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ORIGINAL ARTICLE

Dissociated Representations of Deceptive Intentions and Kinematic Adaptations in the Observer's Motor System

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Abstract

Previous studies showed that observing deceptive actions modulates the activity of the observer's motor system. However, it is unclear whether this modulation reflects the coding of deceptive intentions or the mapping of the kinematic adaptations required to attain deceptive actions. Here, we used single-pulse transcranial magnetic stimulation to measure cortico-spinal excitability (CSE) from hand and forearm muscles while participants predicted the weight of cubes lifted by actors who received truthful information on the object weight and provided 1) truthful (truthful actions) or 2) deceptive (deceptive actions) cues to the observers or 3) who received fooling information and were asked to provide truthful cues (deceived actions). This way, we independently manipulated actor's intentions and kinematic adaptations. We found that, as compared to truthful action observation, CSE increased during observation of deceptive actions, but decreased during observation of deceived actions. Importantly, while the CSE enhancement in response to deceptive intentions lacked muscle specificity, perceiving kinematic alterations in the deceived condition affected CSE only for the hand muscle involved in kinematic adaptations to unexpected object weight. This suggests that actor's intentions and movement kinematics may be coded by the observer's motor system at different hierarchical levels of action representation.

Key words: action observation, action prediction, deceptive intention, motor cortex, transcranial magnetic stimulation

Introduction

Our ability to read others' intentions is a key feature in social life. Everyday interactions often require judging others' intentions by looking at the way they move. Indeed, by observing "how" an action is performed, we try to understand "why" the actor is performing that action, for example, if the actor wants to eat a grasped apple or to place it away (i.e., intention inference). It is well established that different covert intentions lead to overt

differences in others' movements (Becchio et al. 2010; Naish et al. 2013; Ansuini et al. 2015) and observers are able to pick-up and use these differences to infer the underlying intention (Manera et al. 2011; Sartori et al. 2011; see Ansuini et al. 2015 and Catmur 2015 for a review). Even if in most cases we expect to deal with genuine intentions, interpersonal interactions may require to rely on action observation to understand whether a person is honest or deceitful through careful assessment of the

available non-verbal cues (Runeson and Frykholm 1983; Ekman and O'Sullivan 1991; Sebanz and Schiffrar 2009).

Observing another individual's action triggers motor resonance in the observers' motor/mirror neuron system (MNS, Fadiga et al. 2005), which is thought to anticipate the forthcoming action and generate predictions based on kinematics of the observed action (Kilner et al. 2004; Borroni et al. 2005; Aglioti et al. 2008; Urgesi et al. 2010). Recently, a transcranial magnetic stimulation (TMS) study showed that, during the observation of deceptive actions, the detection of kinematic cues violating the predicted action enhanced the motor resonance in the observer's brain (Tidoni et al. 2013). Particularly, seeing deceptive actions facilitated the observers' motor system more than seeing truthful actions, leading the authors to propose that the MNS may code that an agent acts with the intent to fool the observer.

Nonetheless, according to Hamilton and Grafton (2007), actions can be described, and thus they can be understood (Kilner et al. 2007), at many different levels of a hierarchy. Let us consider that we are observing someone grasping a mug from its handle. This action is characterized by an intention level, which describes why the agent is performing that action (to drink). Then, the goal level defines the proximal aim of the action (bringing the mug toward the mouth). In a lower part of the hierarchy, the kinematic level consists of the observed hand-object (handle) interaction. Lastly, the lowest level involves the synergic muscular activation required to attain the movement. Predictive coding models (Kilner et al. 2007) propose that, given an observed action, the MNS allows intention comprehension by generating for each hierarchical level top-down predictions (priors) about lower levels of action representation. When the priors and the incoming sensory information match each other, the overarching intention becomes clear; otherwise, a feedback is sent back to higher levels to adjust the initial prediction and minimize the error signal. Tidoni et al. (2013) suggested that, when someone is facing with deceptive intentions, the alteration of the intentional level is reflected into higher activity of the MNS, which thus shows sensitivity to action intention. However, the implementation of a deceptive action is characterized by the alteration of both the intentional and the kinematic levels. Does the modulation of the observers' motor system reflect the kinematic adaptation of the observed movement rather than the actor's deceptive intention? Alternatively, are both low- and high-level features of deceptive actions coded by the MNS?

Here, we recorded motor-evoked potentials (MEPs) to assess whether and how low- and high-level features of deceptive actions modulate motor-resonance processes when performing a weight discrimination task (WDT). To this aim, we introduced, in addition to "truthful" and "deceptive" actions, a third new condition ("deceived" action) in which the observer faces an action with an altered kinematic pattern, but aimed by a genuine rather than a deceptive intention. In this deceived condition, the actor aims to provide truthful cues to the observer but receives fooling information about the object weight, thus being forced to alter the movement kinematics to adapt to the unexpected object weight. Importantly, since representation of action kinematics in the observer's motor system is thought to mirror the muscle-specific motor role, we compared the modulation of the cortico-spinal excitability (CSE) in one hand and one forearm muscle that differently contribute to the postural adjustments required by unexpected objects' weight (Johansson and Westling 1988; Tidoni et al. 2013). Additionally, given a possible role of emphatic abilities in shaping motor

resonance (Gallese 2003), we measured participants' level of trait empathy.

Material and Methods

Participants

A total of 18 healthy subjects (9 males, aged = 24.8 ± 7.55 years) recruited at the University of Udine took part in this study. We determined the required size for our within-subjects $2 \times 2 \times 3$ design (muscle \times weight \times condition) through the G^* power software (Faul et al. 2009) by setting the expected effect size at 0.25 based on previous MEP study of action deception detection (Tidoni et al. 2013), the significance level at 0.05, and the desired power ($1-\beta$) at 0.80. Two participants were excluded since their performance at the WDT was below the chance level (accuracy of 43% and 44%). Thus, the following evaluations were carried out on data obtained on a sample of 16 participants (7 males). After providing an overview of the study procedure, including technical information about TMS and the task, all subjects, who remained naive to the specific experimental hypothesis throughout the whole experimental session, gave written informed consent for participation. All the experimental procedures were in keeping with the 1975 Declaration of Helsinki, as revised in 1983, and were approved by the Ethics committee of the IRCCS Eugenio Medea. After completing the whole testing session, including also the administration of a dispositional questionnaire (see "Dispositional Empathy Measurement" section), participants received information about the experimental hypothesis and an attendance fee (15 Euros). All participants had normal or corrected-to-normal vision and they were right-handed, except for one who was ambidextrous, as assessed by a standard Handedness Inventory (Briggs and Nebes 1975). None of the participants had contraindications to TMS (Rossi et al. 2009) or complained of any discomfort or adverse effect during the whole procedure.

Stimuli

The experimental stimuli consisted of short video clips depicting (from a lateral view) the right hand of 2 non-professional actors (1 man aged 22 years and 1 woman aged 30 years) while reaching, grasping and lifting a wooden cube (Fig. 1). Two cubes with identical visual appearance (size $6 \times 6 \times 6$ cm) but different weight (100 or 550 g) were used. Crucially, the videos were taken in 3 different conditions. In the first condition (truthful condition), the actors were asked to lift the cube after receiving truthful information about its weight and being asked to provide truthful cues to the observer. In the second condition (deceptive condition), after receiving the same truthful information about the object weight, the actors were asked to provide deceptive cues to the observers, pretending to lift the heavier cube (550 g) as if it weighted less (100 g) and vice versa. The third condition (deceived condition) was obtained by asking the actors to provide truthful cues to the observers (as during the truthful condition), but they received fooling information about the object weight. Thus, extending the experimental design employed in the previous seminal study about detection of deceptive actions (Tidoni et al. 2013), here the inclusion of the deceived condition in addition to the deceptive one allowed us to dissociate the effects of the actor's deceptive intention from that of kinematic adaptations. Indeed, in the truthful condition, the actors performed the action with a genuine intention and displaying the expected kinematic pattern required to lift a light or a heavy object. In the deceptive

