2008; Craighero & Zorzi, 2012). If motor resonance mainly reflects the observed movement kinematics, no difference in results should be present. On the contrary, if motor resonance is also modulated by the to-be-acted-upon object's intrinsic properties, a difference in results should be present. To this purpose, we performed a behavioural study and a TMS study in which we showed participants videos of a grasping action where, in half the trials and from the beginning of the video, the to-be-grasped object (a bar) was substituted by means of software with an object with the same dimensions but different intrinsic properties (a bar with sharp tips in correspondence of the fingers' opposition space and therefore very difficult to grasp with the presented movement). In the behavioural study we asked

participants to detect the time-to-contact of the hand grasping the object; in the TMS study we recorded MEPs from two hand intrinsic muscles at the hand–object contact instant. In both studies, to verify if not only the observed kinematic but also the to-be-grasped object, or the relationship between them, is able to influence observers' behaviour, we compared the results of the two different experimental conditions: observation of a hand recorded during the grasping of a bar and observation of the same hand moving with the same kinematics but grasping a bar with sharp tips in correspondence of the fingers' opposition space.

EXPERIMENT 1: BEHAVIOURAL

Materials and methods

Subjects.   Seven healthy undergraduate students (aged 20–33, four females) of the University of Ferrara took part in the study after giving their informed consent. All participants had normal or corrected-to-normal vision and were naïve as to the aims of the experiment. All of them were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). The study was carried out along the principles laid down in the Helsinki Declaration and procedures were approved by the local ethical committee of the University of Ferrara.

Stimuli and procedure.   Participants were seated on a comfortable chair in front of a desk and watched the videos presented on a monitor (resolution 1024 × 768 pixels) placed at 60 cm distance. They were instructed to watch the videos and to tap with their right index finger on a conducting pad placed on the table at the instant at which the agent in the videos touched the to-be-grasped object (experimental trials), and to refrain from tapping when the agent's hand stopped before touching the object (catch trials). The participant's left arm was relaxed on the arm rest.

We videotaped one video ("flat object video") in which the agent was sitting on a desk with an object made of solid aluminium in the shape of a parallelepiped (a solid body of which each face is a parallelogram) (Figure 1, left) located at 60 cm distance in front of her chest at the centre of her body midline. The parallelepiped was placed with its longer axis facing the agent. The agent reached and grasped the parallelepiped with natural velocity with the fingers' opposition space parallel to her frontal plane, without lifting the object.

To obtain the second video ("sharp tip object video") we captured an image (saved as bitmap image; frame size: 720 × 576) of a polyhedron (a geometric solid in three dimensions with flat faces and straight edges, of the same dimensions as the parallelepiped: 7 cm × 3 cm × 3 cm) made of solid aluminium (Figure 1, right), placed on the desk exactly in the same position of the parallelepiped during videotaping, and we extrapolated the object using Adobe Photoshop 7.0. Then we defragmented the "flat object video" saving each frame
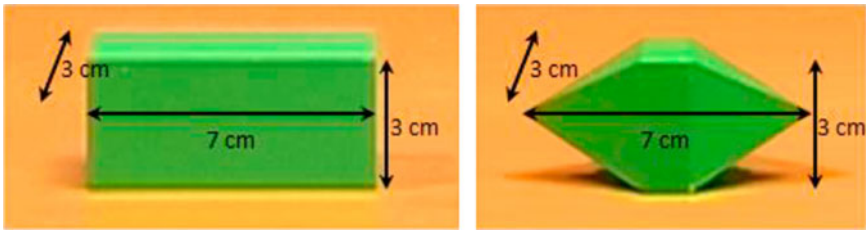
Figure 1.   Objects in the videos. On the left: the object grasped by the experimenter in the flat object videos (parallelepiped). On the right: the object artificially introduced via software in the sharp tip object videos (polyhedron). To view this figure in colour, please see the online issue of the Journal.

as bitmap image (25 frames/second; frame size: 720 × 576) and in each frame we substituted the parallelepiped with the polyhedron: We saved the frames reworked as bitmap images. Thus, we obtained the same number of frames (66 frames) for both videos. Using these frames we edited the two videos by means of Adobe Premiere Pro 1.5: the "flat object video" by using the frames of the original video, and the "sharp tip object video" by using the retouched frames.

Using this graphic trick we obtained a video in which the agent reached and grasped the polyhedron with her fingers just in correspondence of the sharp tips with exactly the same kinematic parameters present in the "flat object video". The two videos had the same duration (2640 ms) and the instant at which the experimenter's index finger touched the object was the same (1880 ms, Frame 47) (Figure 2).

We further manipulated the two videos in order to obtain the catch trials videos in which the agent's hand stopped before touching the objects (1520 ms after the beginning of the video, Frame 38). The last frame was repeatedly presented to obtain the same duration as that of the experimental videos (2640 ms, 66 frames) (Figure 3).

