

Mirroring avatars: dissociation of action and intention in human motor resonance

Paola Borroni,¹ Alessandra Gorini,² Giuseppe Riva,^{2,3} Stéphane Bouchard⁴ and Gabriella Cerri⁵

¹Department of Medicine, Surgery and Dental Sciences, University of Milano Medical School, Milan, Italy

²Istituto Auxologico Italiano IRCSS, Applied Technology for Neuro-Psychology Laboratory, Milan, Italy

³Department of Psychology, Catholic University of the Sacred Heart, Milan, Italy

⁴Cyberpsychology Laboratory, Department of Psychoeducation and Psychology, Pavillon Alexandre-Taché, Université du Québec en Outaouais, Gatineau, Quebec, Canada

⁵Department of Human Physiology, University of Milano Medical School, Milan, Italy

Keywords: action intention, avatar, mirror neuron system, motor resonance, TMS

Abstract

Observation of others' actions induces a subliminal activation of motor pathways (motor resonance) that is mediated by the mirror neuron system and reflects the motor program encoding the observed action. Whether motor resonance represents the movements composing an action or also its motor intention remains of debate, as natural actions implicitly contain their motor intentions. Here, action and intention are dissociated using a natural and an impossible action with the same grasping intention: subjects observe an avatar grasping a ball using either a natural hand action ('palmar' finger flexion) or an impossible hand action ('dorsal' finger flexion). Motor-evoked potentials (MEPs), elicited by single transcranial magnetic stimulation of the hand area in the primary motor cortex, were used to measure the excitability modulation of motor pathways during observation of the two different hand actions. MEPs were recorded from the opponens pollicis (OP), abductor digiti minimi (ADM) and extensor carpi radialis (ECR) muscles. A significant MEP facilitation was found in the OP, during observation of the grasping phase of the natural action; MEPs in the ADM were facilitated during observation of the hand opening phase of the natural action and of both opening and grasping phases of the impossible action. MEPs in the ECR were not affected. As different resonant responses are elicited by the observation of the two different actions, despite their identical intention, we conclude that the mirror neuron system cannot utilize the observer's subliminal motor program in the primary motor cortex to encode action intentions.

Introduction

Observation of actions done by others evokes a resonant response in the observer's motor pathways, mediated by the mirror neuron system (MNS) (Rizzolatti & Sinigaglia, 2010), which reflects the specific motor program encoding the observed action, without producing any movement in the observer. The functional role of this subliminal motor activation remains elusive. The original hypothesis (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996) was that, by reproducing a known neural pattern in the motor system of observers, motor resonance directly encodes the observed action and mediates the immediate understanding of the action and its intention. However, in a more economical explanation such subliminal activation could simply encode the movements comprising the observed action and thus facilitate its repetition, as for instance during motor learning or imitation (Iacoboni *et al.*, 1999; Rizzolatti *et al.*, 2001; Mattar & Gribble, 2005; Vogt *et al.*, 2007). Furthermore, these hypotheses need not be mutually exclusive, if we concede that the activation of the MNS may have different meanings, depending on the level at which

action observation is processed (Blakemore & Frith, 2005; Grafton & Hamilton, 2007).

To separate the above hypotheses it is necessary to dissociate an action from its intention. Here we consider the immediate proximal intention of an action, not its more abstract, distal intention regarding the ultimate reason why it is performed (Hamilton & Grafton, 2006; Pacherie, 2008). As natural actions implicitly contain their motor intentions, we approach this problem with an experimental paradigm in which subjects observe a natural and an impossible hand action with the same intention (grasping a ball). In the two actions 'grasping' is achieved either by a natural sequence (fingers flexed in the natural 'palmar' direction) or by an impossible sequence (fingers flexed in the unnatural 'dorsal' direction). As, by definition, an impossible action cannot be performed by a human actor, we programmed an avatar – a computer-animated graphic representation of a human – to execute the two actions.

The premise here is that natural actions are complex sequences of movements implemented by specific motor programs, whereas impossible actions are sequences of movements that cannot be executed and thus coded by any natural motor program. Therefore, the simplest hypothesis predicts that only the observation of the natural action would engage the MNS and evoke a motor resonant response.

Correspondence: Dr P. Borroni, as above.
E-mail: paola.borroni@unimi.it

Received 16 November 2010, revised 19 April 2011, accepted 25 May 2011

If, however, the MNS were to be engaged by both natural and impossible actions, i.e. if motor resonant responses could be evoked in both conditions (as indeed we see here), then the question of intention could be addressed more incisively. In fact, if motor resonance represents the intention of the action, it should reproduce the observer's own natural grasping program, regardless of the avatar's action – as the intention is the same, MEP responses should be the same during the observation of the natural and impossible grasping. Otherwise, if motor resonance encodes the movements composing the action, it should be a faithful replica of such movements, regardless of the intention – as the movements observed in the natural and impossible grasping are different, MEP responses should be different. Specifically, MEP modulation should reflect the expected activation of the muscles tested in the specific phases of the observed actions. For instance, MEPs in a finger flexor would be expected to show facilitation in the natural sequence during the observation of the grasping phase, in which fingers are flexed to grasp the ball, but not in the impossible sequence, in which fingers are never flexed; similarly, MEPs in a finger abductor muscle would be expected to show facilitation in the opening phase of both the possible and the impossible sequences, when subjects observe the hand open.

Materials and methods

Experiments were carried out on 32 healthy adult volunteers (20 females and 12 males, age 21–36 years), after approval by the ethics committee of the Istituto Auxologico Italiano and written informed consent of each subject.

Motor-evoked potentials (MEPs) were used to measure the excitability modulation of cortical and spinal motoneurons during observation of two different actions (with the same intention) performed by the avatar's right hand.

