

Simulating the Future of Actions in the Human Corticospinal System

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Perception of the final position of a moving object or creature is distorted forward along its actual or implied motion path, thus enabling anticipation of its forthcoming position. In a previous research, we demonstrated that viewing static snapshots that imply body actions activates the human motor system. What remains unknown, however, is whether extrapolation of dynamic information and motor activation are higher for upcoming than past action phases. By using single-pulse transcranial magnetic stimulation, we found that observation of start and middle phases of grasp and flick actions engendered a significantly higher motor facilitation than observing their final postures. Differential motor facilitation during start and end postures was independent of finger configuration at the different hand apertures. Subjective ratings showed that modulation of motor facilitation was not due to the amount of implied motion per se but to the forward direction of the motion path toward upcoming phases. Thus, motor facilitation proved maximal for the snapshots evoking ongoing but incomplete actions. The results provide compelling evidence that the frontal component of the observation–execution matching system is preferentially activated by the anticipatory simulation of future action phases and thus plays an important role in the predictive coding of others’ motor behaviors.

Keywords: anticipatory simulation, human motor system, implied actions, mirror neurons, transcranial magnetic stimulation

Introduction

The full sequence of motion is rarely visible during interactions with a dynamic world. Yet, the human visual system is inherently equipped with the ability to complete missing information (Pessoa et al. 1998; Komatsu 2006). Even when there is no obstacle to our view, the intrinsic delay of our perceptual processing and our motor responses requires an anticipatory representation of the motion sequence in order to interact optimally with moving objects or creatures (Schütz-Bosbach and Prinz 2007; Perrett et al. 2009). This top-down modulation of visual perception may use previous experiences and knowledge on motion to predict and anticipate the forthcoming position of moving entities and thus create a representation of events occurring in the near future (Ingvar 1985). Behavioral studies in humans, for example, have shown that memory for the final position or configuration of a moving object is distorted forward along its path of motion, an effect known as representational momentum (Freyd 1983). In a typical representational momentum experiment, a series of snapshots eliciting the perception of apparent motion is

presented. Observers show a tendency to mislocalize the final position of the moving entity further along the anticipated trajectory. This effect has been demonstrated with a variety of stimuli including dot patterns (Finke and Freyd 1985), common objects (Finke and Shyi 1988), dynamic facial expressions (Yoshikawa and Sato 2008), and human figures (Verfaillie and Daems 2002). It is worth noting that the effect is found even when the actual motion is not present but only implied by static images of moving entities (Freyd 1983). The anticipatory representation of motion demonstrates the ability of our brain to bridge discontinuities in visual inputs by using internal models of the physical rules that govern object motion in the environment, for example, gravity (Hubbard 2005; Zago and Lacquaniti 2005; Motes et al. 2008). Importantly, the perception of movements performed by conspecifics may also rely on the motor representations used during planning and execution of actions (Verfaillie and Daems 2002; Flach et al. 2004; Ramnani and Miall 2004).

Neuroimaging studies in humans (Kourtzi and Kanwisher 2000; Senior et al. 2000) demonstrate that viewing photographs of humans, animals, objects, and natural scenes with implied motion activates the same medial temporal/medial superior temporal area (MT/MST complex) that is also involved in processing real motion (Zeki et al. 1991; Dupont et al. 1994; Tootell et al. 1995). Furthermore, studies in humans (Krekelberg et al. 2005; Lorteije et al. 2007) and monkeys (Krekelberg et al. 2003) suggest that the same populations of cells in extrastriate visual areas code for both implied and real motion. Representational momentum effects, however, seem to involve a larger network of higher-order prefrontal and parietal areas (Amorim et al. 2000; Rao et al. 2004) that may interact with the MT/MST complex during extrapolation of motion information from static images. Moreover, still images implying biological motion activate the lateral occipitotemporal junction (Peigneux et al. 2000), the parietal cortex (Hermsdörfer et al. 2001), and the superior temporal sulcus (Peuskens et al. 2005). In a similar vein, neurons in the monkey’s superior temporal cortex respond to the presentation of both moving body parts and static images of body postures implying preceding action (Jellema and Perrett 2003a, 2003b; Puce and Perrett 2003; Barraclough et al. 2006; Perrett et al. 2009).

By using single-pulse transcranial magnetic stimulation (TMS), we have previously shown that passive viewing of static images implying body actions triggers activation of the human motor system (Urgesi, Moro, et al. 2006). This suggests that the frontal node of the frontoparietal mirror neuron system that matches action observation and execution (di Pellegrino et al.

1992; Rizzolatti and Craighero 2004) may play a major role in the extrapolation of dynamic information from static images that imply body actions. Previous TMS studies have shown that mirror motor facilitation is specific to the muscle involved in the observed action (Fadiga et al. 1995; Romani et al. 2005; Urgesi, Candidi, et al. 2006), is comparable for intransitive body movements and goal-directed actions (Fadiga et al. 1995, 2005; Cattaneo et al. 2009) and can be modulated by the temporal dynamics of the observed actions, simulating the time course of activations during movement execution (Baldissera et al. 2001; Gangitano et al. 2001, 2004; Borroni et al. 2005; Montagna et al. 2005). These findings suggest that mirror facilitations represent action kinematics, more than the goal or the intention beyond an action. Repetitive TMS over the ventral premotor cortex ceased the increase of motor excitability during action observation, suggesting that computation carried out in the frontal node of the mirror neuron system are critical for mirror motor facilitation to occur (Avenanti et al. 2007). These results are well in keeping with a hierarchical model of human action understanding in which the frontal and parietal nodes of the human mirror neuron system have different roles in encoding the action kinematics and the action goals or intentions, respectively (Grafton and Hamilton 2007).