To identify the time instant at which the agent touched the object in the video, we utilized a custom-made light sensor that detected the change of brightness of a square (150 × 150 pixels) that was inserted at the bottom right of the image in each frame of the experimental videos. This square was black and turned white at the frame in which the agent's index finger touched the object (Frame 47). The light sensor was placed on the monitor surface in correspondence of the square to detect the change of square brightness. The signal from the conducting pad used by the participant to respond and the signal from the light sensor were compared by a homemade software program to have a measure of the time lag between the instant at which the agent's index finger touched the object and the participant's response. Errors were considered those trials in which the response preceded or followed the agent's touch of at least 150 ms. The decision to fix such a short range for time response is based on previous results (Craighero et al., 2008; Craighero & Zorzi, 2012) showing that in this type of paradigm the time lags are
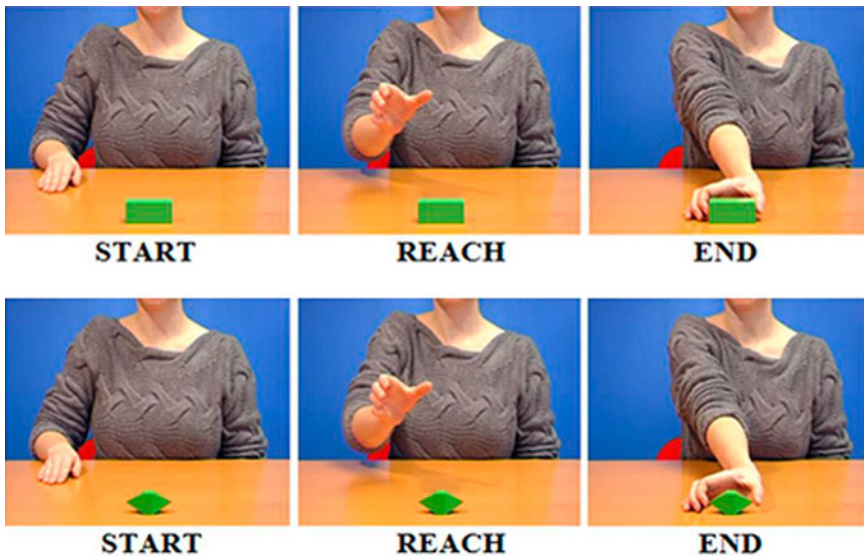
Figure 2.   Experimental trials videos. Three frames extracted from the experimental flat object video (top) and from the experimental sharp tip object video (bottom). (Start: Frame 1; Reach: Frame 25; End: Frame 66). To view this figure in colour, please see the online issue of the Journal.

definitely shorter than the fastest simple reaction time, indicating that subjects are predicting and not reacting at the instant at which the demonstrator touches the object. All trials marked as errors were automatically resubmitted to the participant after the last trial of the experimental sequence (the number of error trials was irrelevant; furthermore, almost all the errors detected were attributable to temporary problems in the conducting pad).

Before the experiment, participants were asked to try to grasp and lift the two objects once, by using the same finger opposition space used in the videos. This test allowed participants to experience for themselves that grasping the sharp tip object using as opposition space the two tips was impossible as it was quite painful. On the contrary, they were easily able to grasp and lift the flat tip object. They afterwards completed a training block in which all videos were presented to familiarize them with the experimental stimuli.

Participants were submitted to an experimental session of 72 trials randomly presented: 60 experimental videos (30 flat object videos and 30 sharp tip object videos) and 12 catch videos (six flat object catch videos and six sharp tip object catch videos). A 2 second black screen was presented between the videos.

Results

Responses given during catch trials were almost absent (no errors or at most two errors for each participant).
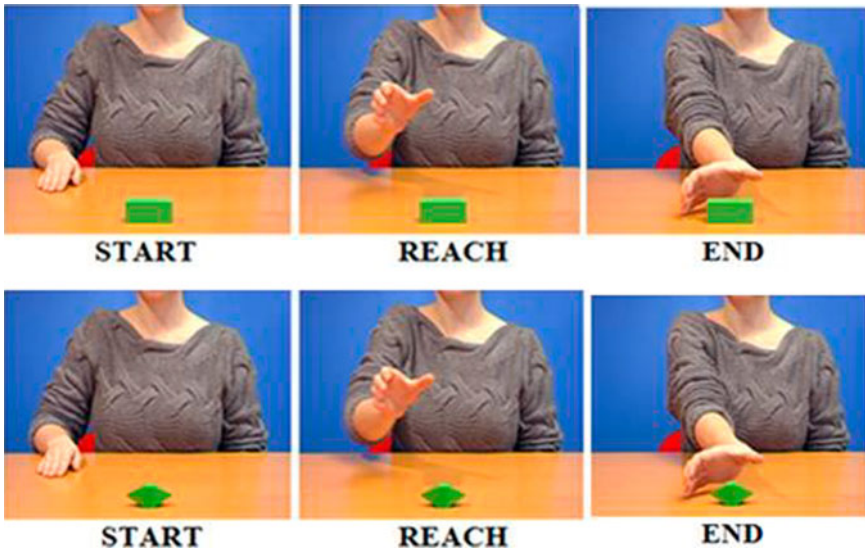
Figure 3. Catch trials videos. Three frames extracted from the catch flat object video (top) and from the catch sharp tip object video (bottom). (Start: Frame 1; Reach: Frame 25; End: Frame 38. Frame 38 was repeated 28 times to obtain the same duration as that of the experimental videos, 66 frames). To view this figure in colour, please see the online issue of the Journal.