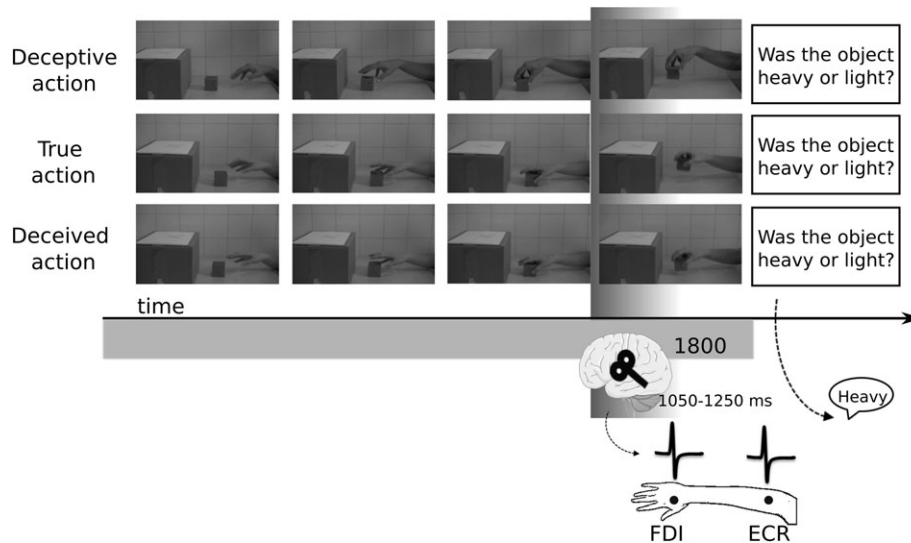


Figure 1. Schematic representation of the events for each trial of the WDT. The picture shows frames extracted from experimental video clips representing the actor reaching and grasping the object in the 3 (deceptive, true, and the deceived) action conditions. For each trial, the TMS pulse could be delivered at a delay randomly varying between 1050 and 1250 ms after the onset of the observed action. For each trial, we recorded the amplitude of the MEPs of 2 different muscles (first dorsal interosseous, FDI, and extensor carpi radialis, ECR) and the participant's verbal response to the WDT.

condition, the fooling intention led the actor to alter the kinematic pattern and to provide misleading information about the object weight. In the deceived condition, the planned kinematics pattern reflected the fooling information provided to the actors and needed to be adjusted once the actual weight of the object was apparent at lifting, thus leading to kinematic alterations in the absence of deceptive intention.

During video clip recording, naïve actors were asked to perform the movements in a natural way according to the experimenter's verbal instructions, which informed them about the weight of the to-be-lifted object. The actors were required to wait for the verbal instruction keeping the eyes closed and to perform the movement only after the presentation of an auditory go signal. In this way, we prevented them to look at the experimenter when he placed the to-be-lifted object on the table. Video clip recording was run in 2 separate blocks. In the first block (genuine intention), the actors were asked to perform the movement in order to provide truthful information about the object weight and to lead a hypothetical observer to understand the object weight. In 75% of the trials of the first block, the instructions provided true information about the object weight (truthful action), while in the remaining intermingled trials deceitful information was provided. Truthful and deceived trials were sorted in a pseudorandom order within the first block. This served a 2-fold purpose. Firstly, the high proportion of true trials allowed us to maintain the unpredictability of the deceived condition and, thus, to successfully deceive the actor. Indeed, the high reliability of the instruction (75%) during the truthful versus the deceptive condition (25%) most likely led the actors to consider the weight information as a valid cue and thus to rely on this information to move in a natural way during each trial. Secondly, to avoid contamination on the truthful condition due to the presence of deceived trials, only truthful video clips recorded at the beginning of the block and following another truthful trial were selected. In the second block (deceptive intention), which always followed the genuine one, we asked the actors to provide deceitful information about the object weight. The deceived and the deceptive actions were repeated 3 times for each object, while the true

actions were repeated 9 times, leading to a total of 30 trials. Before starting each block, the actors were briefly trained to perform the movement (only for the truthful and the deceptive conditions).

For each actor, 6 types of videos were selected following a 2 (object weight: light, heavy) \times 3 (action condition: truthful, deceptive, and deceived) design. Furthermore, to increase stimulus variability, 3 different repetitions of the same type of videos were selected, for a total of 36 video clips (2 actors \times 3 action conditions \times 2 object weights \times 3 repetitions).

The video clips were recorded with a Canon EOS 550D camera and they were further edited with Adobe Premiere Pro CS3 3.0 software. Video clips were cut in order to have the same 1800 ms duration (36 frames presented at 20 Hz) with the hand-object contact occurring at about 700–950 ms after video onset. Since the models were free to move naturally, the exact moment of the hand-object contact was different in each video, but no differences were observed between the 3 conditions ($F(2,33) = 1.79$, $P = 0.184$). Videos were rendered in black and white in order to prevent local changes in skin tone during hand contraction from conveying information about the object weight. Importantly, a kinematic analysis (see “Stimuli kinematic analysis” section) was performed in order to explore which cues were visible in the video clips to allow participants to perform the task. Furthermore, the picture of a static hand not implying action was used for baseline recording (see the Procedure section).

Videos appeared at the center of the screen on a neutral background (subtending approximately $15.96^\circ \times 11.97^\circ$ of visual angle) and they were presented on a 21-in. CRT monitor (resolution: 1024×768 pixels, refresh frequency: 60 Hz). Presentation and randomization of the visual stimuli, TMS triggering, and response recording were controlled by the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, version 2.0).

TMS and Electromyography

Single-pulse TMS was delivered to scalp portion overlying the left motor hand region through a 70-mm-figure-of-eight coil (Magstim polyurethane-coated coil) connected to a Magstim

200 stimulator (Magstim Company, Carmarthenshire, Wales, UK). For each subject, the left motor hand region was functionally localized by means of visual inspection of MEPs recorded simultaneously from the right first dorsal interosseous (FDI) and right extensor carpi radialis (ECR) muscles (Fig. 1). These 2 muscles were selected for their motor role during reaching-to-grasp and lifting movements and sensitivity to genuine versus deceptive intentions during action observation. Indeed, the FDI muscle activity is directly involved in controlling the strength of the grip during lifting (Alaerts et al. 2010a, 2010b; Senot et al. 2011). More importantly, the FDI CSE is more facilitated during the observation of fooling than genuine hand actions exerted upon objects of the same weight (Tidoni et al. 2013). As well, not only is the ECR muscle activity involved in lifting action execution, but the ECR CSE is highly sensitive to changes in the kinematic pattern and exerted force during action observation (Alaerts et al. 2010a, 2010b). However, there is no evidence about the ECR involvement in deceptive behaviors (see electromyography, EMG, recording during action execution).

We determined the optimal position for activation of both muscles (i.e., the scalp position from which maximal amplitude MEPs were elicited) by moving the coil in approximately 0.5 cm steps around the presumed motor hand area and stimulating with a constant, slightly supra-threshold stimulus intensity. The coil was placed tangentially to the scalp with the handle pointing backward and laterally to form a 45° angle with the sagittal plane. This coil orientation induced a posterior-anterior current in the brain. The optimal position of the coil was then marked with a pen on a cap placed on the scalp to ensure correct coil placement throughout the experiment. For the whole experiment, the coil was fastened to an articulated mechanical arm. The resting motor threshold (rMT) was then defined as the minimum stimulus intensity (expressed as percentage of maximum stimulator output) able to produce MEPs of at least 0.05 mV peak-to-peak amplitude in at least 5 out of 10 consecutive trials (Rossini et al. 2015) in the lower threshold muscle (FDI). This procedure was used to avoid saturation of its CSE modulation (Devanne et al. 1997) and possible loss of mirror-like modulation (Loporto et al. 2013). Participants' rMT ranged from 32% to 52% (mean rMT = $42.21 \pm 7.74\%$) of the maximum stimulator output. During the experiment, single-pulse TMS was applied over the identified hotspot at a stimulation intensity corresponding to 130% of the individual's rMT. This procedure allowed us to reliably record MEPs from both muscles.

EMG was recorded with silver disc surface electrodes (1 cm diameters, disposable) positioned on the FDI and ECR muscles in a belly-tendon configuration. Electrode position for the FDI and the ECR muscles was determined by palpation during maximum voluntary muscles activation (i.e., the abduction of the index finger toward the thumb while the experimenter exerted a pressure against the radial side of the index finger in the direction of the middle finger for the FDI muscle; the extension of the wrist toward the radial side while the experimenter exerted a pressure against the dorsum of the hand for the ECR muscle). After skin cleaning, electrodes containing a small amount of water-soluble EEG conductive paste were placed and fixed on each target positions. The reference electrodes were placed over the ipsilateral metacarpal phalangeal joint for the FDI muscle and on the ulnar styloid process for the ECR. The ground electrode was placed at the right elbow. Electrodes were connected to a Biopac MP-36 system (BIOPAC Systems, Inc., Goleta, CA) allowing the amplification, band-pass filtering (5 Hz to 20 kHz, notch filter 50 Hz) and digitization of the EMG signal (sampling rate: 50 kHz). The signal was stored on a personal computer for

display and later offline data analysis. The EMG data were collected for 300 ms starting at 100 ms before the TMS pulse. To ensure full muscular relaxation, EMG signals were sent to loudspeakers before the experimental session to provide participants with an auditory feedback of their muscle relaxation.

Procedure

Participants were seated on a comfortable recliner chair with their right forearm resting on a pillow. They were instructed to keep their hands still and as relaxed as possible. Each participant was tested in a single experimental session lasting approximately 75 min.

Before the beginning of the experiment, participants were asked to lift with their right hand the 2 cubes used in the video clips (3 times for each cube) and they were kindly asked to keep in mind their different heaviness. We introduced this practical training to ensure that participants could rely on stored internal models of the actions during the observation task. Participants were also informed about the 3 possible conditions in which the actors lifted the cube.