In Experiment 1 MEPs were recorded simultaneously from the right opponens pollicis (OP) and abductor digiti minimi (ADM), two muscles normally utilized during the grasping action for finger closing and opening respectively. In Experiment 2 recordings were obtained from the right OP and the extensor carpi radialis (ECR), a muscle involved in the stabilization of the wrist during finger flexo-extension. MEPs were evoked by single-pulse transcranial magnetic stimulation (TMS) of the hand area in the left primary motor cortex of right-handed volunteers. Of the different subjects who participated in each experiment, half observed a 5-s video clip of a natural motor sequence, showing an avatar grasping a small ball positioned on a table, and the other half observed an identical video clip, except just for the frames in which the avatar grasps the ball using an impossible sequence (Fig. 1). We decided that the natural and impossible actions should be observed by two separate groups of subjects because subjects of early pilot experiments, who had observed both, reported that having seen one action influenced how they viewed and interpreted the other. Thus the four experimental groups were: Experiment 1 = OP + ADM/natural ($n = 10$), OP + ADM/impossible ($n = 10$); Experiment 2 = OP + ECR/natural ($n = 6$), OP + ECR/impossible ($n = 6$).

Subjects were sitting in an armchair with prone hands resting on lateral supports and were instructed not to move during the experimental trials. They watched a video on a 17-inch high-resolution computer screen placed at eye level, at a distance of about 1 m. The room was quiet and lights were dimmed to minimize acoustic and visual distractions. Videos started with the same presentation lasting a few seconds, zooming on a male avatar standing near a table where a red ball was resting (see Supporting Information Videos S1 and S2). This scene was shown to familiarize subjects with the whole figure of

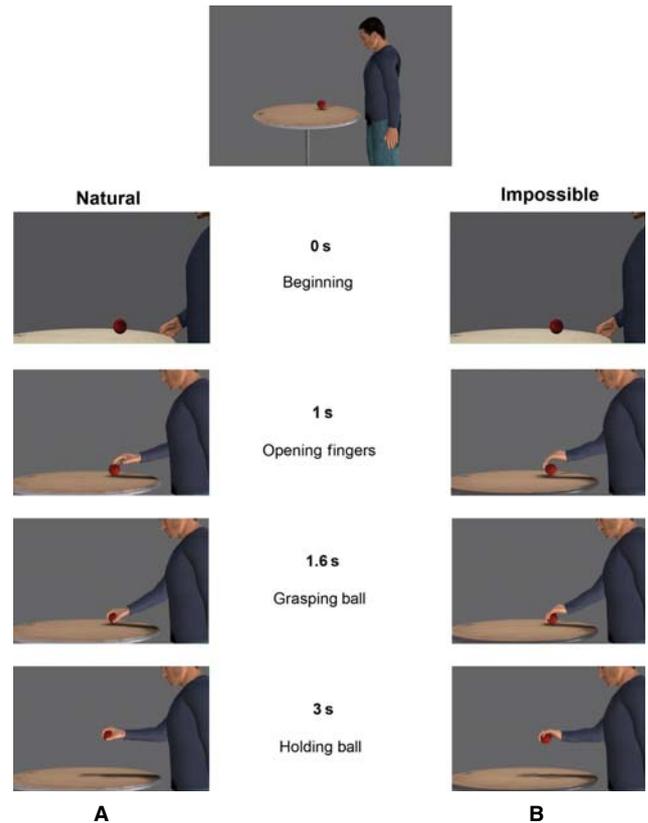


FIG. 1. The four vertical images in each column are frames of the video clip showing the avatar's hand positions at each of the four TMS stimulation delays in the possible (A) and impossible (B) conditions. 0 s (Baseline) = beginning of the avatar's hand movement; 1 s (Opening Fingers) = frame in which the fingers are maximally opened; 1.6 s (Grasping Ball) = frame in which the avatar grasps the ball; 3 s (Holding Ball) frame in which the avatar lowers the ball on the table after having lifted it. The upper middle image shows the entire avatar's body, presented to the subjects at the beginning of the video. Note that the context and the environment in which the two actions were performed were identical.

the avatar; subsequently, during the experimental trials, only the final portion of the video, a close-up of the avatar's hand grasping the ball, was repeated. The close-up part of the videos started with the right hand of the avatar moving from its resting position towards the ball. Then, in the natural grasping video, the hand opened with a finger extension and grasped the ball with a normal 'palmar' finger flexion, while in the impossible grasping video the hand was supinated while opening with finger extension and grasped the ball with an abnormal 'dorsal' finger flexion; after a brief holding phase the sequences were concluded. At the end of the experiment subjects were always asked to describe the observed action – none had any difficulty recognizing it as a grasping action, despite the often explicitly commented strange manner in which it was performed.

Experimental paradigm

Motor-evoked potentials were recorded with self-adhesive bipolar surface electrodes over each muscle belly. Electromyographic signals were amplified, filtered (10 Hz to 1 kHz) and digitally converted (sampling rate 5 kHz). The head of each subject was restrained by a comfortable pillow wrapping around the neck and supported by a fixed head rest. A mechanical arm held a figure-of-eight-shaped coil connected to a magnetic stimulator (Magstim 200; Magstim Co. Ltd,

Whitland, UK; maximal power 2.2 T). The coil was positioned and fixed on the left primary motor cortex so as to activate both selected muscles, and the stimulator output was set at about 110% of the motor threshold of the less excitable muscle (defined as the intensity giving three MEP responses out of six stimuli). Examples of MEPs recorded in the OP muscle are shown in Fig. 2.

The excitability time-course was explored at four relevant randomized delays from the onset of the close-up part of the video: (i) 0 s = Baseline, avatar's hand just beginning to move; (ii) 1 s = Opening phase, moment of maximal finger aperture during the grasping action; (iii) 1.6 s = Grasping phase, moment in which the avatar's fingers grasp the ball; and (iv) 3 s = Holding phase, moment in which the avatar's hand lowers the ball on the table after having lifted it.

For each subject, 100 presentations were obtained, so that overall 25 MEP responses were recorded at each of the four delays (0, 1.0, 1.6 and 3.0 s). Presentations were grouped in five blocks of 20 trials, and subjects were instructed that they could rest at the end of each block. Within each block of 20 trials, MEPs were evoked and recorded five times at each specific delay, chosen in a semi-random order (completing a set of four delays before starting the next set) by the data acquisition program. In order to do this, at the very first frame of the close-up part of the video a synchronizing signal in the video was fed into the computer, which triggered both the TMS stimulator and acquisition program at one of the selected delays. Presentations were spaced by 8-s dark screen intervals (resulting in inter-stimulus intervals lasting a minimum of 10 s). To exclude the possibility of voluntary or involuntary mimic activity of the observer, the background electromyographic activity was monitored in the muscles throughout the whole video presentation.