In order to assess whether participants' response to time-to-contact was modulated by the presence of different objects, the value of the time lag recorded during observation of flat object videos and of sharp tip object videos were compared using a paired-sample *t*-test. The difference between time lag during observation of sharp tip object videos (mean = 29.13 ms, SEM = 11.26) and time lag during observation of flat object videos (mean = -12.37 ms, SEM = 8.94) was statistically significant, $t_6 = -9.397$, $p = .000082$ (Figure 4).

EXPERIMENT 2: TMS

Materials and methods

Subjects. Eighteen healthy undergraduate students (aged 20–21, nine females) of the University of Ferrara took part in the study. None of them had participated in the previous experiment. All participants had normal or corrected-to-normal vision and were naïve as to the aims of the experiment. All of them were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Prior to entering the study, the subjects were screened for possible adverse reaction to TMS (Keel, Smith, & Wassermann, 2001) and a written informed consent was
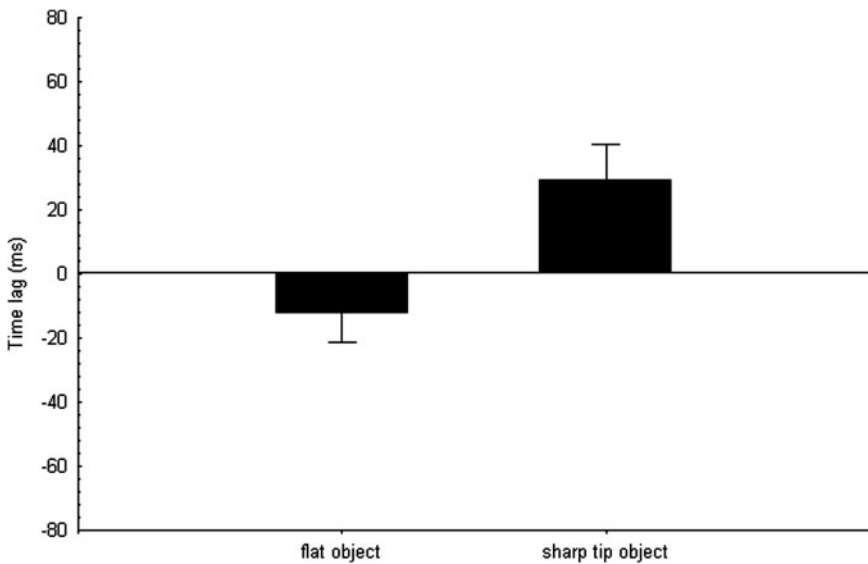
Figure 4.   RT results. Time lag between the instant at which the demonstrator touches the object and subject's response time. Data for flat object videos and sharp tip object videos are shown. Thin lines above histograms indicate standard error of the mean. Ordinates are in milliseconds.

obtained. The experimental procedures were approved by the local Ethics Committee and were performed according to the Declaration of Helsinki.

EMG recordings and TMS.   Surface EMG traces were recorded from first dorsal interosseous (FDI) muscle (see Hasegawa, Kasai, Tsuji, & Yahagi, 2001) and opponens pollicis (OP) muscle (see Fadiga et al., 1995) of the right hand by using 9-mm diameter adhesive Ag/AgCl surface electrodes (Kendall, GbmH, DE), in a belly-tendon montage. Signals were amplified and band-pass filtered (50–1000 Hz) by means of a wireless EMG system (ZeroWire, Aurion srl, IT), then digitized at 2000 Hz and stored on a PC for offline analysis with Signal Software (Version 2.02, Cambridge Electronic Design, UK). EMG recordings started at the beginning of video presentation and lasted for the entire duration of the video. Focal cortical stimulation was performed by means of a figure-of-eight coil (70 mm outer diameter) connected to a Magstim 200 magnetic stimulator (Magstim, Whitland, Dyfed, UK). Magnetic pulses had a nearly monophasic configuration, with a rise time of ∼100 μs, decaying back to zero over ∼0.8 ms. The coil was positioned over the left motor cortex (M1), tangentially to the scalp, with the handle oriented 45° laterally and backwards with respect to the sagittal interhemispheric plane, inducing a medially and anteriorly directed current flow in the underlying cortex, approximately perpendicular to the central sulcus. First

the hand motor area was localized and the "hot spot" for the right FDI defined as the scalp site, at which stimulation evoked the largest MEPs from the homonymous muscle. Then, the resting motor threshold for the FDI muscle (RMT) was identified, according to Rossini and colleagues (Rossini, Barker, Berardelli, Caramia, Caruso, Cracco, … & Tomberg, 1994). The stimulation intensity used in the experimental procedure was set to 120% of RMT of each subject to consistently evoke stable MEPs from all muscles in resting conditions.

Stimuli and procedure.   Participants sat on a comfortable and reclined chair in front of a computer monitor placed at a distance of 60 cm from their eyes. Their head was stabilized by a headrest. The participant's right hand was relaxed and placed supinated over the right armrest. Their left hand was holding a computer mouse attached to the left armrest.

In the present experiment the same videos as in the previous one were used (i.e., flat object video and sharp tip object video).

Participants were submitted to two separate experimental sessions of 138 trials presented in a counterbalanced order between participants. In one experimental session, participants were presented with 69 flat object videos alternating with 69 videos composed of black video frames, of the same duration as the object videos (66 frames, resulting in the presentation of a black screen for 2640 ms). In the other experimental session, the sharp tip object video was substituted for the flat object video.