During the experimental session, participants were administered a 2-alternative forced choice (2AFC) WDT, in which they were instructed to carefully watch the video clips and to indicate for each trial if the cube lifted by the actor was the heavy or the light one. Each trial started with a warning cue lasting 1000 ms and it was followed by the video clip presentation (lasting 1800 ms). The TMS pulse was delivered at a delay randomly varying between 1050 and 1250 ms after the video clip onset (Fig. 1). After the video clip, a frame with the Italian verbal descriptors of the 2 possible weights ("pesante" for heavy and "leggero" for light) written in black on a white background was presented until the response was recorded. Then, a black screen appeared in the inter-trial interval (lasting 7000 ms). This way, the inter-pulse interval was longer than 10 s, thereby avoiding changes in CSE due to repeated TMS pulses (Chen et al. 1997). Participants were required to indicate their response by verbally saying "up" or "down" depending on the position of the verbal descriptor of the predicted object weight, and the experimenter recorded the response by pressing the left or right mouse button. We counter-balanced the up- or down-position of the verbal descriptors in order to avoid participants to plan their response in advance. A verbal, rather than a motor, response was required at the end of each video clip to avoid MEPs contamination (Tokimura et al. 1996; Meister et al. 2003; Gentilucci et al. 2006). Twenty-four repetitions for each of the 3 possible actions with the light or the heavy object were presented, thus leading to a total of 144 trials. All trials were presented and randomized in 4 blocks of 36 trials. In 2 baseline 24-trials blocks administered before and after the WDT, MEPs were recorded while participants observed either a fixation cross (12 trials per block) or a static image of a resting-relaxed hand (12 trials per block). We introduced the static hand in the baseline recording in order to disentangle the eventual effects on CSE due to body part observation from that due to action processing (Naish et al. 2014). Furthermore, before MEPs recording, 12 trials for each of the 3 possible actions were presented, for a total of 36 trials, without delivering any TMS pulse in order to allow participants to familiarize themselves with the experimental stimuli and with the task.

Dispositional Empathy Measurement

After the completion of the TMS session, we measured participants' dispositional empathy to test its role in the motor coding

of action intention and kinematic adaptations. We measured dispositional empathy by means of the Italian version (Bonino et al. 1998) of the Interpersonal Reactivity Index (IRI, Davis 1996). All participants except one filled out the questionnaire. This questionnaire consists of 28 self-report items, and it measures empathy-related dispositions by means of 4 subscales, namely: Perspective Taking (PT), which assesses the tendency to assume the cognitive perspective of another person; Fantasy Scale (FS), which assesses the tendency to imaginatively transpose oneself into fictional characters' feelings and actions; Empathic Concern (EC), which assesses "other-oriented" feeling of sympathy and concern for others in need; and Personal Distress (PD), measuring the self-oriented feeling of personal anxiety and distress when facing others' emotional unease. Importantly, while the PT and the FS subscales tap into cognitive empathy, the EC and the PD subscales are more related to emotional reactivity. It has been proposed that sharing cognitive perspective (rather than emotions) of an observed interaction partner might facilitate successful social behavior in its predictive, deceptive, and counter deceptive purposes (Smith 2006). Furthermore, whereas the PD subscale reflects a self-oriented form of empathy that may interfere with social functioning, high score in the PT, FS and EC scales are associated with other-oriented capacity for empathy (Davis 1996). Thus, we hypothesized to find a relationship between motor coding of deceptive actions and the more mature components of cognitive empathy.

Stimuli Kinematics Analysis

To identify the kinematic differences between the 3 types of actions, we extracted a series of kinematic parameters of the actors' right arm movement by using dedicated software for motion analysis (Kinovea 0.8.15). Particularly, temporal (reaching and lifting duration) and spatial (grip aperture, wrist angle, and index flexion) variables were measured in a frame-by-frame analysis, covering 2 possible time windows: the first one preceding the contact with the object (reaching phase) and the second one starting with the lifting of the object (lifting phase).

"Reaching duration" was defined as the time (in ms) required by the actor's hand to reach the object since the beginning of the videos up to the frame showing the first hand-object contact. "Lifting duration" was defined as the time interleaving between the frame at which the vertical position (measured as y-axis pixels and then converted to mm) of the dorsal part of the wrist started to rise up and the frame at which it reached the 130% of its position at the contact point.

For data reduction, the 3 spatial parameters were measured in the last 200 ms before the contact time for the reaching phase and in the initial 200 ms after the beginning of the lifting phase. This ensured that the spatial parameters were measured at comparable action points in all video clips. The "grip aperture" (GA) was measured as the distance between the tips of the thumb and of the index finger (in mm). The "wrist angle" (WA, in degrees) was measured at the palmar side of the radiocarpal joint and was defined by the line connecting the lateral epicondyle of the humerus with the radial styloid process and the line connecting the thumb metacarpal joint with the radial styloid process. The proximal interphalangeal "index-finger angle" (IA, in degrees) was defined by the line connecting the distal with the proximal interphalangeal joint of the index finger and the line connecting the index finger metacarpal joint with the proximal interphalangeal joint of the index finger. To provide a synthetic measure of kinematics changes for the 3

actions, we calculated the displacement of the 3 spatial parameters in the considered interval by calculating the difference between the parameter values measured at the 2 extreme frames (last frame–first frame; Fig. 2).

EMG Recording During the Execution of True, Deceived, and Deceptive Action

To better delineate the involvement of the 2 recorded muscles during action execution, we studied the EMG activity of the FDI and ECR muscles during the execution of the same types of actions represented in the video clips. Thirteen additional participants (5 males; aged = 22.53 ± 4.27 years) non-participating in the main experiment were asked to reach, grasp, lift, and place a cube on a box with their right hand while EMG activity from the right FDI and ECR muscles was recorded. We used exactly the same objects, setting, and instruction procedures as those adopted during video recording. Participants were told to perform the movements in a natural way according to the verbal instructions that informed them about the weight of the to-be-lifted object. They were required to wait for this verbal instruction keeping their eyes closed and to perform the movement only after the presentation of an auditory go signal. In this way, we prevented participants from looking at the experimenter when she placed the to-be-lifted object on the table. The EMG recording in each trial started 200 ms before the go signal and lasted for 5200 ms. Like during the video clips recording, the EMG experiment was run in 2 separate blocks. In the first (genuine intention) block participants were asked to perform the movement in order to provide truthful information about the object weight and to lead an hypothetical observer to understand the object weight. In 75% of the trials of the first block, the instructions provided true information about the object weight (truthful action), while in the remaining interspersed trials deceitful information was provided. The 1:3 proportion between truthful and deceived action trials served the purpose of maintaining the unpredictability of the deceived condition. In the second (deceptive intention) block, which always followed the genuine one, we asked participants to provide deceitful information about the object weight. The deceived and the deceptive actions were repeated 5 times for each object, while the true actions were repeated 15 times, leading to a total of 50 trials. Actions were executed in a pseudorandom order within each block. Before starting each block, participants were briefly trained to perform the movement (only for the truthful and the deceptive conditions). During the execution of the movement, an experimenter carefully observing the action signaled the time of the hand-object contact by setting a marker on the EMG trace.

Data Analysis

All the analyses were performed using Analysis of Variance (ANOVA) designs implemented in STATISTICA software (StatSoft, version 10, StatSoft Inc, Tulsa, OK). Estimates of the effect size were obtained using partial eta-squared (η_p^2). Post hoc analysis was performed using the Duncan test correction. The significance threshold was set at 0.05 for all statistical tests.

Kinematics Data

Reaching and lifting durations of the 36 videos and the GA, WA, and IA displacement indices for the reaching and lifting phases were entered into separate factorial ANOVAs with action