Data analysis

Motor-evoked potential responses in each subject and for each muscle were measured as peak-to-peak amplitude. In each subject single MEP values in all four delays were normalized to the average of MEP values in the first delay (Baseline, time = 0 s, avatar's hand just beginning to move). After normalization, responses at each delay were averaged across all subjects, as illustrated in Figs 3 and 4. Average values of MEPs in the first delay are shown in Table 1.

In both experiments, data were analysed with a $4 \times 2 \times 2$ three-way repeated-measures ANOVA with delay (0, 1.0, 1.6 and 3.0 s) and muscle (OP-ADM or OP-ECR) as within-subject factors and movement (natural and impossible) as between subject factor. Dunn's *t*-test,

with Bonferroni correction for multiple comparisons was subsequently used to evaluate differences between different delays in each separate experimental group. Statistical analysis was conducted using SPSS software (SPSS Inc., Chicago, IL, USA).

Results

Excitability of the neural pathways controlling the experimental muscles was modulated by observation of both natural and impossible grasping actions. MEP modulation was differently affected by observation of the different delays during the different grasping actions. The avatar's hand was just as effective as a human hand (Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Montagna *et al.*, 2005) in evoking a resonant MEP modulation of hand muscles during the observation of a grasping action.

Experiment 1

Normalized OP and ADM MEP modulation data were analysed by means of a $4 \times 2 \times 2$ repeated-measures ANOVA, with delay (0, 1.0, 1.6 and 3.0 s) and muscle (OP-ADM or OP-ECR) as within-subject factors and movement (natural and impossible) as between-subject factor. A significant main effect was found for the delay factor ($F_{3,954} = 7.014$, $P < 0.001$), indicating that considering both muscles in both movement conditions together, MEP modulation was different at the different delays. A significant main effect was also found for the muscle factor ($F_{1,318} = 5.066$, $P < 0.025$), indicating that, pooling all different delays and movements, the normalized MEP average amplitude was different in the two muscles; this effect is mainly due to the larger amplitude of ADM MEPs in the impossible movement condition (see Table 1). The muscle/movement and muscle/delay interactions were significant ($F_{1,318} = 5.066$, $P < 0.025$; $F_{3,954} = 6.728$, $P < 0.001$, respectively) indicating that MEPs recorded from the two muscles were modulated differently in the two movement conditions and across the different delays. Most importantly, the three-way interaction between muscle, delay and movement was significant ($F_{3,954} = 11.214$, $P < 0.001$), indicating that MEP facilitation patterns were different when all three factors are considered.

Multiple comparisons, performed on the data from the four experimental conditions (Dunn's *t*-test, Bonferroni-corrected level of significance $P < 0.01$), revealed that during the observation of the natural action, OP MEPs were significantly facilitated in the Grasping phase compared with all other phases (Grasping-Baseline $P < 0.01$,

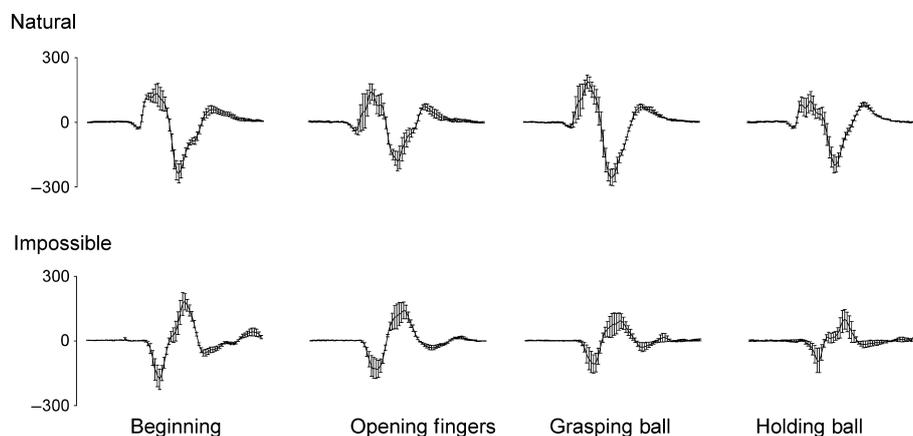


FIG. 2. Examples of MEP amplitude modulation (μV) in the OP muscle from two representative subjects during observation of the possible (top) and impossible (bottom) videos, recorded at the four experimental delays (0, 1, 1.6 and 3 s). Each trace represents the mean (\pm SE) of 20 recordings.