In each session single pulse TMS was randomly delivered in 12 videos with objects and in 12 videos with black frames. In total, 48 MEPs were recorded from each subject.

In both object and black frames videos TMS was delivered in correspondence with Frame 47, which related with the instant at which the experimenter's index finger touched the object in the object video (1880 ms from the beginning of the video). In order to precisely trigger TMS, the same device used in the previous experiment was used: a custom-made light sensor that detected the change of brightness of a square (150 × 150 pixels) that was inserted at the bottom right of the image in each frame of the videos. This square was black and turned white at Frame 47. The light sensor was placed on the monitor surface corresponding to the square to detect the change of square brightness and trigger the TMS pulse.

To ensure that participants would maintain their focus on the videos, randomly in 18 object video trials of each session, among those without TMS, a beep of 100 ms duration was presented before (1360 ms from the beginning of the video) or after (2400 ms) the instant at which the experimenter touched the object (1880 ms). At the end of these videos presentation the following question was presented at the centre of the computer screen: "Before or after?" Participants were required to press the left mouse button with their left middle finger in the case of the beep being presented before the touch instant, and the

right mouse button with their left index finger in the case of the beep being presented after the touch instant.

Before the experiment, participants were asked to try to grasp and lift the two objects once, by using the same finger opposition space used in the videos. This test allowed participants to experience for themselves that grasping the sharp tip object using as opposition space the two tips was impossible as it was quite painful. On the contrary, they were easily able to grasp and lift the flat tip object. They also completed a training block without TMS comprising 36 trials (18 object videos and 18 black frame videos). In some object videos the auditory signal was present and participants were required to give the response.

Data analysis.   Trials showing EMG activity prior to TMS were discarded from further analysis (less than 3% of all trials, equally distributed between the conditions). After calculation on a trial by trial basis of MEPs area from rectified EMG, MEPs area values were normalized (z-scores) separately for every subject to reduce intersubject variability. Offline analysis of MEPs area was carried out with MATLAB (Version 9.a, The Mathworks Inc., Natick, USA). MEPs areas mean values for each experimental condition (black frames video, flat object video, sharp tip video), each muscle, and each participants were calculated. Data were entered in two separate one-way repeated measures analyses of variance (ANOVA), in which the three-level factor condition was considered. Pairwise comparisons with the Newman-Keuls method were conducted whenever appropriate. The significance level was always set at .05.

Results

None of the subjects ever made any mistake answering the question related to the temporal relationship between the auditory signal and the instant of touch.

The one-way ANOVA performed for the FDI muscle showed a significant result for the main effect of condition, $F(2, 34) = 4.18$, $MSE = 0.087$, $p = .0238$. Pairwise comparisons revealed that MEPs areas were statistically significant greater during observation of flat object videos (Mean = 0.134, $SD = 0.357$) than during observation of sharp tip object videos (Mean = -0.128, $SD = 0.222$) and black frames videos (Mean = -0.09, $SD = 0.174$). MEPs areas recorded during the last two conditions were not statistically different (Figure 5).

The one-way ANOVA performed for the OP muscle showed a significant result for the main effect of condition, $F(2, 34) = 5.54$, $MSE = 0.107$, $p = .0082$. Pairwise comparisons revealed that MEPs areas were statistically significant greater during observation of flat object videos (Mean = 0.143, $SD = 0.351$) than during observation of sharp tip object videos (Mean = -0.136, $SD = 0.269$) and black frames videos (Mean = -0.199, $SD = 0.194$). MEPs areas recorded during the last two conditions were not statistically different (Figure 6).
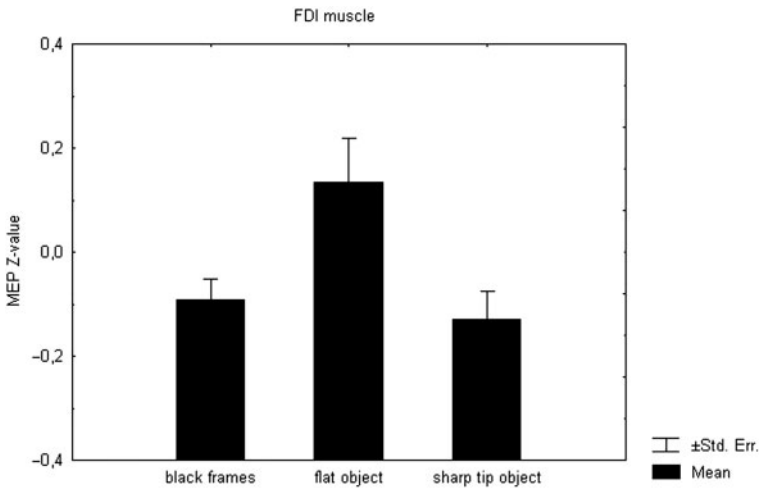
Figure 5. FDI MEPs results. *Z*-value MEPs amplitudes recorded from the first dorsal interosseous (FDI) muscle during the three experimental conditions. Black frames: during the observation of videos showing black frames. Flat object: during the observation of the original video showing a hand grasping the parallelepiped. Sharp tip object: during the observation of the modified video showing a hand grasping the polyhedron. Thin lines represent standard error of the mean.