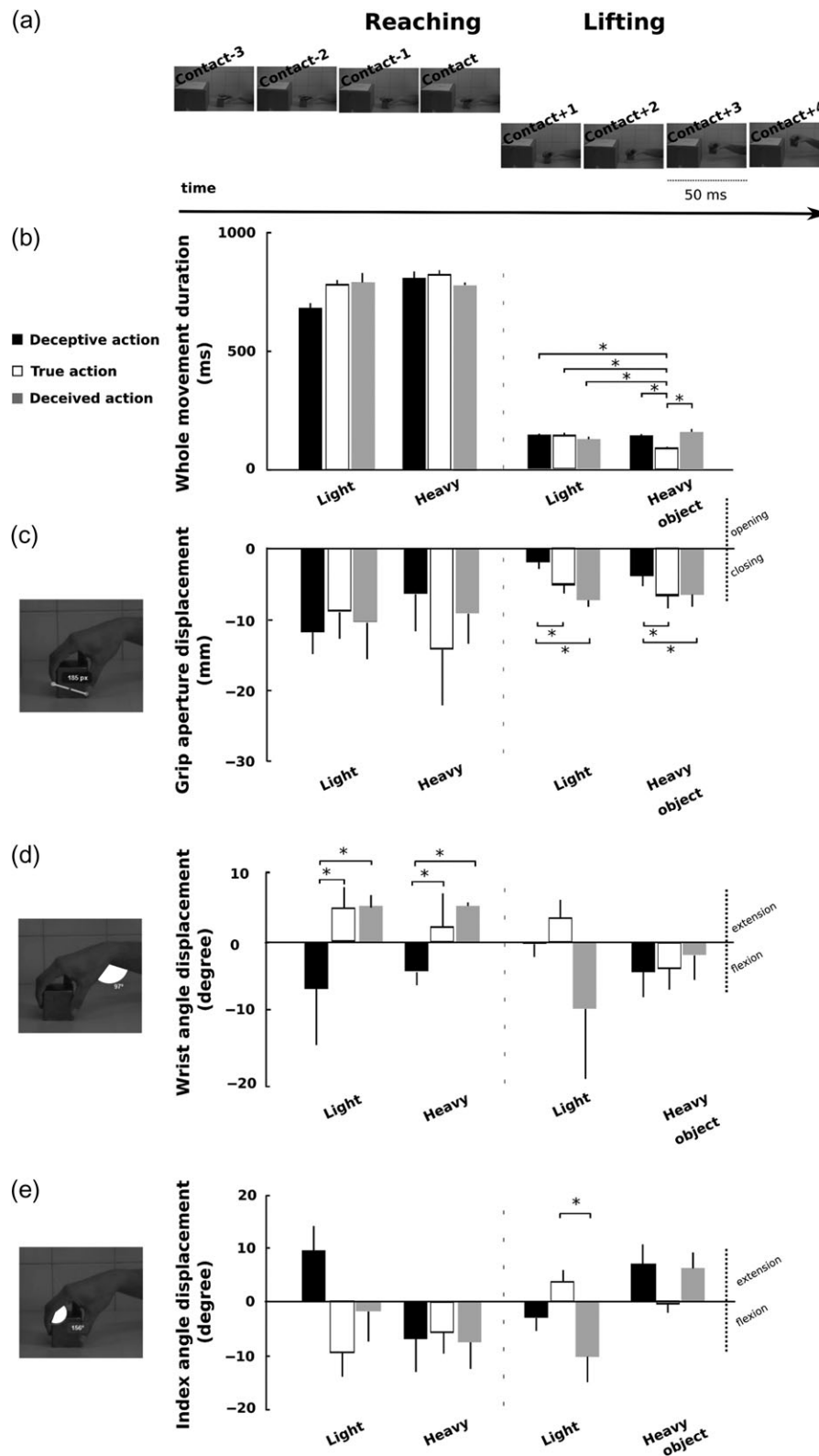


Figure 2. Kinematic parameters (Mean \pm SE) during the reaching and the lifting phase of the 3 actions performed by the actor upon the light or the heavy object. Asterisks indicate significant comparisons ($P < 0.05$). (a) The pictures depict the 4 consecutive frames covering the reaching phase (i.e., the first contact point frame and the preceding 3 frames, for a total of 200 ms) and the 4 consecutive frames covering the lifting phase (i.e., the last frame preceding the lifting onset and the following 3 frames, for a total of 200 ms). (b) Whole movement duration. Bars represent the whole duration of the reaching (on the left) and lifting movement (on the right) performed during the deceptive (black bars), true (white bars), and deceived (gray bars) actions performed on the light and the heavy objects. The whole reaching duration was defined as the time (in ms) occurring between the beginning of the movement and the first hand-object contact. The whole lifting duration corresponds to the time interleaving between the frame at which the vertical position of the dorsal part of the wrist started to rise up and the frame at which it reached

(3 levels: deceptive, truthful, and deceived conditions) and object weight (2 levels: heavy, light) as between-movies factors.

EMG Data During Action Execution

EMG data were processed offline. For each trial the signal was rectified and the data points of the recording were averaged into bins of 200 ms. The mean rectified EMG signal (in mV) in each bin was measured starting from 200 ms before the go signal up to 5000 ms later (26 bins). For each trial, the mean EMG signal of the first artifact-free bin was used as a baseline. To allow comparison between conditions and between participants, the mean EMG signal for each trial was expressed as a percentage from its baseline. Then, trials of the same condition were averaged by aligning the recordings on the moment of the hand-object contact, as marked on the EMG trace. The 12.16% of the trials were removed from the analysis because of failure in data acquisition or because participants started the movement before the go signal. Two participants were excluded from the analyses since they came up as outliers (being their signal greater than 2 SD from the group mean) for more than 4 consecutive bins.

For data reduction, actions were subdivided into 2 phases corresponding to the reaching and the lifting phases. Specifically, the reaching phase was defined by considering the 5 bins (1000 ms) before the contact with the object, while the lifting phase included the 5 bins (1000 ms) after the contact. The data for each muscle and for each phase were entered into separate repeated-measures ANOVAs with action condition (3 levels: deceptive, truthful, and deceived actions), object (2 levels: light or heavy), and bins (5 levels corresponding to the 5 bins) as within-subject variables.

Behavioral Data

Behavioral performance at the 2AFC WDT was analyzed using signal detection theory (SDT) and calculating measures of task sensitivity d' , which is a bias-independent index of participant's perceptual sensitivity to difference between stimuli, and of response criterion (or bias, c), which expresses to which extent one response is more probably over the other regardless of sensitivity (Green and Swets 2000). For calculating SDT parameters, "light-object" responses to light-object stimuli were considered as hits and "light-object" responses to heavy-object stimuli as false alarms. A preliminary analysis (2 sessions \times 3 action conditions repeated-measure ANOVA) showed no difference between the patterns of results in the initial behavioral session without TMS and in the TMS experimental session ($F < 1$ for the main effect of session and the action \times session interaction; $F(2,30) = 24.593$; $P < 0.001$ for the main effect of action condition), thus ruling out that previous exposure to the stimuli during the initial behavioral session affected performance. Therefore, only the data from the main TMS experimental session were further considered to ensure comparability with the MEPs data. The individual d' and the c values were entered into 2 separate 1-way repeated-measured ANOVAs with action condition (deceptive, truthful, and deceived) as a within-subjects variable. Furthermore, the d' values in the 3

action conditions were compared against zero by means of one-sample t-test (one tailed) to verify if participants were above chance in the discrimination of the object weight.

MEP Data

EMG pre-TMS activity was visually monitored during the whole duration of the experiment to ensure MEPs were recorded during full muscle relaxation. Trials with visible background EMG activity ($>100 \mu\text{V}$) preceding the TMS pulse were removed from the analysis. For all the remaining trials, we extracted the peak-to-peak amplitude (expressed in mV) of MEPs recorded from the FDI and ECR muscles during the eye-closed and static hand observation trials of the 2 baseline blocks (Pre, Post) and during the observation of deceptive, truthful, and deceived actions in the main experimental blocks. MEP amplitudes values were then averaged for each experimental condition, separately for each participant and for the 2 muscles, and used for further analyses. MEPs exceeding 2 SD from the respective mean peak-to-peak amplitude were excluded as outliers. To reduce skewness, the mean MEP amplitudes values for the remaining trials (87.76%, SD = 9.78% for the FDI muscle, and 89.75%, SD = 13.36% for the ECR) were submitted to a logarithmic transformation with log10 and constant value of 1 (Osborne, 2002). Then, we first compared MEPs recorded during the baseline sessions by means of a $2 \times 2 \times 2$ RM ANOVA with Time (Pre, Post), observed object (fixation cross, static hand), and muscle (FDI, ECR) as within-subjects factors. Once we verified that no changes in CSE occurred for the 2 muscles between the beginning and the end of the experimental session and that observing a resting-relaxed hand did not increase CSE as compared to observing a fixation cross, we calculated a measure of motor facilitation by subtracting the individual mean amplitude values of MEPs recorded at baseline (collapsing the fixation cross and static hand trials collected at the beginning and at the end of the TMS session) from those of MEPs recorded in each experimental condition. The resulting difference values were entered into a $3 \times 2 \times 2$ repeated-measures ANOVA with condition (3 levels: deceived, deceptive, or truthful actions), object weight (2 levels: heavy or light), and muscle (2 levels: FDI and ECR) as within-subjects variables.

To explore the relationship between cortico-spinal responses to the observation of our action conditions and the subjective measures of dispositional empathy we computed, separately for the 2 muscles, the Pearson correlation coefficients between the normalized mean MEP amplitudes in the 3 action conditions and the individual scores at the 4 subscales of the IRI. A False Discovery Rate correction procedure was used to control P -value for multiple correlation testing within each condition (4 correlations).