Notably, mirror motor facilitation of the first dorsal interosseous (FDI) muscle was present during observation of static snapshots representing the middle postures of a mimicked grasping action, where the hand had maximal grasp aperture (Urgesi, Moro, et al. 2006). In contrast, it was absent not only during observation of a resting, relaxed hand but also during observation of the end posture of the same action, where the hand had maximal finger closure. What remains unknown is whether mirror motor facilitation is selectively linked to the extraction of dynamic information about the upcoming or past action phases. In particular, no study has thus far addressed the issue of whether the motor facilitation found during observation of implied action stimuli derives from mere reading out of muscle contraction and joint configuration or from the anticipatory simulation of the temporal deployment of the action depicted in a given snapshot.

Here, we addressed this issue by exploring any differential modulation of motor potentials evoked by single-pulse TMS while participants observed static snapshots representing the start, middle, or end postures of 2 different right-hand actions: grasping a ball (grasp) or flicking a ball with the index finger (flick; Fig. 1). We chose these 2 actions because finger configuration in the start phase of grasp actions was comparable with the end posture of flick actions, whereas the end posture of grasp actions was comparable with finger configuration in the start phase of flick actions. Thus, experimental stimuli may allow one to distinguish the corticospinal encoding of the finger aperture and the temporal phase of the observed action. We tested whether motor resonance is linked to the creation of an internal representation of finger configuration independently of the temporal phase of the observed action. Were this the case, maximal FDI facilitation should be obtained during observation of grasp-start postures and flick-end postures, where the index finger was maximally extended (Gangitano et al. 2001). In contrast, were motor resonance influenced by the anticipatory simulation of the deployment of actions in the future, corticospinal facilitation should be found during observation of start and middle postures of both grasp and flick actions, where the actions were still ongoing, but not during observation of end

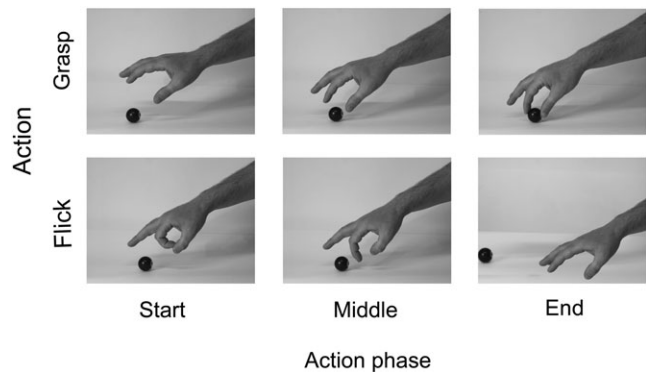


Figure 1. Examples of the experimental stimuli and factorial design. Participants viewed color pictures depicting the initial (start), intermediate (middle), and final (end) phases of 2 actions, namely, grasping a ball (grasp) and flicking a ball (flick). The crucial experimental manipulation was the finger configuration in the different phases of the 2 actions. Indeed, finger configuration in the start phase of grasp actions was comparable with the end posture of flick actions, whereas the end posture of grasp actions was similar to the finger configuration in the start phase of flick actions.

postures, where the actions were complete. Because the index finger was maximally extended in the grasp-start postures and maximally flexed in the flick-start postures, maximal motor facilitation during observation of both grasp and flick start phases cannot be ascribed to mere reading out of finger kinematics. This result would, thus, support the view that mirror corticospinal facilitation is specific for the observation of postures representing ongoing, but incomplete actions, and largely independent of mere reading out of finger configuration.

Materials and Methods

Participants

Eighteen healthy individuals (7 women) aged 19–37 (mean 22.1 years) were recruited at the University of Udine for the action observation TMS experiment. Furthermore, 6 additional individuals (3 women) aged 24–33 (mean 27.7 years), who did not participate in the TMS experiment, were recruited at the University of Bologna for the action execution experiment. All participants were right handed according to a standard handedness inventory (Briggs and Nebes 1975). They had normal or corrected-to-normal visual acuity in both eyes and were naïve as to the purposes of the experiment. Information about the experimental hypothesis was provided only after the experimental tests had been completed. Participants gave their written informed consent and received credits for their participation in the study. The procedures were approved by the Ethics Committee of the IRCCS Eugenio Medea and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. None of the participants had neurological, psychiatric, or other medical problems or any contraindication to TMS (Wassermann 1998). No discomfort or adverse effects during TMS were reported or noticed.

Stimuli

Stimuli were color pictures taken with a digital camera during the execution of right-hand precision grasp and flick actions by 4 male (aged 22–28 years) and 4 female (aged 23–29 years) models. Presenting 8 different hand stimuli allowed minimizing habituation and loss of attention. For each model, we selected 3 snapshots at the initial (start), intermediate (middle), and final (end) phases of the 2 action sequences (Fig. 1). Pictures were modified by means of the Adobe Photoshop software (Adobe Systems Incorporated, San Jose, CA). Pictures depicting the 6 different hand postures of the same model were matched for color, luminance, and viewing perspective. A total of 48 stimuli were created.

They were presented on a neutral background and subtended a $15.96^\circ \times 11.97^\circ$ region viewed from a distance of 100 cm.