Both analyses compared the average of 12 MEPs collected during objects videos with the average of 24 MEPs collected during black frames videos. We preferred to unbalance the total number of observations for each condition in order to compare the same number of observations collected for each condition in each session. We decided to do this in light of the fact that doubling the observations increases the variability. However, to be sure that the different number of observations did not influence our results, we performed two further ANOVAs in which, for black frame trials, we averaged six randomly extracted values from one session and six from the other session, in order to give the average of 12 values. The results confirmed those previously obtained: for the FDI muscle, $F(2, 34) = 4.11$, *MSE* $= 0.095$, $p = .0251$; for the OP muscle, $F(2, 34) = 5.97$, *MSE* $= 0.107$, $p = .006$.

DISCUSSION

For the first time the present work directly investigated, on equal terms of kinematics, the role of to-be-grasped object intrinsic properties on motor resonance during action observation. The intrinsic characteristics of the object could be congruent or incongruent with the kinematics that was maintained always the same. The artificial substitution via software of the bar with a bar of the same width but with two sharp tips in correspondence of the fingers'
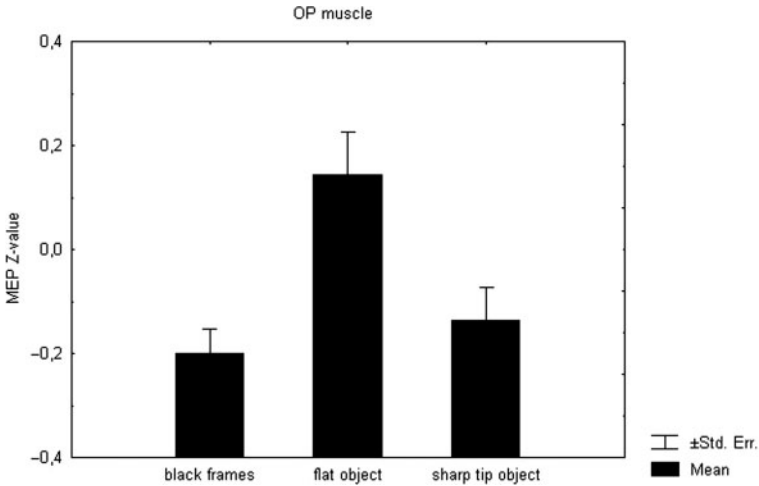
Figure 6. OP MEPs results. Z-value MEPs amplitudes recorded from the opponens pollicis (OP) muscle during the three experimental conditions. Black frames: during the observation of videos showing black frames. Flat object: during the observation of the original video showing a hand grasping the parallelepiped. Sharp tip object: during the observation of the modified video showing a hand grasping the polyhedron. Thin lines represent standard error of the mean.

opposition space rendered the presented grasping movement not suitable to grasp the object. In fact, during action execution, the presence of the two sharp tips would drive people to dramatically modulate velocity and force, in the case the same fingers' opposition space was used, or to completely change the way of grasping the object.

In the behavioural study participants were instructed to watch the videos and to tap the table at the instant at which the agent touched the to-be-grasped object. It is important to be reminded that in both videos the object was touched at Frame 47, since the movement of the hand was the same and the width of the objects was the same. Results showed that the difference between time lag during detection of sharp tip object videos and time lag during detection of flat object videos was statistically significant. In particular, response during sharp tip object videos was delayed. Present results confirm those of a previous experiment (Craighero et al., 2008) in which the same task was requested but grasping actions were online performed by the experimenter in front of the subject. The to-be-grasped object was a plastic parallelepiped (9 cm × 6 cm × 2.5 cm) which was grasped either with fingers' opposition space parallel to subject's frontal plane or perpendicular to it. The first type of grasping has been categorized as "not suitable" and the latter one as "suitable" on the basis of a preliminary experiment demonstrating that participants almost constantly selected the suitable grasping when requested to grasp that object. Results showed that responses recorded during detection of not suitable grasping were

statistically delayed with respect to those recorded during detection of suitable grasping. Whereas in Craighero et al.'s (2008) study the comparison was between same object and different kinematics, in the present experiment it was between same kinematics and different objects. However, results are pretty the same and we may conclude that what is influencing participants' behaviour in time-to-contact detection is the relationship between to-be-grasped object's intrinsic properties and hand movement kinematics. This observation supports the conclusions stated in previous papers (Craighero et al., 2008; Craighero & Zorzi, 2012) claiming that during grasping observation the observer automatically activates the sensory motor representation cued by the to-be-grasped object. When the to-be-detected action corresponds to the activated sensory motor representation, response should be faster than when it does not correspond to it, as suggested by motor priming, the classical effect showing that an observed action facilitates a compatible action (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001), indicating that stimuli and responses are represented in a commensurable format (Brass et al., 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Wohlschlager & Bekkering, 2002; see Prinz, 2002). When observers see a motor event that shares features with a similar motor event present in their motor repertoire, they are primed to repeat it. The greater the similarity between the observed event and the motor event, the stronger the priming is (Prinz, 2002).