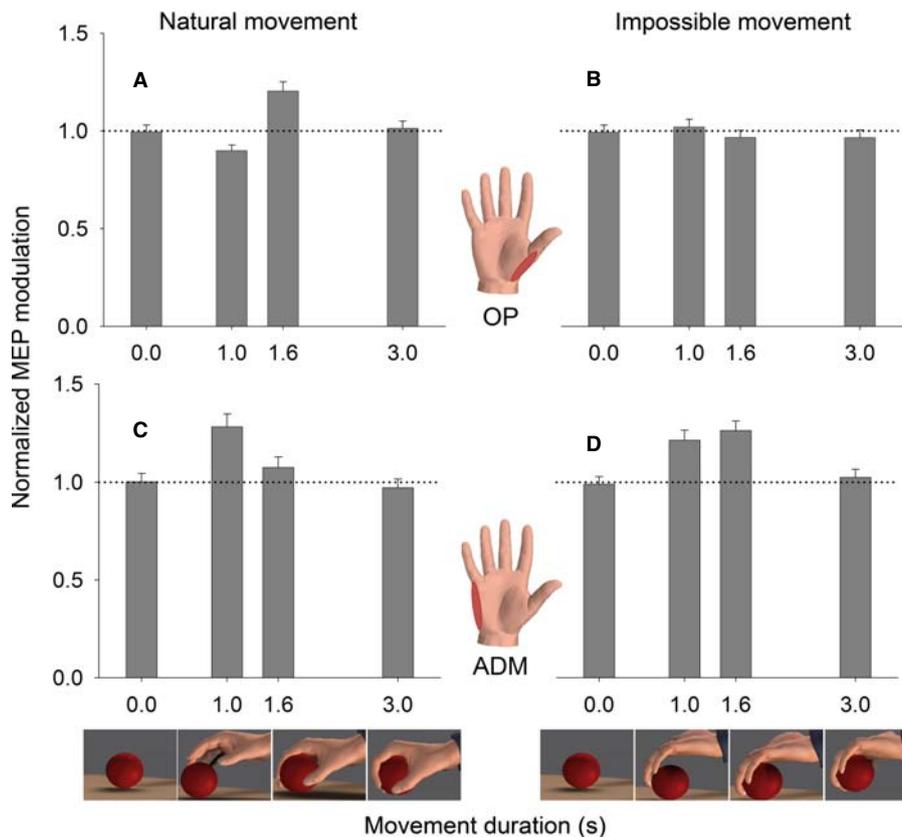


FIG. 3. MEP amplitude variations in OP and ADM muscles (vertical gray bars, means \pm SE) recorded at four selected delays (0, 1, 1.6 and 3 s) during the observation of the avatar's possible or impossible grasping action. The small figures on the bottom are the video frames illustrating positions of the hand at the four delays. OP MEPs in the natural action (A) were significantly facilitated during the Grasping phase with respect to all other phases (see text). OP MEPs in the impossible action (B) were not modulated significantly. ADM MEPs in the natural action (C) were significantly facilitated in the Opening phase with respect to all other phases. In the impossible action (D) ADM MEPs in the Opening and Grasping phases were not different from each other, but were significantly facilitated with respect to the Baseline and Holding phases.

Grasping-Opening $P < 0.001$, Grasping-Holding $P < 0.01$), which were not different from each other (Fig. 3A), while ADM MEPs were significantly facilitated during observation of the natural action in the Opening phase with respect to those in all other phases (Opening-Baseline $P < 0.01$, Opening-Grasping $P < 0.01$, Opening-Holding $P < 0.001$), which were not different from each other (Fig. 3C). During observation of the impossible grasping, OP MEPs were not modulated in any phase of the observed movement (Fig. 3B). ADM MEPs in the Opening and Grasping phases were not different from each other, but significantly facilitated with respect to those in the Beginning and Holding phases (Opening-Baseline $P < 0.001$, Opening-Holding $P < 0.01$, Grasping-Baseline $P < 0.001$, Grasping-Holding $P < 0.001$), which were not different from each other (Fig. 3D).

Thus, OP and ADM MEPs were facilitated in a pattern fully consistent with the normal activation of these muscles during the execution of the observed actions: the thumb opponent was facilitated during the observation of fingers closing around the ball (Grasping phase in the natural action), and the little finger abductor during finger opening and extension (Opening phase in the natural action; Opening and Grasping phases in the impossible action).

Experiment 2

Normalized OP and ECR MEP modulation data were also analysed by means of a $4 \times 2 \times 2$ repeated-measures ANOVA. No significant main effect was found for any of the factors (delay, muscle or movement).

Both delay/movement and muscle/movement interactions were significant ($F_{3,786} = 9.278$, $P < 0.001$ and $F_{1,262} = 28.542$, $P < 0.001$ respectively), indicating that MEP amplitude in the natural and impossible movements was affected differently at the different delays, and that MEPs recorded from the two muscles were modulated differently in the two movement conditions. As in Experiment 1 the muscle/delay/movement interaction was significant ($F_{3,786} = 13.178$, $P < 0.001$) indicating that MEP facilitation patterns were different when all three factors were considered.

The pattern of facilitation in the OP muscle was very similar to that obtained in the previous experiment – during the observation of the natural action OP MEPs were significantly facilitated during the Grasping phase (Dunn's t -test multiple comparisons, Bonferroni-corrected level of significance $P < 0.01$; Grasping-Baseline $P < 0.001$, Grasping-Opening $P < 0.001$, Grasping-Holding $P < 0.001$) with respect to those in all other phases, which were not different from each other (Fig. 4A). In this experiment, during the observation of the impossible action, OP MEPs were significantly dis-facilitated in the Grasping phase with respect to Baseline ($P < 0.001$, Fig. 4B), but not with respect to the Opening and Holding phases. This dis-facilitation of the OP with respect to Baseline was probably due to the small number of subjects and disappeared if the OP data from Experiments 1 and 2 were merged ($n = 16$; Dunn's t -test multiple comparisons, Bonferroni-corrected level of significance $P < 0.01$), while the facilitation of this muscle during the Grasping phase of the natural action was confirmed by

TABLE 1. Mean MEP amplitudes (\pm SD) of the first delay (Baseline = 0 s) in all the different conditions of both experiments

Experiment	Action	Muscle	MEP amplitude (μ V)
1	Natural	OP	352.48 \pm 285
		ADM	319.65 \pm 271
	Impossible	OP	385.59 \pm 352
		ADM	423.98 \pm 359
2	Natural	OP	466.94 \pm 340
		ECR	382.81 \pm 281
	Impossible	OP	334.78 \pm 268
		ECR	274.35 \pm 197

merging the data (Grasping-Baseline $P < 0.001$, Grasping-Opening $P < 0.001$, Grasping-Holding $P < 0.001$). No significant modulation was measured in the ECR muscle, in either natural and impossible conditions (Fig. 4C and D).

Discussion

The excitability of motor pathways controlling hand muscles normally involved in grasping (OP and ADM) was modulated by the observation of both the natural and the impossible grasping actions. Observation of the two different actions elicited different motor resonant responses, despite the fact that these actions shared an identical intention, suggesting that intention is not encoded by the MNS in the subliminal motor program produced by the primary motor

cortex. In fact, the lack of a motor resonant response in the OP muscle during the observation of the impossible grasping implies that in this condition observers do not utilize their own natural motor program for grasping – flexion of the thumb – to encode the grasping intention, but have no difficulty understanding it. Furthermore, although the resonant motor program developed in both OP and ADM muscles provides a coherent neural representation of the natural action, during the observation of the impossible action the resonant program evoked in the ADM muscle codes for finger opening, while no resonant program is evoked in the OP muscle to code for thumb closing. This pattern of activation would not be useful in representing the grasping intention of that action in the observer's motor pathways.