Electromyography (EMG) Recording and TMS

Motor-evoked potentials (MEPs) were recorded simultaneously from the FDI and abductor digiti minimi (ADM) muscles of the right hand. It is worth noting here that the FDI muscle is strongly involved in the execution of both grasp and flick actions; by contrast, the ADM muscle does not play a major role in the execution of either action. EMG recordings were performed through surface Ag/AgCl cup electrodes (1-cm diameter) placed in a belly-tendon montage. Responses were amplified, band-pass filtered (20 Hz to 2 kHz), and digitized by means of a Viking IV EMG equipment (Nicolet Biomedical, Madison, WI). The sampling rate of the EMG signal was 20 kHz. A prestimulus recording of 80 ms was used to check for the presence of EMG activity before the TMS pulse. To make sure there was no unwanted background EMG activity before the magnetic pulse, the signal from both muscles was additionally displayed in separate channels set at high sensitivity (50 μ V). Moreover, during the preliminary session EMG signals were sent to loudspeakers to provide participants with an auditory feedback of their muscle relaxation. Focal TMS was performed by means of a 70-mm figure-of-8 stimulation coil (standard Magstim plastic-covered coil), connected to a Magstim Rapid (The Magstim Company, Carmarthenshire, Wales), producing a maximum output of 2 T at the coil surface (pulse duration, 250 μ s; rise time, 60 μ s). The coil was placed tangentially on the scalp, with the handle pointing backward and laterally 45° away from the midline, approximately perpendicular to the line of the central sulcus. This orientation induced a posterior-anterior current in the brain, which tends to activate corticospinal neurons indirectly via excitatory synaptic inputs (Di Lazzaro et al. 1998). We chose the above coil orientation based on the finding that the lowest motor threshold is achieved when the induced electric current in the brain is flowing approximately perpendicular to the central sulcus (Brasil-Neto et al. 1992; Mills et al. 1992).

During the recording session, the coil was positioned over the left motor cortex in correspondence with the optimal scalp position (OSP), defined as the position from which MEPs with maximal amplitude were recorded. The OSP was detected by moving the intersection of the coil in 1-cm steps around the motor hand area of the left motor cortex and by delivering TMS pulses at constant intensity. Participants wore a tightly fitting bathing cap on which the scalp position for stimulation was marked. The coil was held by hand, and its position with respect to the mark was checked continuously to easily compensate for small movements of the participants' head during data collection. The resting motor threshold (rMT), defined as the lowest stimulus intensity able to evoke 5 of 10 MEPs with an amplitude of at least 50 μ V, was determined by holding the stimulation coil over the OSP for the FDI muscle. Because we aimed to evaluate the differential modulation of MEPs recorded from the FDI muscle during observation of the different phases of actions, OSP and rMT were determined for the FDI. Thus, stimulation conditions were optimal to obtain facilitation of FDI MEPs in the less activating conditions, too. It is worth noting, however, that modulation of FDI, but not of ADM MEPs, was also obtained in previous studies (Urgesi, Candidi, et al. 2006; Urgesi, Moro, et al. 2006) where OSP and rMT were determined by using the ADM. Stimulation intensity during the recording sessions was 120% of the rMT and ranged from 48% to 86% (mean = 62.7%) of the maximum stimulator output. Using this procedure, a clear and stable signal was obtained from both the targeted muscles in all participants. The distance between the OSPs for the targeted muscles (FDI and ADM) turned out to be within the spatial resolution of the employed coil (ca. 1 cm; Krings et al. 1998). The MEP peak-to-peak amplitude (in mV) was collected and stored on a computer for offline analysis.

Procedure

Each participant was tested in a single experimental session lasting approximately 90 min. They sat in a comfortable armchair in a dimly lit room in front of a 15-in. monitor (resolution 1024×768 pixels; refresh frequency 60 Hz). They were instructed to keep their right hand on a pillow and to fully relax their muscles with the help of the auditory feedback coming from the loudspeakers. When muscular contractions

were detected, stimulus presentation was suspended, and participants were invited to keep again full muscular relaxation. Before starting the recording session, participants were presented with examples of the stimuli and were informed that they were to be presented with static images depicting the start, middle, and end postures of precision grasp and flick actions performed by different male and female models. Subjects were also instructed to pay attention to the stimuli presented on the screen and were informed that, when requested at a given point during the experiment, they were to report the gender of the hand presented in the trial. The request was performed during 25% of trials according to a random selection procedure with the constraint of an equal distribution among the different conditions. The experimenter asked the participants to report the gender of the observed model at the end of the selected trials. However, no overt response was required at any time during stimuli presentation and MEP collection. The 6 types of pictures were randomly presented in 4 blocks of 24 trials. In each block, 4 stimuli per condition were presented with a random presentation of male and female models. A short rest was allowed before proceeding to a different block. Sixteen trials were presented for each of the 6 observation conditions (2 presentations for each of the 8 model hands), for a total of 96 trials. We also recorded 2 series of 8 MEPs while participants observed a white-colored fixation cross presented on a black background. One series was recorded at the beginning and the other at the end of the experimental session. Comparisons of MEP amplitudes in the 2 series allowed us to check for any corticospinal excitability change related to TMS per se. Stimulus-presentation timing, EMG recording, and TMS triggering, as well as randomization of stimuli in a block, were controlled using E-prime V1.2 software (Psychology Software Tools Inc., Pittsburgh, PA) running on a PC. Stimuli remained on the screen for 1500 ms.