On the basis of these conclusions, we tested if the finding of motor activity during action observation in humans (Buccino et al., 2001, 2004; Fadiga et al., 2005) mainly reflects the seen movements (Rizzolatti & Craighero, 2004) or if it is also modulated by the to-be-acted-upon object's intrinsic properties. We compared MEPs recorded from first dorsal interosseous muscle and opponens pollicis muscle while participants were watching the same two videos used in the behavioural experiment. If only movement kinematics was able to influence motor resonance, the prediction was that no difference in MEPs should be present between the two videos, given that the TMS pulse was delivered exactly at the same time instant of the trajectory (Frame 47), which corresponded to the instant in which experimenter's index finger touched the object, in both videos. Results did not support this prediction given that MEPs areas were statistically significant greater during observation of flat object videos than during observation of sharp tip object videos. In particular, MEPs recorded during sharp tip object videos did not differ from those recorded during the control condition (black frames videos), revealing that the motor system of the observer is not involved or it is suppressed/inhibited during observation of an incongruence between the sensory motor representation cued by the to-be-grasped object and the observed action. This result reflects those found during two similar experimental conditions proposed in previous papers. The first one was shown by Gangitano, Mottaghy, and Pascual-Leone (2004) in a condition in which subjects were watching a video clip of a hand approaching and grasping a ball and in which

maximal finger aperture was substituted with an unpredictable closure. Results showed that FDI motor excitability was suppressed during the observation of the incongruent action, as if the activated motor plan was discarded when features of the presented movement ceased to match those of the attended one. The second one was found in an experiment recording tongue corticospinal modulation during attended verbal stimuli (D'Ausilio, Jarmolowska, Busan, Bufalari, & Craighero, 2011), showing that the presentation of an incongruent phonemic cue cancelled the modulation of tongue corticospinal excitability present when the cue was congruent with the predicted stimulus. This interpretation of the results hypothesizes the presence of a feedforward anticipatory mechanism based on contextual cues which is constantly verifying incoming information as an online feedback-based control strategy. In the present study, contextual cues are represented by the to-be-grasped object's intrinsic properties and incoming information by hand movement kinematics. Such control strategy is indeed not new in motor neuroscience. In fact, the relationship between action and perception, at the level of motor control, is thought to be organized around similar principles. People may use internal predictive models to generate goal-directed actions (Desmurget & Grafton, 2000). More specifically, during goal-directed action, internal models provide sensory expectations that are used to monitor and control movements. Analogously, it has been argued that the same internal modelling mechanisms are reused when we encode another's action in terms of our own motor repertoire (Fadiga et al., 1995; Fazio, Cantagallo, Craighero, D'Ausilio, Roy, Pozzo, … & Fadiga, 2009; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004). In this sense, the motor system might furnish an attentional-like mechanism able to prime perceptual processes (Rizzolatti & Craighero, 1998; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994).

An alternative possible interpretation of the results is that motor resonance is influenced not by hand movement kinematics but only by the to-be-grasped object's intrinsic properties and that the statistically significant difference between MEPs recorded during observation of the two videos is essentially determined by the different involvement of the hand area of the motor cortex (see Lemon, Johansson, & Westling, 1995) during the final positioning of the digits prior to touch for grasping the two objects, a phase particularly demanding in terms of sensorimotor control. When we reach out to grasp and lift a small object, the first goal is to adequately position the tips of the digits onto its surfaces such that a stable grasp can be established. The transport and shaping of the hand reflect a precise coordination to achieve the necessary spatiotemporal features for arresting the reach, and for an appropriate closure of the fingers around the object (Iberall, Bingham, & Arbib, 1986; Jeannerod, 1984, 1986). Once the digits contact the object, the goal is to generate the necessary fingertip forces to lift it. This action evolves in a series of phases each delineated by discrete mechanical events and associated responses in tactile afferents from the

digits (Johansson & Westling, 1984, 1987, 1988; Westling & Johansson, 1987). The magnitudes of the fingertip forces are parameterized by implicit memory information of both the friction at the digit–object interface and the object's weight, acquired during previous manipulation of the object (for a review, see Johansson & Cole, 1994). In the present experiment, participants had a clear experience of grasping and lifting the two objects, given that prior to starting the task they were asked to try to do it once, and they were perfectly aware of the pain produced by the sharp tips over the fingertips when lifting the object. It can be that to accomplish the task of indicating if the auditory signal was delivered before or after the instant at which the experimenter's hand touched the object, participants internally simulated the grasping action. A possibility is that the reduction in corticospinal excitability during observation of sharp tip object videos reflected participants' awareness of the necessity to reduce reaching velocity and of the need to avoid too much pressure on the tips and consequently decreasing the application of force.

Both interpretation of the results, however, indicate a crucial role of the to-be-grasped object's intrinsic properties in modulating motor resonance during grasping action observation. Present results exclude the possibility that the involvement of the motor system found during action observation may be merely determined by a passive subliminal reenacting of the observed movement kinematics and support the idea that motor resonance is an active process considering kinematics, context cues, and past motor experience to predict others' actions outcomes (Stapel, Hunnius, & Bekkering, 2012) and to check the appropriateness of the observed action with respect to the predicted goal. Further support to this last observation is given by an experiment testing with bifocal TMS whether the observation of goal-directed reach to grasp actions may lead to specific changes in the short-latency connections linking the anterior intraparietal cortex (AIP) and the ventral premotor cortex (PMv), with M1 (Koch, Versace, Bonnì, Lupo, Lo Gerfo, Oliveri, & Caltagirone, 2010). Results showed that AIP-M1 and PMv-M1 cortico-cortical interactions were specifically activated when observing successful reaching to grasp goal-directed actions, in which the hand posture was congruent with the goal of the action performed by the actor. On the other hand, they were not modified when the same goal-directed actions were performed wrongly with an inappropriate grasping posture. A similar profile of excitability was observed in the same paper (Koch et al., 2010) when testing specific intracortical facilitatory circuits in M1, known to reflect the activity in cortico-cortical pathways transmitting information from PMv.