The neural pattern of the observer's resonant motor program, on the other hand, reproduced faithfully the observed movements composing both the natural and the impossible grasping actions, as illustrated by the following considerations regarding the data. Motor pathways to the OP muscle were activated during the observation of the natural but not of the impossible grasping. From the motor point of view this is not surprising, as thumb flexion is a movement comprising the first action, but not the second, given that in the impossible grasping the thumb is always extended. ADM MEPs, by contrast, were facilitated by the observation of both possible and impossible grasping, and in fact, the fifth finger is actively abducted during the Opening phase in the natural action and of both Opening and Grasping phases in the impossible action.

Therefore, during observation of the natural action the excitability of corticospinal fibers, and of their target spinal motoneurons driving the muscles, changed in a consistent and predictable way, at specific

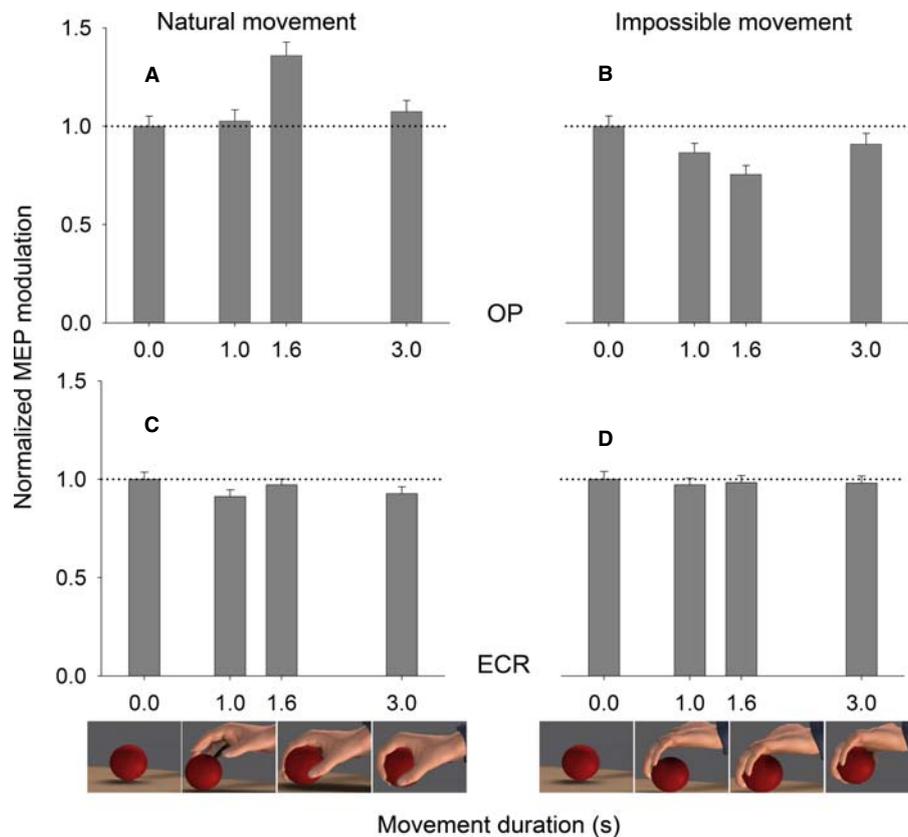


FIG. 4. MEP amplitude variations in the OP and ECR muscles (vertical gray bars, means \pm SE) recorded at four selected delays (0, 1, 1.6 and 3 s) during the observation of the avatar's natural or impossible grasping action. The small figures on the bottom are the video frames illustrating positions of the hand at the four delays. In the natural action (A) OP MEPs were significantly facilitated in the Grasping phase compared with all other phases, which were not different from each other (see text). OP MEPs in the impossible action (B) in the Grasping phase were significantly dis-facilitated with respect to the Baseline phase only. ECR MEPs were not different from each other in either the natural or the impossible action (C and D, respectively).

points in times during the observed action, i.e. following the same temporal pattern it would have followed had the action been actually performed. As a consequence, MEPs in both OP and ADM were modulated consistently with the motor commands that would have been dispatched to each muscle during the actual execution of the grasping action – facilitation of the OP for the opposition of the thumb when the avatar's hand was closing around the ball and in the ADM for the abduction of the fifth finger during hand opening. Consistently, during the observation of the impossible action the MEP facilitation was observed only in the ADM muscle; this facilitation also mirrored the motor program necessary to obtain the movements observed, i.e. the abduction of the fifth finger during hand opening but also during the closing of the hand around the ball, as in this case the grasping was achieved by a 'dorsal' finger flexion, in which the fifth finger is actively abducted.

An alternative interpretation of the OP data is that the lack of modulation in the OP muscle during the observation of the impossible action is due to a global failure of impossible actions to evoke a motor resonant response, because they are either totally novel or mechanically unfeasible. In this case an inferential mechanism, different from the embodied simulation, would be utilized by observers to understand the observed action and its intention (Brass *et al.*, 2007; Grammont, 2010). The MNS may not be engaged by an impossible action because (i) it is simply not recognized as belonging to the observer's natural motor repertoire, (ii) it evokes a feeling of something bizarre or uncomfortable for the acting person or (iii) it is seen as an action that can only be performed by an avatar (i.e. it is only virtual). In all these cases observation of the impossible grasping could fail to evoke a corresponding motor program capable of modulating the excitability of motor pathways and thus MEP amplitude. This interpretation is, however, dispelled by the ADM results. To date, no studies have investigated the effect of the observation of impossible actions on motor resonance and only a few that of impossible movements (Romani *et al.*, 2005; Avenanti *et al.*, 2007), utilizing simple intransitive finger movements. These studies have shown that motor pathways are facilitated during the observation of impossible movements. The present results in the ADM muscle confirm these findings, and exclude the alternative interpretation, by showing that motor pathways are activated during the observation of both natural and impossible grasping in a way that is fully consistent with the functional utilization of this muscle during active movement. Thus the first hypothesis, stating that the observation of the impossible action does not evoke a motor resonant response because it does not engage the observer's MNS, can be rejected.