On each trial, the magnetic pulse was randomly delivered between 500 and 16.7 ms before the offset of the stimulus to avoid any priming effects that could affect MEP size. A 9-s blank screen was presented before the next trial. Therefore, the interpulse interval ranged from 10 to 10.5 s. The choice of the interpulse interval was based on research by Chen et al. (1997) who showed that even 1 h of repetitive TMS at 0.1 Hz did not induce any change in corticospinal excitability. Thus, the procedure allowed us to rule out any experimental effect due to TMS per se.

To ensure that all participants correctly discriminated between precision grasp and flick snapshots, an action discrimination task was administered at the end of the TMS session. The different start, middle, and end postures of the 2 actions were randomly presented on the computer monitor and participants had to indicate whether each image depicted a precision grasp or a flick action by pressing the left and the right button of the computer mouse, respectively. In keeping with the TMS session, stimulus duration was 1500 ms. Response accuracy was recorded and stored for automatic analysis.

In a further post-TMS session, the experimental stimuli were presented in random order for 1500 ms on the computer monitor. For each picture, participants were asked to judge the perceived intensity of the implied motion by marking with the mouse cursor a vertical, 10-cm visual analog scale (VAS), where 0 cm was "no effect" and 10 cm was "maximal effect imaginable." Two blocks were presented in a counterbalanced order in which participants were required to judge the intensity of the perception of the implied action of the hand or of the implied motion of the ball suggested by each of the 48 experimental stimuli.

Action Execution Experiment

To establish whether the corticospinal response to the observation of the different visual stimuli reflected mere read out of the level of muscle contraction rather than anticipatory coding of the observed actions, we recorded the EMG signals from the FDI and ADM muscles during actual execution of grasping and flicking actions. The participants of the action execution experiment stood in front of a table where an object with a similar size as that of the ball depicted in the experimental stimuli (2.5-cm diameter) was placed and fixed on a support. The object was connected to the computer and had a built-in button that was pressed during grasping and flicking movements, thus signaling the end phase of the movements. Movement execution was

guided by a sequence of 2 different tones (3 and 2 kHz, respectively) that were generated by a computer (sinus waves: 150-ms duration, intertone interval: 1 s) and signaled the starting phase (go signal) and the end of the actions (corresponding to the end phase of the visual stimuli). Therefore, the grasping and flicking movements were performed with a 0.5-Hz frequency (following the 1-Hz pace of the metronome). Before proceeding to the EMG recording session, the participants of the action execution experiment were presented with the different experimental visual stimuli and were asked to repeatedly mimic the target action (grasp or flick) with their right hand. After a variable and self-paced number of repetitions of the target-mimed action, participants actually performed the target action by grasping or flicking the object with their right hand (and thus clicking the mouse button). This event generated a trigger signal that ceased the metronome for 2 s and was used to analyze the EMG activity. A block of 15 trials was recorded for each action (grasp, flick). The order of the blocks was counterbalanced across subjects.

The EMG signals were recorded from the right FDI and the ADM muscle by means of a Biopac MP-150 (Biopac Corp., Goletta, CA) EMG equipment, band-pass filtered (20 Hz to 2 kHz, sampled at 20 kHz), digitized, and stored on a computer for offline analysis. Mean EMG responses were time locked to the finger-object contact (button press) and computed by averaging the root square rectified EMG signal across trials using 200-ms epochs over an interval of 1.2 s. The first 3 epochs covered the reaching component of the movements. Epochs 4 and 5 covered the grasping or flicking components and roughly corresponded to the start and middle phases of the visual stimuli. The last epoch included the 200-ms interval after button press and corresponded to the end phase of the visual stimuli.

Data Handling

Task compliance during action observation was good, as assessed by immediate verbal report of the gender of the presented hand. For each observation condition, we calculated the individual mean peak-to-peak amplitudes of MEPs recorded from the FDI and ADM muscles, the percentage of correct responses in the action discrimination task, and the mean VAS judgments of the perceived intensity of the implied hand action and of the implied object motion. Inspection of recognition performances in the action discrimination task revealed that 1 male and 1 female participant were below the chance level for pictures depicting the end posture of flick actions (0% and 38%, respectively). Because these 2 participants seemed to have systematically categorized stimuli depicting the flick-end postures as grasp action, their data were not included in the analysis. Thus, final analyses were based on data from 16 participants.

Visual inspection of the EMG recordings confirmed full muscular relaxation in all participants during MEP recording. Trials with background EMG activity preceding the TMS pulse or with an MEP amplitude deviating more than 2 standard deviation (SD) from the mean for each observation condition were discarded (4.2% of the total). No more than 3 MEPs for each observation condition were discarded and mean values were obtained from at least 13 MEPs per condition for each participant. A paired-sample *t* test (2-tailed) was used to compare the amplitude of MEPs recorded from the FDI and ADM muscles in the 2 series of fixation-cross trials presented at the beginning and at the end of the experimental session. The individual mean amplitude of MEPs recorded in the 2 fixation-cross series served as baseline. For each muscle, individual mean raw amplitudes of MEPs recorded during the 6

observation conditions were expressed as percentage of baseline values. Individual normalized MEP amplitudes were entered into a $2 \times 2 \times 3$ repeated-measure analysis of variance (ANOVA) with muscle (FDI, ADM), type of action (grasp, flick), and action phase (start, middle, and end) as within-subjects variables.