Results

Kinematics Analysis

Only a main effect of weight (weight: $F(1,30) = 5.08$, $P = 0.032$, $\eta_p^2 = 0.145$) emerged from the analysis of reaching duration, indicating that the movement lasted longer for heavy than for light objects, regardless of the action condition. No other effects

the 130% of its position at the contact point. (c-e) Spatial kinematic parameters. The pictures on the left represents: (c) the GA parameter, measuring the distance between the tips of the thumb and of the index finger (in pixels and then converted in mm); (d) the WA parameter; and (e) the index angle parameter. The graphs represent mean displacements, measured as the difference in the spatial parameter value at the last frame minus its value during the first frame considered in the reaching and in the lifting phases. For the GA (c), positive values indicate opening movement, while negative values indicate closing movement of the thumb and the index finger. For the wrist (d) and index (e) angle parameters, positive values indicate extension movement, while negative values indicate flexion movement.

were observed. Conversely, the ANOVA performed on the lifting duration revealed a significant interaction between weight and action condition ($F(2,30) = 4.77$, $P = 0.016$, $\eta_p^2 = 0.241$), because the truthful lifting of heavy objects lasted less than the lifting in all other types of videos (all $P < 0.048$). Thus, the lifting of heavy objects was delayed for both deceptive and deceived actions as compared to truthful lifting movements, suggesting that, even if this temporal kinematics parameter can be intentionally altered by deceptive intentions (Brault et al. 2012; Tidoni et al. 2013), it cannot dissociate between intentional deception and kinematics adjustment behavior (Fig. 2).

Considering the spatial parameters, no main effects or interactions were found for the GA displacement index during the reaching phase (all $P > 0.55$). Conversely, during the lifting phase, the ANOVA revealed only a main effect of action condition ($F(2,30) = 4.29$, $P = 0.023$, $\eta_p^2 = 0.222$), due to a smaller closure (i.e., less negative differences) of the index and thumb fingers for the deceptive actions with respect to the truthful ($P = 0.034$) and the deceived ($P = 0.013$) actions, which in turn did not differ ($P = 0.595$).

A different pattern of results emerged from the analysis performed on the WA displacement. The ANOVA on the reaching phase revealed a main effect of action condition ($F(2,30) = 3.409$, $P = 0.046$, $\eta_p^2 = 0.185$), with the WA displacement during the deceptive action being different with respect to that during either truthful ($P = 0.049$) or deceived actions ($P = 0.028$), which in turn did not differ ($P = 0.71$). Importantly, while for the truthful and the deceived conditions the positive values of the displacement index indicate wrist extension, for the deceptive condition the negative values indicate that the actor was flexing the wrist. No main effects or interaction resulted from the analysis of the WA displacement during the lifting phase (all $P > 0.30$). Thus, independently from the object weight, the actor was using wrist flexion during the reaching phase in order to disguise the observer.

Considering the IA displacement, while the main effects of action condition and weight and their interaction were non-significant during the reaching phase (all $P > 0.16$), we found a main effect of weight ($F(1,30) = 6.858$, $P = 0.014$, $\eta_p^2 = 0.186$) and a significant interaction between weight and action condition ($F(2,30) = 4.69$, $P = 0.017$, $\eta_p^2 = 0.238$) during the lifting phase. Crucially, post hoc comparisons showed that the lifting of the light object in the deceived condition involved a stronger flexion (i.e., more negative values) of the index finger as compared to the lifting of the same object in the truthful condition ($P = 0.012$). Thus, the displacement of the IA differentiated the truthful and the deceived conditions during lifting, but not during reaching.

EMG Data During Action Execution

The 3-way ANOVA performed on the EMG ratio of the FDI muscle in the reaching phase revealed a significant main effect of bins ($F(4,40) = 16.14$, $P < 0.001$, $\eta_p^2 = 0.617$) and a significant bins \times action condition interaction ($F(8,80) = 2.22$, $P = 0.035$, $\eta_p^2 = 0.181$). This interaction was due to a weaker activation of the FDI in the deceptive condition with respect to both the deceived ($P = 0.014$) and the truthful ($P < 0.001$) conditions in the last bin of the reaching phase, without any other differences between action conditions (all $P > 0.10$) (Fig. 3).

Conversely, the 3-way ANOVA performed on the FDI for the lifting phase revealed a significant main effect of weight ($F(1,10) = 5.62$, $P = 0.039$, $\eta_p^2 = 0.359$), a significant main effect of bins ($F(4,40) = 8.38$, $P < 0.001$, $\eta_p^2 = 0.456$), a significant condition

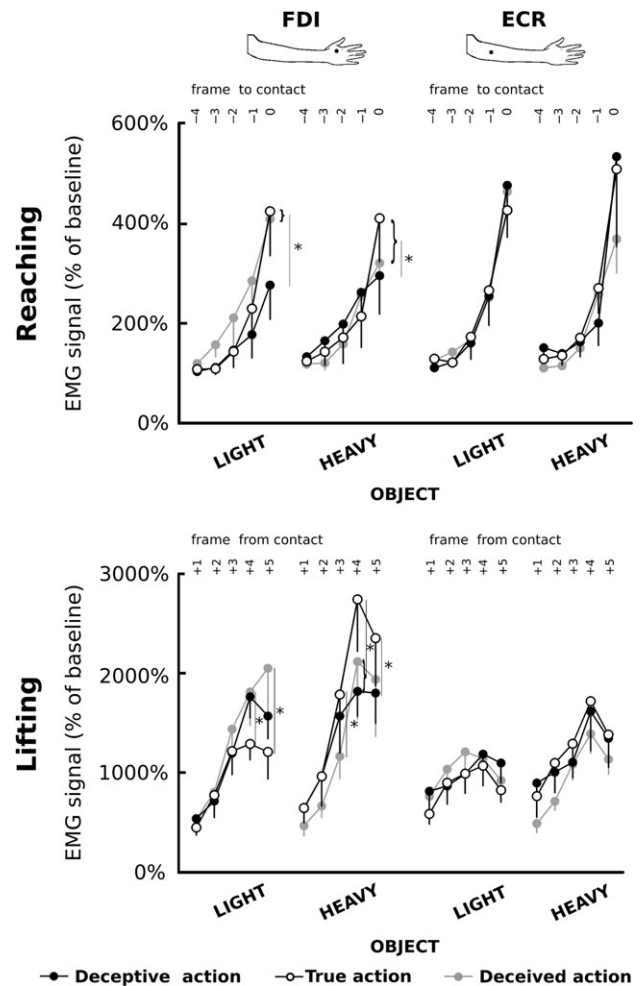


Figure 3. Mean (\pm SE) values of the EMG (rectified) signal, expressed as percentage of the baseline, recorded from the FDI (on the left) and ECR (on the right) muscles during the execution of deceptive (black dots), truthful (white dots), and deceived (gray dots) actions. Values are reported separately for the light and heavy objects as a function of the bins preceding (reaching phase, upper panel) or following (lifting phase, lower panel) the contact with the object. Asterisks indicate significant differences between the 3 action types at each bin ($P < 0.05$).

\times weight interaction ($F(2,20) = 4.54$, $P = 0.024$, $\eta_p^2 = 0.312$), a significant weight \times bins interaction ($F(4,40) = 3.34$, $P = 0.019$, $\eta_p^2 = 0.251$) and, crucially, a significant 3-way interaction between condition, weight, and bins ($F(8,80) = 2.49$, $P = 0.018$, $\eta_p^2 = 0.199$).

By considering the comparisons between the 3 conditions for each object weight at each bin, post hoc tests highlighted that no differences were detectable between the deceived and the truthful conditions in the initial 3 bins of the light object lifting (all $P > 0.34$). However, these 2 action conditions differed in the last 2 bins of the light object lifting due to a higher activation of the FDI muscle during the deceived condition with respect to the truthful condition (fourth bin: deceived action: mean = $1823.59 \pm 337.38\%$, truthful action: mean = $1299.53 \pm 159.78\%$, $P = 0.042$; fifth bin: deceived action: mean = $2064.84 \pm 572.69\%$, truthful action: mean = 1219.64 ± 276.67 , $P = 0.001$). The deceived and the truthful conditions did not differ during the first, the second, and the fifth bins of the heavy object lifting (all $P > 0.05$), but they were different in the central part (i.e., third and fourth bins). Crucially, differently from what

was observed during the lifting of the light object, here we found that the FDI activity was lower during the execution of deceived versus truthful actions (third bin: deceived action: mean = $1172.80 \pm 224.66\%$, truthful: mean = $1799.51 \pm 408.96\%$, $P = 0.016$; fourth bin: deceived action: mean = $2130.89 \pm 578.95\%$, truthful: mean = $2760.62 \pm 523.15\%$, $P = 0.007$). Thus, we observed that, once the actual weight of the object became known in the deceived condition, the FDI muscle was involved in adjusting the lifting of the object according to its actual weight. In particular, in the central and last phases of truthful lifting, the FDI muscle was more activated for the heavy than for the light object (third bin: $P = 0.023$; fourth bin: $P < 0.001$; fifth bin: $P < 0.001$), in keeping with the sensitivity of the hand muscles to object weight (Alaerts et al. 2010a, 2010b; Senot et al. 2011; Tidoni et al. 2013). Importantly, this weight-sensitivity was reflected into a reduced activation of the FDI while the actors were lifting an object that was expected to be lighter than its actual weight as compared to when they received truthful information. Conversely, in keeping with the greater flexion of the index finger during the deceived lifting of the light object that was obtained in the kinematic analysis of stimuli, the FDI activity was higher when lifting an object that was expected to be heavier than its actual weight, thus confirming that FDI activity allowed to dissociate the deceived and the truthful action conditions.