Interestingly, a significant response in the ADM is elicited in the Opening phase during the natural grasping, even though in the video the fifth finger is only partially visible in the background, consistent with the behavior of mirror neurons in the ventral premotor cortex of the monkey that can be activated by observed actions only partially seen by the animal (Umiltà *et al.*, 2001). This ADM result also strongly suggests that the lack of modulation in the OP muscle during the observation of the impossible action is not due to the fact that the thumb is not fully visible in the forefront. Similarly, although the wrist was always perfectly visible, observation of either natural or impossible actions did not evoke a motor resonant response in the ECR muscle.

Finally, we interpret the absence of MEP modulation in both OP and ADM during observation of the Holding phase in either natural and impossible actions as a consequence of the fact that this is not a critical phase of the grasping action, whereas the essence of grasping is embodied in the hand opening and closing movements. Similarly, we propose that the lack of modulation in the ECR muscle during the observation of either natural or impossible actions results from the fact

that this muscle is mainly involved in stabilizing the wrist during the grasping movement and thus is not directly involved in the primary moving action.

The present results appear to be at odds with a recent report showing that MEPs in the OP muscle are modulated by the goal and not by the muscular pattern necessary to grasp an object with 'reverse pliers' (Cattaneo *et al.*, 2009). However, we believe that the two studies explore radically different processes because an action acquires fundamentally different properties once it is performed with a tool. In the study by Cattaneo *et al.*, MEPs were recorded from the OP muscle during observation of grasping actions performed with normal or 'reverse' pliers, both with and without the presence of a small object to be grasped (goal). In the absence of the goal, the modulation of MEP amplitude reflected the muscular pattern involved in the execution of the observed action, i.e. necessary to use the pliers. During the observation of goal-directed actions, MEPs were instead modulated in opposite ways with the two pliers, with reverse pliers increasing MEP amplitude during object grasping, despite the hand-opening movement necessary to obtain it. This different modulation, however, could be due not so much to the presence of the goal *per se*, but to the fact that goal has changed from grasping the pliers with the hand to grasping the object with the pliers, so that the tool has become a natural extension of the body (Iriki *et al.*, 1996; Maravita & Iriki, 2004; Ferrari *et al.*, 2005; Hihara *et al.*, 2006; Umiltà *et al.*, 2008). Recordings from bimodal neurons in the somatosensory cortex suggest that during tool use their visual receptive fields are altered to include the entire length of the tool, providing a modified neural representation of the hand schema in which the tool has been incorporated (Iriki *et al.*, 1996). Similar recordings from neurons in the ventral premotor cortex and even some neurons in the primary motor cortex of monkeys that had learned to use a tool to grasp objects show that the tool is coded in the motor system as if it were an artificial hand (Umiltà *et al.*, 2008).

A second important result of our study is that simple movements, as long as they can be programmed and executed by the observer, can be effectively coded by the MNS in the primary motor cortex, even when embedded in impossible actions. In order for these simple movements to evoke a motor resonant response it might be necessary that they be essential components of goal-oriented actions, i.e. the presence of the goal may confer salience to these movements (Avenanti *et al.*, 2007; Gazzola *et al.*, 2007; Cattaneo *et al.*, 2009), which may not have evoked a motor resonant response, especially if embedded in a novel, non-familiar action. This hypothesis will have to be tested in future studies. The underlying mechanism may be similar to what has been proposed for motor learning and imitation (Iacoboni *et al.*, 1999; Wolpert *et al.*, 2003; Buccino *et al.*, 2004) – the MNS can be activated by viewing known elementary modular movements easily recognized by a naive observer and only subsequently recombined in new motor sequences. In this view the existence of a goal might become the premise, not the consequence, of motor resonance, so that recognizable simple movements can be encoded even when they are part of actions that do not belong to the observer's motor repertoire, as long as the motor intention of the action is familiar. This would support the hypothesis that it is not motor resonance that makes intention understanding possible, but it is intention understanding that makes motor resonance useful for other aspects of action perception, such as anticipating how an action will unfold (Kilner *et al.*, 2004; Csibra, 2007) or motor learning. In fact, it would seem that if the MNS is able to select and activate a specific motor program to match the observed action, then the action must have already been understood elsewhere, upstream to primary motor areas.

In this perspective, once information has been gathered about an observed action and its intention by higher sensory-motor brain areas

(e.g. premotor and parietal cortices, Gallese *et al.*, 1996; Fogassi *et al.*, 2005; Hamilton & Grafton, 2006; Kilner *et al.*, 2007; Gallese, 2009; Rizzolatti & Sinigaglia, 2010), and this very information has made the observed action relevant for the observer, it could also be transmitted to and utilized by the primary motor cortex, where it could play an important role in 'simpler' cognitive functions of the motor system, such as motor learning and imitation. If we consider the immediate results of motor resonance, in fact, we see that the subliminal activation of a motor program results in a specific and functionally well-timed increase in excitability of cortical and spinal motoneurons (Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Strafella & Paus, 2002; Borroni *et al.*, 2005; Montagna *et al.*, 2005), i.e. in a lower threshold for their activation, should they be solicited to produce actual movement. In other words, the immediate effect of motor resonance is to favor the repetition of the action observed.