In conclusion, present results support the idea that during grasping action observation the motor system of the observer is experiencing not only the seen movements but also the grasp of the object and when these two experiences are in contrast it ceases to be involved, interrupting the feedforward anticipatory mechanism able to predict others' action consequences.

REFERENCES

Borroni, P., & Baldissera, F. (2008). Activation of motor pathways during observation and execution of hand movements. *Social Neuroscience*, *3*, 276–288. doi:10.1080/17470910701515269

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22. doi:10.1016/S0001-6918(00)00024-X

Brass, M., Bekkering, H., Wohlschlager, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*, 124–143. doi:10.1006/brcg.2000.1225

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *Neuroimage*, *14*, 1416–1423. doi:10.1006/nimg.2001.0944

Brighina, F., La Bua, V., Oliveri, M., Piazza, A., & Fierro, B. (2000). Magnetic stimulation study during observation of motor tasks. *Journal of the Neurological Sciences*, *174*, 122–126. doi:10.1016/S0022-510X(00)00271-9

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., … & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language*, *89*, 370–376. doi:10.1016/S0093-934X(03)00356-0

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*, 478–484. doi:10.1006/nimg.2000.0635

Clark, S., Tremblay, F., & Ste-Marie, D. (2004). Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. *Neuropsychologia*, *42*, 105–112. doi:10.1016/S0028-3932(03)00144-1

Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, *40*, 492–502. doi:10.1016/S0028-3932(01)00134-8

Craighero, L., Bonetti, F., Massarenti, L., Canto, R., Fabbri Destro, M., & Fadiga, L. (2008). Temporal prediction of touch instant during observation of human and robot grasping. *Brain Research Bulletin*, *75*, 770–774. doi:10.1016/j.brainresbull.2008.01.014

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. A. (1998). Visuomotor priming. *Visual Cognition*, *5*, 109–125. doi:10.1080/713756780

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1673–1692. doi:10.1037/0096-1523.25.6.1673

Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, *8*, 347–349. doi:10.1097/00001756-199612200-00068

Craighero, L., & Zorzi, V. (2012). Hand-foot motor priming in the presence of temporary inability to use hands. *Visual Cognition*, *20*, 77–93. doi:10.1080/13506285.2011.639315

D'Ausilio, A., Jarmolowska, J., Busan, P., Bufalari, I., & Craighero, L. (2011). Tongue corticospinal modulation during attended verbal stimuli: Priming and coarticulation effects. *Neuropsychologia*, *49*, 3670–3676. doi:10.1016/j.neuropsychologia.2011.09.022

Deiber, M. P., Passingham R. E.,Colebatch, J. G.,Friston, K. J.,Nixon, P. D., & Frackowiak, R. S. (1991). Cortical areas and the selection of movement: A study with positron emission tomography. *Experimental Brain Research*, *84*, 393–402. doi:10.1007/BF00231461

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*, 423–431. doi:10.1016/S1364-6613(00)01537-0

de Vignemont, F., & Haggard, P. (2008). Action observation and execution: What is shared? *Social Neuroscience*, *3*, 421–433. doi:10.1080/17470910802045109

Ellis, R., & Tucker, M. (2000). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology*, *91*, 451–471. doi:10.1348/000712600161934

Fadiga, L., Craighero, L., & Olivier E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, *15*, 213–218. doi:10.1016/j.conb.2005.03.013

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.

Fazio, P., Cantagallo, A., Craighero, L., D'Ausilio, A., Roy, A. C., Pozzo, T., … & Fadiga, L. (2009). Encoding of human action in Broca's area. *Brain*, *132*, 1980–1988. doi:10.1093/brain/awp118

Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*, 769–771. doi:10.1038/nature01861

Franca, M., Turella, L., Canto, R., Brunelli, N., Allione, L., Andreasi, N. G., … & Fadiga, L. (2012). Corticospinal facilitation during observation of graspable objects: A transcranial magnetic stimulation study. *PLoS ONE*, *7*, e49025. doi:10.1371/journal.pone.0049025

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609. doi:10.1093/brain/119.2.593

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, *12*, 1489–1492. doi:10.1097/00001756-200105250-00038

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2004). Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *European Journal of Neuroscience*, *20*, 2193–2202. doi:10.1111/j.1460-9568.2004.03655.x

Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *Neuroimage*, *7*, 232–243. doi:10.1006/nimg.1998.0324

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage*, *6*, 231–236. doi:10.1006/nimg.1997.0293

Grèzes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*, 212–222. doi:10.1016/S0028-3932(01)00089-6

Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in Brain Research*, *159*, 253–260.