Moving to the post hoc comparisons between the deceptive and the true conditions, no difference was found during the lifting of the light object (all bins: $P > 0.053$) and in the first 3 bins of the lifting of the heavy object (all $P > 0.36$). Conversely, the FDI activity was higher during the true than the deceptive condition in the final part of the heavy object lifting, namely in the fourth bin (true: mean = $2760.62 \pm 523.15\%$, deceptive: mean = $1830.95 \pm 252.03\%$, $P < 0.001$) and in the fifth bin (true: mean = $2369.82 \pm 487.11\%$, deceptive: mean = $1814.82 \pm 307.33\%$, $P = 0.029$). Again, this modulation of the FDI activity according to the deceptive versus genuine intention of the actor, being dependent from the object weight, might reflect the higher activation of the FDI muscle in the truthful lifting of the heavy object. Indeed, during the truthful lifting, but not during the deceptive (or the deceived) lifting, the recorded activation of this muscle significantly increased when participants lifted the heavy object with respect to when they lifted the light one (third bin: $P = 0.023$; fourth bin: $P < 0.001$; fifth bin: $P < 0.001$). No differences were found between deceived and deceptive actions performed on the light or heavy object (all $P > 0.06$).

The ANOVA performed on the ECR EMG ratio in the reaching phase revealed only a significant main effect of bins ($F(4,40) = 18.15$, $P < 0.001$, $\eta_p^2 = 0.644$), which reflected higher activity of the ECR muscle in the fourth bin with respect to the first ($P = 0.018$) and second ($P = 0.018$) ones and in the fifth bin with respect to the previous ones (all $P < 0.001$). Concerning the lifting phase, the ANOVA showed a main effect of weight ($F(1,10) = 17.86$, $P = 0.002$, $\eta_p^2 = 0.641$), a main effect of bins ($F(4,40) = 6.71$, $P < 0.001$, $\eta_p^2 = 0.401$), and a significant 2-way bins \times weight interaction ($F(4,40) = 5.93$, $P < 0.001$, $\eta_p^2 = 0.372$). Post hoc comparisons revealed that the activity of the ECR in the last 2 bins was higher for the lifting of the heavy object than for the lifting of the light one (all $P < 0.001$). Crucially, in this case, the 3-way interaction between action condition, weight, and bins was far from significance ($F(8,80) = 0.518$, $P = 0.839$), thus ruling out a different involvement of this forearm muscle during the true, deceptive, and deceived lifting of the 2 objects. In sum, while the differential activation of the FDI for the lifting of the light and heavy objects provided information on whether the action was

truthful, deceptive, or deceived, the activity of the ECR muscle did not differentiate between these action conditions.

Behavioral Data

The repeated-measures ANOVA run on the d' values revealed a significant main effect of action condition ($F(2,30) = 22.48$, $P < 0.001$, $\eta_p^2 = 0.6$). Post hoc comparisons showed that participants were less accurate in judging the weight of the object when the actor tried to deceive them (deceptive condition: mean = -0.197 , SE = 0.137) with respect to either when the actor was fooled (deceived condition: mean = 0.562 , SE = 0.089 ; deceptive vs. deceived condition: $P < 0.001$) or during the truthful condition (truthful condition: mean = 0.473 , SE = 0.085 ; deceptive vs. truthful condition: $P < 0.001$), without differences between these 2 last genuine conditions (deceived vs. truthful condition: $P = 0.661$) (Fig. 4).

Importantly, the results of the repeated-measures ANOVA performed on the response criterion c showed no main effect of action condition ($F(2,30) = 2.45$, $P = 0.103$, $\eta_p^2 = 0.140$), thus ruling out changes in response bias during the WDT.

Lastly, t-tests comparisons revealed that performance was higher with respect to the chance level for the deceived and the truthful actions (deceived: $t(15) = 5.92$, $P < 0.001$; truthful: $t(15) = 5.57$, $P < 0.001$), but not for the deceptive action condition (deceptive: $t(15) = -1.44$, $P = 0.171$), indicating that participants were not able to recognize the object weight above chance when the actor was trying to deceive them.

These results indicate that our manipulation was effective in fooling the observers. Furthermore, they show that intentionally fooling, but not accidentally adjusted kinematics hindered the ability in discriminating object weight. Indeed, participants were able to estimate the actual object weight even when the actor was fooled and hence engaged in attuning the movement to accomplish the action.

MEP Data

No difference was found between MEP values recorded at the baseline sessions at the beginning and at the end of the experimental session (time: $F(1,15) = 0.13$, $P = 0.719$) independently of the observed stimulus (i.e., fixation cross or static hand) or of the recorded muscle (all $F(1,15) < 4.5$, $P > 0.05$). Consequently, baseline motor excitability did not change during the experiment nor was it affected by the observation of a static hand. Furthermore, our thresholding procedure allowed us to record comparable MEP amplitudes from both muscles.

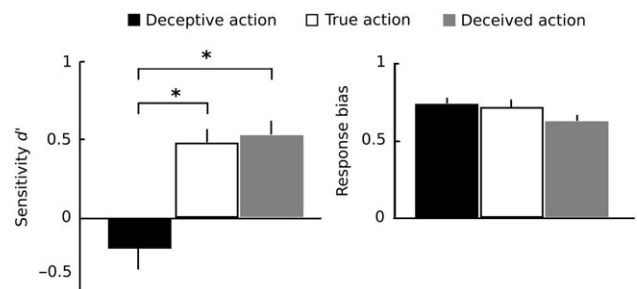


Figure 4. Effects of the observation of the deceptive (black bars), true (white bars), and deceived (gray bars) actions on participants' ability to perform the WDT. Values correspond to mean (\pm SE) sensitivity (d' , left) and response bias (right) for each condition. Asterisks indicate significant post hoc comparisons ($P < 0.05$).

By considering the analysis performed on the differential normalized indices of MEP amplitude modulation during the WDT, the 3-way action condition \times weight \times muscle repeated-measures ANOVA revealed a significant intercept effect ($F(1,15) = 13.53$, $P = 0.002$, $\eta_p^2 = 0.474$), indicating that overall MEP amplitudes during action observation were higher than at baseline (0 level). MEP amplitudes, however, were differently modulated depending on the type of action that was observed (action condition: $F(2,30) = 11.24$, $P < 0.001$, $\eta_p^2 = 0.428$). Post hoc analysis showed that MEPs were more enhanced during the observation of deceptive actions (mean = 0.059, SE = 0.027, $P = 0.011$) than during the observation of truthful (mean = 0.044, SE = 0.027) and deceived actions (mean = 0.033, SE = 0.022, $P < 0.001$). Comparable MEP amplitudes were, conversely, obtained overall from the 2 muscles during the observation of truthful and deceived actions ($P > 0.05$). The main effect of object weight and the interaction between object weight and action were not significant. We also found a significant main effect of muscle ($F(2,30) = 6.86$, $P = 0.019$, $\eta_p^2 = 0.313$), due to higher activation of the FDI muscle (mean = 0.055, SE = 0.034, $P = 0.019$) with respect to the ECR muscle (mean = 0.036, SE = 0.028), and crucially a significant interaction between action and muscle ($F(2,30) = 8.12$, $P = 0.002$, $\eta_p^2 = 0.351$), suggesting that the 3 actions modulated the MEPs recorded from the 2 muscles with different patterns. For the FDI muscle, we found that, respect to truthful actions (mean = 0.053, SE = 0.022), CSE increased during the observation of deceptive actions (mean = 0.074, SE = 0.022, $P < 0.001$), but it decreased during the observation of deceived ones (mean = 0.037, SE = 0.017, $P < 0.001$). For this hand muscle, the difference between deceptive and deceived actions was also significant ($P < 0.001$). The ECR CSE was enhanced during observation of deceptive actions (mean = 0.044, SE = 0.018) as compared to truthful (mean = 0.034, SE = 0.017, $P = 0.014$) and deceived actions (mean = 0.028, SE = 0.015, $P < 0.001$). However, in this case, no significant difference was obtained between deceived and truthful actions ($P > 0.09$) (Fig. 5). Thus, while observation of deceptive actions increased the CSE of both muscles, observation of unintentionally altered kinematics in deceived actions reduced CSE in a muscle-specific fashion. Indeed, CSE was reduced during the observation of deceived versus truthful actions only for the FDI muscle,

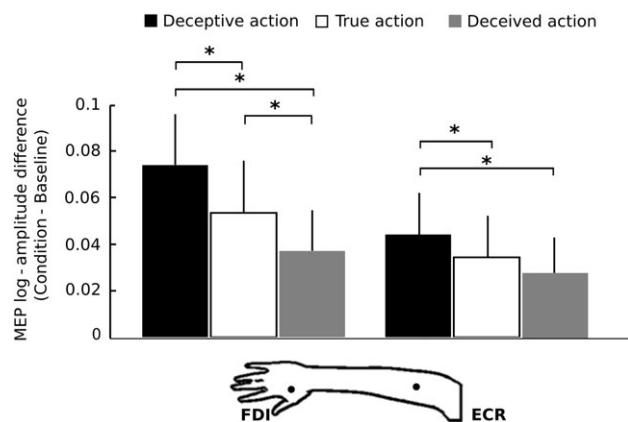


Figure 5. Effects of the observation of the deceptive (black bars), true (white bars), and deceived (gray bars) actions on CSE recorded from the right FDI (on the left) and the right ECR (on the right) muscles. Values correspond to the difference between the log values of the MEP amplitude [$\log(\text{mean MEP amplitude value in mV} + 1)$] during each experimental condition and at baseline. Error bars indicate SEs. Asterisks indicate significant post hoc comparison ($P < 0.05$).

whose kinematics allowed differentiating truthful and deceived actions in the videos.