The individual percentages of correct responses in the action discrimination task, the mean VAS judgments of the perceived intensity of the implied hand action and of the implied object motion were entered into separate 2×3 repeated-measures ANOVAs, with type of action and action phase as within-subjects variables. Furthermore, for each observation condition, we computed the Pearson correlation coefficients between the normalized FDI MEP amplitudes and 1) the VAS judgments of the perceived intensity of the implied hand action; 2) the VAS judgments of the perceived intensity of the implied object motion. Only the FDI MEP amplitudes were entered into the correlation analysis because ADM MEPs were not significantly modulated by any observation condition. The EMG signals recorded during action execution were analyzed by means of a $2 \times 2 \times 6$ ANOVA with muscle (FDI, ADM), type of action (grasp, flick), and time (6 epochs) as within-subjects variables. All post hoc pairwise comparisons were carried out using the Newman-Keuls test. A significance threshold of $P < 0.05$ was set for all statistical tests.

Results

MEP Amplitude

Table 1 shows the mean raw MEP amplitudes recorded from the FDI and ADM muscles during the 2 baseline blocks and the 6 observation conditions. Mean raw MEP amplitudes during the 2 baseline blocks run at the beginning and at the end of the experimental session were not significantly different for either the FDI ($t_{15} = 0.729$, $P = 0.478$) or the ADM muscle ($t_{15} = -0.06$, $P = 0.954$). This indicates that TMS per se did not induce any changes in corticospinal excitability in our experimental session.

To test whether mirror motor facilitation is higher during extrapolation of dynamic information about the upcoming action phases than the past ones, we compared normalized MEP amplitudes during observation of static snapshots depicting the start, middle, and end postures of grasp and flick actions (Fig. 2). The 3-way ANOVA yielded a significant main effect of muscle ($F_{1,15} = 7.9$, $P = 0.013$), with FDI normalized MEPs (mean \pm standard error of the mean [SEM]: $103.92\% \pm 9.35\%$) being higher than ADM normalized MEPs ($87.88\% \pm 7\%$). Thus, motor facilitation during observation of grasp and flick actions was higher for the FDI muscle, which is involved in the actual execution of the same movements. The main effects of type of action ($F_{1,15} < 1$) and action phase ($F_{2,30} = 2.19$, $P = 0.129$) were nonsignificant. Crucially, however, we found a significant interaction between muscle and action phase ($F_{2,30} = 5.03$, $P = 0.013$). Pairwise post hoc tests showed that MEPs recorded from the FDI (Fig. 2a) were more facilitated during observation of start ($108.64\% \pm 9.62\%$) and middle postures ($109.26\% \pm 11.28\%$) than during observation of end postures ($93.85\% \pm$

Table 1
Amplitudes of MEPs recorded during baseline and observation conditions

	Baseline		Grasp			Flick		
	B1	B2	Start	Middle	End	Start	Middle	End
FDI	1.28 (± 0.18)	1.19 (± 0.19)	1.33 (± 0.19)	1.3 (± 0.17)	1.17 (± 0.17)	1.41 (± 0.22)	1.42 (± 0.20)	1.28 (± 0.19)
ADM	0.79 (± 0.13)	0.79 (± 0.18)	0.66 (± 0.12)	0.67 (± 0.14)	0.61 (± 0.1)	0.73 (± 0.17)	0.75 (± 0.16)	0.75 (± 0.15)

Mean (\pm SEM) peak-to-peak amplitudes (in mV) of MEPs recorded from the FDI and ADM muscles during the 2 fixation-cross, baseline conditions run at the beginning (B1) and at the end (B2) of the experimental session, and during the 6 observation conditions.

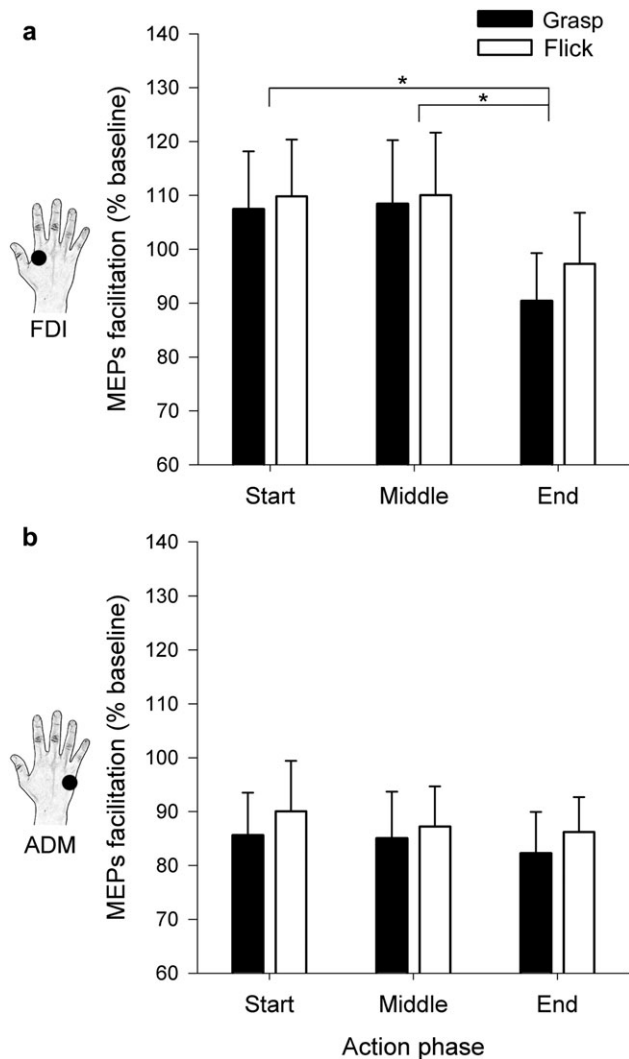


Figure 2. Muscular facilitation during observation of the different implied action phases. Amplitudes of MEPs recorded from the FDI (a) and ADM (b) muscles during the 6 observation conditions are expressed as value percentages of the MEPs recorded during the baseline (viewing a fixation cross). MEPs facilitation was higher during the observation of the start and middle phases of the 2 actions with respect to their final postures. Error bars indicate SEM. * $P < 0.05$.