Hasegawa, Y., Kasai, T., Tsuji, T., & Yahagi, S. (2001). Further insight into the task-dependent excitability of motor evoked potentials in first dorsal interosseous muscle in humans. *Experimental Brain Research*, *140*, 387–396. doi:10.1007/s002210100842

Iberall, T., Bingham, G., & Arbib, M. A. (1986). Opposition space as a structuring concept for the analysis of skilled hand movements. *Experimental Brain Research*, *15*(Suppl.), 158–173.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153–168). Hillsdale, NJ: Lawrence Erlbaum Associates.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, *16*, 235–254. doi:10.1080/00222895.1984.10735319

Jeannerod, M. (1986). The formation of finger grip during prehension: A cortically mediated visuomotor pattern. *Behavioral Brain Research*, *19*, 99–116. doi:10.1016/0166-4328(86)90008-2

Johansson, R. S., & Cole, K. J. (1994). Grasp stability during manipulative actions. *Canadian Journal of Physiology and Pharmacology*, *72*, 511–524. doi:10.1139/y94-075

Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, *56*, 550–564. doi:10.1007/BF00237997

Johansson, R. S., & Westling, G. (1987). Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, *66*, 141–154. doi:10.1007/BF00236210

Johansson, R. S., & Westling, G. (1988). Programmed and reflex actions to rapid load changes during precision grip. *Experimental Brain Research*, *71*, 59–71.

Keel, J. C., Smith, M. J., & Wassermann, E. M. (2001). A safety screening questionnaire for transcranial magnetic stimulation. *Clinical Neurophysiology*, *112*, 720. doi:10.1016/S1388-2457(00)00518-6

Koch, G., Versace, V., Bonnì, S., Lupo, F., Lo Gerfo, E., Oliveri, M., & Caltagirone, C. (2010). Resonance of cortico-cortical connections of the motor system with the observation of goal directed grasping movements. *Neuropsychologia*, *48*, 3513–3520. doi:10.1016/j.neuropsychologia.2010.07.037

Lemon, R. N., Johansson, R. S., & Westling, G. (1995). Corticospinal control during reach, grasp, and precision lift in man. *Journal of Neuroscience*, *15*, 6145–6156.

Makris, S., Hadar, A. A., & Yarrow, K. (2011). Viewing objects and planning actions: On the potentiation of grasping behaviours by visual objects. *Brain and Cognition*, *77*, 257–264. doi:10.1016/j.bandc.2011.08.002

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652. doi:10.1038/379649a0

Matsumura, M., Kawashima, R., Naito, E., Satoh, K., Takahashi, T., Yanagisawa, T., & Fukuda, H. (1996). Changes in rCBF during grasping in humans examined by PET. *Neuroreport*, *7*, 749–572. doi:10.1097/00001756-199602290-00017

Montagna, M., Cerri, G., Borroni, P., & Baldissera, F. (2005). Excitability changes in human corticospinal projections to muscles moving hand and fingers while viewing a reaching and grasping action. *European Journal of Neuroscience*, *22*, 1513–1520. doi:10.1111/j.1460-9568.2005.04336.x

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113. doi:10.1016/0028-3932(71)90067-4

Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de) synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage*, *31*, 153–159. doi:10.1016/j.neuroimage.2005.12.003

Prinz, W. (2002). Experimental approaches to imitation. In A. N. Meltzoff & W. Prinz (Eds.), *The imitative mind: Development, evolution and brain bases* (pp. 143–162). Cambridge, UK: Cambridge University Press.

Proverbio, A. M. (2012). Tool perception suppresses 10–12Hz μ rhythm of EEG over the somatosensory area. *Biological Psychology*, *91*, 1–7. doi:10.1016/j.biopsycho.2012.04.003

Rizzolatti, G., & Craighero, L. (1998). Spatial attention: Mechanisms and theories. In M. Sabourin, F. Craik, & M. Robert (Eds.), *Advances in psychological science: Vol. 2. Biological and cognitive aspects* (pp. 171–198). Hove, UK: Psychology Press.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192. doi:10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40. doi:10.1016/0028-3932(87)90041-8

Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV* (pp. 231–265). Cambridge, MA: MIT Press.

Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., … & Tomberg, C. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalography and Clinical Neurophysiology*, *91*, 79–92. doi:10.1016/0013-4694(94)90029-9

Stapel, J. C., Hunnius, S., & Bekkering, H. (2012). Online prediction of others' actions: The contribution of the target object, action context and movement kinematics. *Psychological Research*, *76*, 434–445. doi:10.1007/s00426-012-0423-2

Symes, E., Ellis, R., & Tucker, M. (2007). Visual object affordances: Object orientation. *Acta Psychologica (Amsterdam)*, *124*, 238–255. doi:10.1016/j.actpsy.2006.03.005

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 830–846. doi:10.1037/0096-1523.24.3.830

Westling, G., & Johansson, R. S. (1987). Responses in glabrous skin mechanoreceptors during precision grip in humans. *Experimental Brain Research*, *66*, 128–140. doi:10.1007/BF00236209

Wohlschlager, A., & Bekkering, H. (2002). Is human imitation based on a mirror-neurone system? Some behavioural evidence. *Experimental Brain Research*, *143*, 335–341. doi:10.1007/s00221-001-0993-5