No significant correlations were found between the normalized amplitudes of MEPs recorded from the 2 muscles and the individual scores at the 4 IRI subscales (all $P > 0.14$), suggesting that trait empathy did not influence motor resonance during the observation of the 3 action conditions of the current experiment.

Discussion

Several previous studies have shown that observing others' actions facilitates the observer's motor system (Fadiga et al. 2005; Avenanti et al. 2013). However, it is unclear whether such facilitation reflects the mapping of low-level action descriptors, as suggested by the match with the observed or inferred pattern of muscle activation in terms of muscle somatotopy and temporal deployment (Gangitano et al. 2001; Borroni et al. 2005; Urgesi et al. 2006; Valchev et al. 2015), or the higher-level aspects such as goals (Cattaneo et al. 2009, 2013; Cavallo et al. 2013) and intentions (Tidoni et al. 2013), as suggested by the generalization of effects across muscles (Borroni et al. 2008) or effectors (Senna et al. 2014; Finisguerra et al. 2015). In the present study, we aimed to test whether the modulation of the observer's motor system during observation of deceptive actions (Tidoni et al. 2013) reflects the decoding of the actor's intentions or the mapping of the kinematic adaptations required to fool the observer. We presented observers with videos of an actor reaching and lifting an object following a well-organized pattern of muscle activity. Importantly, each action could be performed with the goal of providing deceitful (i.e., deceptive condition) or truthful (i.e., truthful and deceived conditions) information, thus with fooling or genuine intentions. Furthermore, actions could be performed with an expected kinematic pattern (i.e., truthful actions) or present kinematic alterations that were aimed by either deceitful (i.e., deceptive actions) or genuine (i.e., deceived actions) intentions. Thus, by independently manipulating the intention and kinematic hierarchical levels of action representation (Hamilton and Grafton 2007), we could assess how they entail the observer's motor system. We found that, as compared to observing truthful actions, observing kinematic alterations determined by deceptive intentions induced a muscle-independent CSE facilitation, while observing kinematic alterations determined by genuine intentions induced a muscle-specific CSE inhibition. This pattern of modulation was not affected by the different levels of dispositional empathy reported by the observers. Taken together, our results suggest that both intention and kinematic hierarchical levels of action representation modulate the motor system, but they likely do so through 2 dissociable mechanisms, as reflected by different direction of CSE modulation and muscle specificity.

Deceptive Intentions but not Kinematic Adaptations Fool the Onlookers

In everyday life, we can discriminate the weight of an object by observing its lifting movement. Our behavioral results confirmed the ability to recognize an object weight by observing honest actors lifting it in a typical way. Indeed, subtle weight variations introduce specific kinematic changes of the actor's reaching and lifting movements and the observer is sensitive to this information (Runeson and Frykholm 1981; Hamilton et al. 2004). In particular, the kinematic analysis of our truthful

action videos showed that heavy as compared to light objects triggered movements characterized by longer reaching duration and shorter lifting duration, as well as by higher FDI contraction. Thus, as far as our kinematic and EMG analyses allowed us to ascertain, movement duration and index finger flexion were a trustful cue to estimate object weight. Crucially, differences in lifting duration according to object weight were masked during performance of actions with deceptive intention, since the actors tended to prolong the lifting of the heavy object in order to minimize the postural cues that may inform on the object weight. In a similar vein, the actors tended to exaggerate the flexion of the wrist during the reaching phase and to reduce the closure of the index and thumb fingers during the lifting phase (with reduced FDI contraction) when they acted with the intent to fool the observer (deceptive actions) as compared to when they acted with genuine intentions (truthful and deceived actions). These effects were independent from the object weight. Providing exaggerated body-related cues that induce others to make incorrect action predictions and minimizing or delaying informative postural cues are fundamental aspects of effective deception (Brault et al. 2010; Brault et al. 2012). Here, we showed that these alterations of movement kinematics succeeded in blurring the observer's sensitivity in predicting object weight by observing reaching-to-grasp and lifting movements. Importantly, accidental alterations of movement kinematics to adapt to unexpected object weight (Johansson and Westling 1988) could be detected and used by the observers to predict the actual object weight in the deceived condition, as no difference in the observers' predictions of truthful and deceived actions was found. In particular, the kinematic analysis showed that, while movement duration, wrist flexion and GA could not help to make a distinction between truthful and deceived actions, the index finger was more flexed (and the FDI more contracted) during the lifting of an object that was expected to be heavier as compared to the corresponding truthful actions. Thus, while the exaggerated flexion of the wrist and the alterations of movement duration successfully fooled the observers in the deceptive condition, the sudden adjustments of the index finger kinematics while grasping an unexpected-weight object could be promptly detected by the observers in order to update their predictions on the actual object weight in the deceived condition. Importantly, these 2 conditions elicited different patterns of modulation on the observer's motor cortex.

The Muscle-Independent CSE Enhancement “Mirrors” Deceptive Intention

Understanding others' behavior seems to imply the matching of the observed action kinematics with the motor program that would be required for the observer to produce the same action (Calvo-Merino et al. 2006). This matching process is used to anticipate the future course of actions (Kilner et al. 2004; Wilson and Knoblich 2005; Aglioti et al. 2008; Urgesi et al. 2010) and predict the underlying intention (Kilner et al. 2007). Compatibly with the role of motor simulation in action understanding studies showed that performing a given action influences the perception of others' movements (Kilner et al. 2003; Hamilton et al. 2004). For instance, constraining observers to lift a light or a heavy box affected their perceptual judgments about the weight of objects lifted by another individual (Hamilton et al. 2004). Furthermore, it has been proposed that the detection of a conflict between the observed kinematics and the motor pattern that the observers predict through their

stored internal model may allow the recognition of deceptive intents in others' behavior (Ekman and O'Sullivan 1991; Bond et al. 1992; Wolpert et al. 1995; Grèzes et al. 2004a).

In keeping with a strong link between action simulation and the ability to detect deception, Tidoni et al. (2013) demonstrated that perceiving deceptive actions facilitates the observers' motor system more than observing truthful actions. Our findings for the deceptive condition are in keeping with those of Tidoni et al. (2013) and can be explained in the light of the predicting coding framework (Wilson and Knoblich 2005; Kilner et al. 2007). In this view, the increase in CSE in the deceptive condition may reflect the increase in the prediction error, generated by the mismatch between the priors related to both the intention and the action kinematics and the incoming information, and the need to adjust the predictions in order to minimize the error.

Crucially, however, the deception-related facilitation of motor activity in Tidoni et al.'s (2013) study was highly muscle-specific, since it differently involved the hand and forearm muscles according to their motor role during actual execution of deceptive versus truthful actions. Conversely, here we found a muscle-independent CSE facilitation that cannot be explained by a direct mapping of the observed kinematics to attain deceptive behavior. Indeed, no differences were present between the deceptive and the 2 conditions with genuine intent for the kinematic parameters involving the index finger, since both the index angle and the GA were not affected by deceptive intention. Moreover, while the MEPs for both muscles were more facilitated during the observation of deceptive versus truthful actions, the EMG activity of the FDI muscle was lower during the execution of deceptive versus truthful actions. In a similar vein, even if changing wrist kinematics was used to fool the observers, this involved an exaggerated flexion, which maps the motor role of wrist flexor muscles (e.g., flexor carpi radialis as in Tidoni et al. 2013), but not of the ECR muscle (Borroni et al. 2005). This was also suggested by the analysis of EMG activity during the actual execution of the same movements, which showed that the ECR was not modulated during the execution of deceptive versus truthful actions. Thus, we suggest that the muscle-independent facilitation of the observer's motor cortex during observation of deceptive actions in the present study was specifically triggered by coding deceptive intentions rather than by coding the altered kinematic pattern required to accomplish a fooling action.