8.76%; $P < 0.001$ for both comparisons). Instead, comparable FDI MEPs were obtained during observation of start and middle postures ($P = 0.864$). Furthermore, no modulation during observation of the 3 phases of grasp and flick actions was obtained for MEPs recorded from the ADM (Fig. 2b, $P > 0.7$ for all comparisons), a muscle not involved in the actual execution of either actions. Although FDI MEPs were higher than ADM MEPs during observation of start ($P < 0.001$) and middle postures ($P < 0.001$), no between-muscle difference was obtained during observation of end postures ($P = 0.23$). The 2-way interactions between muscle and type of action ($F_{1,15} < 1$) and between type of action and action phase ($F_{1,15} < 1$) were nonsignificant. Importantly, the nonsignificant effect of the 3-way interaction between muscle, type of action, and action phase ($F_{2,30} < 1$) showed that the greater motor facilitation during observation of start and middle postures versus end postures was independent of the finger configuration in the different phases of the 2 actions. Indeed, planned

comparisons showed that FDI MEPs were lower during observation of grasp end postures than during observation of grasp start ($F_{1,15} = 12.47$, $P = 0.003$) and middle postures ($F_{1,15} = 5.71$, $P = 0.03$). In a similar vein, FDI MEPs were lower during observation of flick end postures than during observation of flick start ($F_{1,15} = 4.81$, $P = 0.044$) and middle postures ($F_{1,15} = 5.04$, $P = 0.04$).

Action Discrimination

Action discrimination performance was above 90% for all observation conditions, suggesting that participants were able to discriminate whether the static snapshot stimuli were taken from grasp or flick action sequences. The ANOVA on percent correct responses revealed a significant main effect of type of action ($F_{1,15} = 6.95$, $P = 0.019$), because responses for grasp snapshots ($98.85\% \pm 0.46\%$) were more accurate than responses for flick action snapshots ($94\% \pm 1.76\%$). Nonsignificant effects of action phase ($F_{2,30} = 1.39$, $P = 0.265$) and of the interaction between type of action and action phase ($F_{2,30} = 2.6$, $P = 0.091$) were found. Indeed, recognition performance was comparable between the 3 phases of grasp (start: $98.44\% \pm 1.22\%$; middle: $98.88\% \pm 0.6\%$; end: $99.25\% \pm 0.51\%$) and flick actions (start: $97.75\% \pm 0.75\%$; middle: $92.25\% \pm 3.03\%$; end: $92.38\% \pm 2.79\%$). This suggests that the difference between the motor facilitation during observation of start and middle postures and that obtained during observation of end postures cannot be ascribed to different abilities in recognizing the actions represented in the different pictures.

VAS Ratings Concerning Implied Motion of Each Stimulus

To test the relationship between motor facilitation and the perceived intensities of implied hand action and implied object motion, we compared VAS ratings on pictures representing the start, middle, and end postures of grasp and flick actions. The ANOVA on implied hand action VAS ratings (Fig. 3a) showed significant main effects of type of action ($F_{1,15} = 4.86$, $P = 0.04$), action phase ($F_{2,30} = 9.89$, $P < 0.001$), and their interaction ($F_{2,30} = 7.47$, $P = 0.002$). Post hoc tests showed that the subjective perception of implied hand action was higher for start than for middle ($P = 0.021$) and end ($P < 0.001$) grasp postures. Middle grasp postures suggested higher implied hand action perception than the corresponding end postures ($P = 0.018$). Thus, perception of implied hand action was maximal for the initial phases of grasp actions, which showed ongoing but incomplete movements. In contrast, no difference was observed between the perceived intensity of implied hand action suggested by the start, middle, and end postures of flick actions ($P > 0.76$ for all comparisons). Importantly, ratings of implied hand action perception for flick end postures were higher than ratings for grasp end postures ($P < 0.001$) and were not significantly different than ratings for grasp start postures ($P = 0.38$). Because grasp start postures activated the motor system to a greater extent than flick end postures, modulation of motor facilitation cannot be ascribed to different intensities of implied hand action perception for start, middle, and end postures.