Although these results demonstrate that the representation of action intentions cannot be based on the neural pattern of the observer's resonant motor program in the primary motor cortex, they do not exclude the possibility that intention may be encoded as a sensory-motor representation in some higher area of the MNS, such as premotor or parietal cortex (Gallese *et al.*, 1996; Fogassi *et al.*, 2005; Hamilton & Grafton, 2006; Kilner *et al.*, 2007; Rizzolatti & Sinigaglia, 2010). The available evidence about the role played by the MNS in understanding actions and their intentions (Fogassi *et al.*, 2005; Iacoboni *et al.*, 2005; Brass *et al.*, 2007; de Lange *et al.*, 2008; Umiltà *et al.*, 2008; Cattaneo *et al.*, 2009) is compelling but not definitive. The results of the experiments that originally led to the formulation of the direct-matching theory (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996), namely the recording of mirror neurons in the ventral premotor cortex (and subsequently parietal cortex) of macaque monkeys, have been revolutionary in their power to unify the neural substrate of action perception and action execution, and there is now ample evidence that premotor/parietal circuits are activated by action observation also in the human brain (Rizzolatti & Sinigaglia, 2010). From the theoretical point of view, the direct-matching theory relies on three reasonable but unproven assumptions. First, that the premotor/parietal circuits would follow the same functional rules in both the production and the perception of movement – being involved in the organization of complex actions rather than simple movements (Fogassi *et al.*, 2001; Umiltà, 2004) during execution, it is assumed that the activation of the premotor/parietal cortex during observation would represent this same level of organization. Second, that the activity of the premotor/parietal cortex in organizing complex actions in execution implies the translation of abstract intention into practical action when, in fact, the question of where and how in the brain ideomotor transformations takes place is one of the fundamental unresolved issues of motor control (Stock & Stock, 2004). Third, even conceding that ideomotor transformations took place in premotor/parietal circuits, that the activation of this brain area during action observation would automatically give access to the more abstract intentional content of the action. The above assumptions, in turn, find their conceptual origin in the classical theoretical postulate that an 'efference' copy of a descending motor command is normally utilized by the agent as a neural simulator, and thus as a predictor, of the sensory-motor consequences of the movement such command would engender (von Holst & Mittelstaedt, 1950; Sperry, 1950; Bubic *et al.*, 2010; Press *et al.*, 2010). The application of this concept to the MNS requires a further extension of the theoretical forward model, in which reading of the motor neural pattern of activation induced by observation would be the functional equivalent of the 'efference' copy and could be utilized by the observer to simulate and predict the sensory-motor consequences of an observed movement (Wolpert

et al., 2003) thus understanding its intention (Kilner *et al.*, 2007). Although theoretically engaging as a working hypothesis, such broad interpretation, which requires a series of important assumptions, is somewhat overreaching with respect to our actual knowledge of the neural mechanisms underlying it. Although a recent elegant study has shown that the primary somatosensory cortex is activated during voluntary movement in the absence of sensory feedback and pointed to the ventral premotor cortex as a likely candidate area of origin of the efference copy during voluntary movement (Christensen *et al.*, 2007), the complex interactions between movement (executed or observed) and sensory consequences (predicted or experienced) are far from understood.

From a more practical point of view, the experimental approach to how intentions of observed actions are coded in the MNS has been confounded by addressing at times proximal intentions (the motor goal of an action, e.g. grasping an object), at times distal intentions (the ultimate goal of an action, e.g. grasping an object for different purposes), in different experimental conditions (with or without the use of tools) and at different levels of the sensori-motor system (motor, premotor and parietal cortex). The complexity of the data is probably an inevitable consequence of the complexity of the problem; however, if the hypothesis that comprehension of an observed action and its intention are based on the activation of a motor program in the observer's motor pathways is to be confirmed, then questions about what aspects of the action are understood, what is meant by motor program, which pathways are involved and whether this is true for any kind of action must be answered.

The present study tries to address some of these questions by recalling the physiological constraints and neural properties of the motor system that necessarily underlie and define its function in both action execution and perception (Borroni *et al.*, 2008; Cabinio *et al.*, 2010). As motor programs are mediated by the primary motor cortex, which organizes the precise spatial and temporal muscle activation necessary to perform an action, it is relevant to ask whether observers understand actions by reading subliminal motor programs in the primary motor cortex. Our results suggest that they do not – although our experimental subjects developed a perfectly good motor resonant response during observation of both natural and impossible grasping actions, they would not have been able to understand the goal of the impossible grasping based on a direct reading of the neural pattern of the resonant motor program. This program is coding for finger opening, a motor strategy obviously never used to grasp, while it is not coding for thumb closing, a motor strategy obviously necessary to grasp. The results effectively dissociate the coding of the single movements composing an observed action from the coding of its proximal intention and demonstrate that low-level kinematics, not intentions of actions, are encoded in the neural pattern of the observer's resonant motor program in the primary motor cortex.

Supporting Information

Additional supporting information may be found in the online version of this article:

Video S1. Normal grasping action video clip observed by subjects.

Video S2. Impossible grasping action video clip observed by subjects.

Please note: As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset by Wiley-Blackwell. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Acknowledgements

This study was supported by grants PUR 2008 (12-1-5201001-76), from the Università degli Studi di Milano and Project for International Scientific and Technological Cooperation (SAL-53, no. 16970), from the Regione Lombardia. We thank Roma Siugzdaite for her help with statistical analysis.

Abbreviations

ADM, abductor digiti minimi; ECR, extensor carpi radialis; MEP, motor evoked potential; MNS, mirror neuron system; OP, opponens pollicis; TMS, transcranial magnetic stimulation.