Nevertheless, the discrepancy between the high degree of topographic specificity reported in the previous study of deceptive action detection (Tidoni et al. 2013) and the muscle-independent facilitation that we have found here may be explained by the differences between the tasks used in the 2 studies. Crucially, task differences were 2-fold: the presence of the deceived condition, which was present in our study and absent in the study by Tidoni et al. (2013), and the feature of the observed action that participants had to discriminate in the 2 tasks, namely the actual weight of the object in our study and actor's deceptive intention in the Tidoni et al.'s (2013) study. Concerning the first aspect, differences can be due to the fact that, in the absence of deceived trials, participants could rely on the detection of kinematic alterations to perform a dichotomic discrimination between a deceptive and a genuine action, because kinematic alterations co-varied with deceptive intention. Thus, the modulation of motor facilitation obtained in such a 2AFC deception detection task may reflect either the coding of deceptive intentions or the mapping of the associated kinematic alterations. Conversely, since also deceived trials

were included in our study, the detection of kinematic alterations per se could not be used to discriminate genuine versus deceptive intentions, because kinematic alterations were also present for the deceived actions, which were driven by genuine intentions. In this way, the modulation of motor facilitation obtained in the 2AFC WDT might reflect only the coding of deceptive intention. Regarding the second aspect, we can speculate that our WDT taps on a more ecological situation, in which other individuals may perform movements with kinematic alterations even in the absence of a deceptive intention and the observer needs to infer which is the intention underlying such alterations in order to predict and react to their behavior rather than just saying if they are fooling or not. During the observation of interacting partners, intention comprehension is crucial in so far as it allows predicting what they are actually doing, rather than only understanding if they are attempting to deceive or not. In fact, in some competitive settings (e.g., sport) we can assume that others are trying to fool us, but predicting the outcome of their fooling actions may still be a challenging task that is crucial for planning an appropriate response. In our study, not only was the detection of kinematic alterations insufficient to detect a deceptive intention but also the participants had to infer the actual weight of the object by taking into account the observed kinematics and the inferred intention of the actor. These task differences might explain the different degree of muscle specificity in motor facilitation obtained in the 2 studies. Indeed, recent studies have demonstrated the high flexibility of motor resonance in the observers' brain, as the amount of motor facilitation can be modulated by the instructions given to the participants (Bardi et al. 2015) and can reflect either direct mirroring or complementing an observed action according to contextual variables (Sartori et al. 2013).

Here, by presenting both deceptive and deceived actions in a WDT we could dissociate the processing of deceptive intention and the detection of kinematic alterations and provided evidence that the activity of the observer's motor system can mirror the intentional level of observed actions beyond processing kinematic alterations.

The Muscle-Specific CSE Decrease Mirrors Kinematic Adaptations

While the muscle-independent facilitation during observation of deceptive actions cannot be explained by mapping the observed kinematics, the muscle-specific decrease in CSE for the FDI, but not for the ECR muscle, during the observation of deceived actions with respect to the observation of true actions seems to directly map the observed kinematic alterations. Indeed, from a kinematic point of view, the 2 conditions underlined by a genuine intention (i.e., truthful and deceived actions) differed only for a more limited displacement of the index angle during the deceived condition, but no differences were observed for the wrist parameters. In a similar vein, the analysis of the EMG activation during action execution revealed that only the FDI, but not the ECR activity changed during the lifting of an object with an unexpected weight. Coherently, MEPs data showed a muscle-specific decrease of CSE for the FDI muscle, but not for the ECR muscle. This effect might reflect the mapping of the amount of displacement of the index angle during the lifting phase. For instance, Cattaneo et al. (2013) showed that the CSE of the observer's finger muscles correlated with the velocity of the movements to operate pliers. Similarly, we observed a decrease in CSE for the FDI muscle during the observation of deceived actions, which were, indeed,

characterized by slower index finger displacement with respect to the truthful condition.

Alternatively, in the predictive coding framework (Wilson and Knoblich 2005; Kilner et al. 2007), the muscle-specific decrease of the FDI CSE in the deceived condition might reflect the observation of unpredicted movements. In this condition, once the object weight became known, the actors altered their lifting behavior, particularly for the index finger parameters. Thus, after a prediction was made on the basis of the initial reaching and grasping movements, the new sensory information conflicted with the predicted kinematics, leading to a decrease of the activity of the inaccurate motor representation. This interpretation is in keeping with previous studies showing CSE decrease during the observation of unpredicted movements. For example, Gangitano et al. (2004) reported suppression of mirror-like facilitation when participants saw an unnatural grasping obtained by delaying finger aperture. A similar suppression effect was obtained by Tomeo et al. (2013) when expert goalkeepers observed kicking actions containing incongruent body kinematics and by Mattiassi et al. (2014) when the observers viewed a sequence of 2 incongruent finger movements, even if the first movement was masked not to be consciously detected by the participants. In a similar vein, when the observers expected a specific kinematic pattern depending on a semantic cue informing on the object weight (Senot et al. 2011) or affordance (Janssen et al. 2015) or on the context of the action (Amoruso and Urgesi 2016), observation of an action pattern that disconfirmed their expectations suppressed motor resonance.

In other ways, studies have found increased motor facilitation while participants observed (Romani et al. 2005; Avenanti et al. 2007) or imagined (Bufalari et al. 2010) impossible movements, which violate the biomechanical constraints of the human body, or in experts during observation of erroneous piano fingerings (Candidi et al. 2014) or basketball throws (Aglioti et al. 2008). In all these cases, however, the observed movement was incorrect and mismatched the (correct) kinematic pattern to successfully obtain the action outcome. Thus, the increase of motor facilitation obtained in these studies likely reflected the detection of erroneous motor performance. Conversely, in our deceived action condition, abrupt kinematics alterations occurred once the actors lifted an object of unexpected weight, but these alterations were aimed at successfully adapting the movement to the actual object weight. Thus, in our case and in all those studies (Senot et al. 2011; Tomeo et al. 2013; Mattiassi et al. 2014; Janssen et al. 2015) showing suppression of motor facilitation for unpredicted actions, the expected motor representation was incorrect and the observers had to rely on the incoming kinematic adaptations to understand the actual action outcome. In sum, we propose that the muscle-specific CSE decrease during observation of deceived actions might be due to the discrepancy between the kinematics pattern erroneously predicted on the basis of the reaching and grasping phases and the kinematic pattern correctly predicted on the basis of the observed adaptations during the lifting phase.

Previous neuroimaging studies (Grèzes et al. 2004a, 2004b) have shown that violations of the observer's predictions engage a network of temporal, prefrontal, and cerebellar areas. In particular, Grèzes et al. (2004b) used an action observation condition in which the actors could or could not have correct information about the weight of the to-be-lifted object and the observer had to judge if the actor had correct expectations about the object weight. In a further study, Grèzes et al. (2004a) compared this condition with a deception detection task, in which the actors always had correct information about the

weight of the to-be-lifted object, but they could try to deceive the observer. In both studies, participants were asked to make judgments about mental states (i.e., weight expectations or deceptive intention) by observing action kinematics and noticing the kinematic alterations required to adapt to unexpected object weight or to deceive the observer. Accordingly, actions judged as reflecting false belief and actions judged as reflecting deceptive intention were both associated to activations in the superior temporal sulcus, lateral orbitofrontal cortex, dorsomedial frontal cortex, and cerebellum. Nevertheless, the 2 conditions differed because of greater activation for noticing deceptive intentions in areas involved in affective processing, namely in the amygdala and the anterior cingulate cortex. However, since the 2 conditions were not administered within the same task and to the same group of observers, it was not clear whether these activations reflected detection of kinematic alterations, false belief or deceptive intention. By presenting deceived and deceptive actions within the same WDT, our study attempted to dissociate the motor response to kinematic adaptations and actor's intention.

Conclusions

The results of the present study show that the observer's motor system may code both the intention and the kinematic aspects of deceptive actions. In particular, while we corroborate previous findings showing that observing deceptive intentions increases motor facilitation during action observation, by implementing a condition in which the observers are faced with kinematic alterations not aimed by deceptive intentions, we were able to dissociate the effects of intention and kinematics coding. We found that processing kinematic adaptations embedded in non-deceptive actions induced a muscle-specific reduction rather than an increase of motor facilitation. Thus, the increase of motor facilitation for deceptive actions, which was not muscle-specific, is likely to reflect processing of the underlying intention rather than of the kinematics to attain fooling behavior. This suggests that both low- and high-level aspects of observed actions seem to be mapped onto the observer's motor system. The different direction of their modulation on motor facilitation and the different level of muscle specificity, however, might suggest that they are mediated by different neurophysiological mechanisms.

Classical views of MNS activity suggests that the direct matching of the observed kinematics on the observer's motor representations might underlie the ability to attribute an intentional meaning to the movement of others (Rizzolatti and Sinigaglia 2007). However, it is also possible that high-level processes involving mentalizing system areas (i.e., medial prefrontal cortex but also the temporal-parietal junction and posterior cingulate cortex) might mediate the intentional modulation of motor resonance (e.g., Catmur 2015).

Although the present single-pulse TMS study cannot elucidate the source of the modulations of M1 activity according to intention and kinematics, combining this paradigm with a systematic investigation of the role of fronto-parietal MNS and mentalizing system areas might offer a promising tool to investigate the different and complementary contributions of these networks to social perception and cognition.

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Notes

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