The ANOVA on VAS ratings of implied object motion (Fig. 3b) yielded significant effects of type of action ($F_{1,15} = 55.78$, $P < 0.001$), action phase ($F_{2,30} = 27.23$, $P < 0.001$), and their interaction ($F_{2,30} = 41.86$, $P < 0.001$). Post hoc tests showed that the subjective perception of implied object motion was higher for start, middle, and end flick postures than for start,

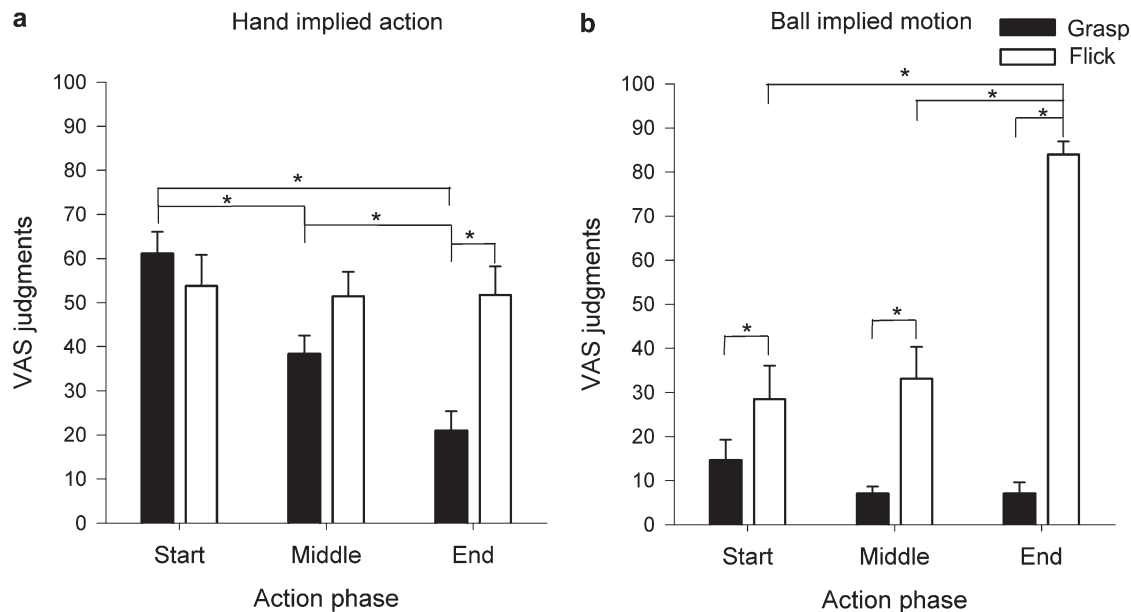


Figure 3. Subjective judgments of perceived intensity of the different implied hand actions and implied object motion. Mean VAS ratings on pictures representing the start, middle, and end postures of grasp and flick actions. (a) VAS ratings of the perceived intensity of the implied hand action were maximal for start and middle grasp postures, whereas no difference was observed between the 3 phases of flick actions. (b) VAS ratings on the perceived intensity of the implied object motion were higher for flick than for grasp action phases and were maximal for flick end postures, which exerted minimal facilitation on cortico-spinal excitability. Error bars indicate SEM. * $P < 0.05$.

middle, and end grasp postures ($P < 0.015$ for all comparisons). The ratings of implied object motion for the start, middle, and end postures of grasp actions did not differ from one another ($P > 0.15$ for all comparisons). In contrast, ratings of implied object motion perception were higher for the end postures than for the start ($P < 0.001$) and middle postures ($P < 0.001$) of flick actions. Thus, maximal perception of implied motion of the object was suggested by the end posture of flick actions. Because observing the end postures of flick actions did not activate the FDI motor representations, modulation of motor facilitation during observation of the different phases of grasp and flick actions cannot be ascribed to the perception of implied object motion.

The absence of association between motor facilitation and implied motion perception was further corroborated by the analysis of the correlation between motor facilitation and implied motion perception ratings for each stimulus. Indeed, nonsignificant correlations were found between the individual mean normalized FDI MEP amplitudes and the VAS ratings of implied hand action (all $-0.35 < r_s < 0.42$, all $P_s > 0.11$) and implied object motion perception (all $-0.39 < r_s < 0.36$, all $P_s > 0.1$).

Muscle Activation during Action Execution

The analysis of the mean root square EMG signal recorded during action execution (Fig. 4) revealed a significant main effect of muscle ($F_{5,25} = 28.81$, $P = 0.003$), accounted for by the higher EMG signal recorded in the FDI (0.123 ± 0.009 mV) with respect to the ADM muscle (0.080 ± 0.004 mV), a main effect of time ($F_{5,25} = 50.66$, $P < 0.001$) and, most importantly, a significant muscle \times time interaction ($F_{5,25} = 60.33$, $P < 0.001$). The effect of the interaction was accounted for by the stronger increase over time of the EMG activity recorded from the FDI muscle in comparison to that recorded from the ADM muscle. The FDI EMG activity remained constant between the epochs 1 and 2

($P = 0.827$) and between the epochs 2 and 3 ($P = 0.211$). Importantly, a significant increase was found between epoch 3 and epoch 4 (200–400 ms before the finger contacted the ball; $P = 0.002$). Maximum increase was found at epoch 5 (0–200 ms before the finger-object contact), corresponding to the flexion phase of grasping and to the extending phase of flicking, and epoch 6 (0–200 ms after the contact), corresponding to the end phase of the experimental visual stimuli. Crucially, the EMG signal during epochs 5 and 6 was comparable ($P = 0.86$) and was higher than that during all the previous epochs (all $P_s < 0.001$). A smaller but significant increase during epochs 5 and 6 was detected also in the ADM muscle (all $P_s < 0.001$), reflecting the postural adjustments of the hand during grasping or flicking with the index finger. The EMG signal during the epochs 5 and 6 was higher in the FDI than in all the epochs of the ADM muscle (all $P_s < 0.001$). No other significant main effect or interaction was found in the ANOVA (all $F_s < 2.14$, all $P_s > 0.09$), suggesting a similar time course of muscle activation during execution of grasp and flick actions.