References

- Avenanti, A., Bolognini, N., Moravita, A. & Aglioti, S.M. (2007) Somatic and motor components of action simulation. *Curr. Biol.*, **17**, 2129–2135.
- Blakemore, S. & Frith, C. (2005) The role of motor contagion in the prediction of action. *Neuropsychologia*, **43**, 260–267.
- Borroni, P., Montagna, M., Cerri, G. & Baldissera, F. (2005) Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. *Brain Res.*, **1065**, 115–124.
- Borroni, P., Montagna, M., Cerri, G. & Baldissera, F. (2008) Bilateral motor resonance evoked by observation of a one-hand movement: role of the primary motor cortex. *Eur. J. Neurosci.*, **28**, 1427–1435.
- Brass, M., Schmitt, R.M., Spengler, S. & Gergely, G. (2007) Investigating action understanding: inferential processes versus action simulation. *Curr. Biol.*, **17**, 2117–2121.
- Bubic, A., von Cramon, D.Y. & Schubotz, R.I. (2010) Prediction, cognition and the brain. *Front. Hum. Neurosci.*, **4**, 1–15.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G.R., Zilles, K. & Rizzolatti, G. (2004) Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron*, **42**, 323–334.
- Cabinio, M., Blasi, V., Borroni, P., Montagna, M., Iadanza, A., Falini, A. & Cerri, G. (2010) The shape of motor resonance: right or left handed? *NeuroImage*, **51**, 313–323.
- Cattaneo, L., Caruana, F., Jezzini, A. & Rizzolatti, G. (2009) Representation of goal and movements without overt motor behavior in the human motor cortex: a transcranial magnetic stimulation study. *J. Neurosci.*, **29**, 11134–11138.
- Christensen, M.S., Lundbye-Jensen, J., Geertsen, S.S., Petersen, T.H., Paulson, O.B. & Nielsen, J.B. (2007) Premotor cortex modulates somatosensory cortex during voluntary movements without proprioceptive feedback. *Nat. Neurosci.*, **10**, 417–419.
- Csibra, G. (2007) Action mirroring and action interpretation: an alternative account. In Haggard, P., Rosetti, Y. & Kawato, M. (Eds), *Sensorimotor Foundations of Higher Cognition. Attention and Performance XXII*. Oxford University Press, Oxford, pp. 435–459.
- Fadiga, L., Fogassi, L., Pavesi, G. & Rizzolatti, G. (1995) Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.*, **73**, 2608–2611.
- Ferrari, P.F., Rozzi, S. & Fogassi, L. (2005) Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *J. Cogn. Neurosci.*, **17**, 212–226.
- Fogassi, L., Gallese, V., Buccino, G., Craighero, L., Fadiga, L. & Rizzolatti, G. (2001) Cortical mechanisms for the visual guidance of hand grasping movements in the monkey. A reversible inactivation study. *Brain*, **124**, 571–586.
- Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F. & Rizzolatti, G. (2005) Parietal lobe: from action organization to intention understanding. *Science*, **308**, 662–667.
- Gallese, V. (2009) Motor abstraction: a neuroscientific account of how action goals and intentions are mapped and understood. *Psychol. Res.*, **73**, 486–498.
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996) Action recognition in the premotor cortex. *Brain*, **119**, 593–609.
- Gangitano, M., Mottaghy, F.M. & Pascual-Leone, A. (2001) Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, **12**, 1489–1492.
- Gazzola, V., Rizzolatti, G., Wicker, B. & Keysers, C. (2007) The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *NeuroImage*, **35**, 1674–1684.
- Grafton, S.T. & Hamilton, A.F.de.C. (2007) Evidence for a distributed hierarchy of action representation in the brain. *Hum. Mov. Sci.*, **26**, 590–616.
- Grammont, F. (2010) Can I really intend more than what I am able to do? In Grammont, F. & Legrand, D. (Eds), *Naturalizing Intention in Action*. MIT Press, Cambridge, MA, pp. 117–139.
- Hamilton, A.F.de.C. & Grafton, S.T. (2006) Goal representation in the human anterior intraparietal sulcus. *J. Neurosci.*, **26**, 1133–1137.
- Hihara, S., Notoya, T., Tanaka, M., Ichinose, S., Ojima, H., Obayashi, S., Fujii, N. & Iriki, A. (2006) Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. *Neuropsychologia*, **44**, 2636–2646.
- von Holst, E. & Mittelstaedt, H. (1950) Das Refferenzprinzip. *Naturwissenschaften*, **37**, 464–476.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C. & Rizzolatti, G. (1999) Cortical mechanisms of human imitation. *Science*, **286**, 2526–2528.
- Iacoboni, M., Molnar-Szakas, I., Gallese, V., Buccino, G., Mazziotta, J.C. & Rizzolatti, G. (2005) Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.*, **3**, 529–535.
- Iriki, A., Michio, T. & Yoshiaki, I. (1996) Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport*, **7**, 2325–2330.
- Kilner, J.M., Vargas, C., Duval, S., Blakemore, S. & Sirigu, A. (2004) Motor activation prior to observation of a predicted movement. *Nat. Neurosci.*, **7**, 1299–1301.
- Kilner, J.M., Friston, K.J. & Frith, C.D. (2007) Predictive coding: an account of the mirror neuron system. *Cogn. Process.*, **8**, 159–166.
- de Lange, F.P., Spronk, M., Willems, R.M., Toni, I. & Bekkering, H. (2008) Complementary systems for understanding action intentions. *Curr. Biol.*, **18**, 454–457.
- Maravita, A. & Iriki, A. (2004) Tools for the body (schema). *Trends Cogn. Sci.*, **8**, 79–86.
- Mattar, A.A.G. & Gribble, P.L. (2005) Motor learning by observing. *Neuron*, **46**, 156–160.
- 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. *Eur. J. Neurosci.*, **22**, 1513–1520.
- Pacherie, E. (2008) The phenomenology of action: a conceptual framework. *Cognition*, **107**, 179–217.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. (1992) Understanding motor events: a neurophysiological study. *Exp. Brain Res.*, **91**, 176–180.
- Press, C., Gherri, E., Heyes, C. & Eimer, M. (2010) Action preparation helps and hinders perception of action. *J. Cogn. Neurosci.*, **22**, 2198–2211.
- Rizzolatti, G. & Sinigaglia, C. (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.*, **11**, 264–274.
- Rizzolatti, G., Fogassi, L. & Gallese, V. (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.*, **2**, 661–670.
- Romani, M., Cesari, P., Urgesi, C., Facchini, S. & Aglioti, S.M. (2005) Motor facilitation of the human cortico-spinal system during the observation of biomechanically impossible movements. *NeuroImage*, **26**, 755–763.
- Sperry, R.W. (1950) Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. Comp. Physiol. Psychol.*, **43**, 482–489.
- Stock, A. & Stock, C. (2004) A short history of ideo-motor action. *Psychol. Res.*, **68**, 176–188.
- Strafella, A.P. & Paus, T. (2002) Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport*, **11**, 2289–2292.
- Umiltà, M.A. (2004) Frontal cortex: goal-relatedness and the cortical motor system. *Curr. Biol.*, **14**, R204–R206.
- Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. & Rizzolatti, G. (2001) I know what you are doing: a neurophysiological study. *Neuron*, **31**, 155–165.
- Umiltà, M.A., Escola, L., Intskirvell, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V. & Rizzolatti, G. (2008) When pliers become fingers in the monkey motor system. *Proc. Natl Acad. Sci. USA*, **105**, 2209–2213.
- Vogt, S., Buccino, G., Wolschlag, A.M., Canessa, N., Shah, N.J., Zilles, K., Eichhoff, S.B., Freund, H., Rizzolatti, G. & Fink, G.R. (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. *NeuroImage*, **37**, 1371–1383.
- Wolpert, D.M., Doya, K. & Kawato, M. (2003) A unifying computational framework for motor control and social interaction. *Phil. Trans. R. Soc. Lond. B, Biol. Sci.*, **358**, 593–602.