Discussion

We explored the possible functional involvement of the human motor system in the anticipatory representation of observed actions by recording the cortico-spinal facilitation during observation of snapshots depicting specific finger configuration (e.g., large or small finger aperture) and snapshots depicting specific temporal phases (e.g., start or end of hand actions). In particular, we tested whether mirror motor facilitation during implied action stimuli observation was higher when extrapolating dynamic information about upcoming than past action phases. We found that observing the start and middle postures of grasp and flick actions engendered a significantly higher motor facilitation than observing their final postures. In contrast, observing the final postures of both grasp and flick

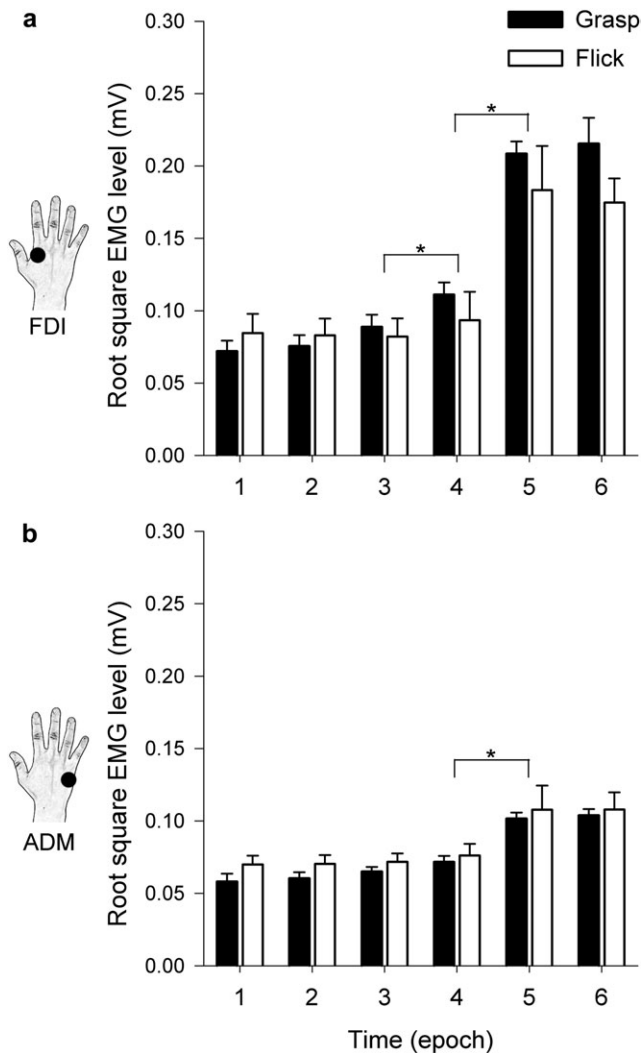


Figure 4. Time course of muscular activation during action execution. Mean root square EMG signals recorded from the FDI (a) and ADM (b) muscles during execution of grasp and flick actions. Results were pooled across 6 epochs, each lasting 200 ms. The first 3 epochs covered the reaching component, whereas epochs 4 and 5 covered the grasping or flicking components of the movements, corresponding to the start and middle phases of the visual stimuli. The last epoch corresponded to the end phase of the visual stimuli. Error bars indicate SEM. * $P < 0.05$.

actions did not activate the motor system. Importantly, the finger configuration in the start posture of grasp actions was comparable with the end posture of flick actions, whereas finger configuration of the end posture of grasp actions was comparable with that in the start position of flick actions. Furthermore, the EMG recording during action execution showed that muscular activation increased over time during both grasp and flick actions, reaching its maximum during the middle and end phases of the movements. Thus, differential mirror motor facilitation during start and end postures cannot be ascribed to 1) mere reading out of finger aperture and muscular activation at different postures; nor to 2) any differential ability in recognizing the actions represented in the static snapshots because action discrimination performance was comparable for the 3 action phases. The modulation of motor facilitation was independent of the perceived intensity of hand or object implied motion in start, middle,

and end postures. Indeed, although ratings of implied hand action were maximal for start and middle grasp postures, no difference was observed between the 3 phases of flick actions. On the other hand, ratings of the implied object motion were maximal for flick end postures, which exerted minimal facilitation on corticospinal excitability. Thus, a main point of novelty of the present study is that the motor facilitation contingent upon extrapolation of dynamic information from static snapshots is higher for the anticipation of the upcoming than past action phases.

Somatotopic Mirror Motor Mapping of Implied Body Actions

Single-pulse TMS studies demonstrate that the mirror motor facilitation contingent on observation of dynamic displays of body actions (Strafella and Paus 2000; Gangitano et al. 2001; Borroni et al. 2005; Fadiga et al. 2005; Montagna et al. 2005; Romani et al. 2005; Urgesi Candidi, et al. 2006) specifically involves the muscles that would be recruited during the actual execution of the actions. In keeping with the only other TMS study (Urgesi, Moro, et al. 2006) on this issue, the present results show that, even in the absence of explicit dynamic information, cortical-spinal muscle representations are facilitated by the observation of static snapshots evoking the perception of implied actions. Moreover, we demonstrate that MEP modulation during observation of static photographs of pincer grasp and flick actions follows the same mapping rule of actual movements. Indeed, the MEP facilitation was selective for the FDI muscle, which is activated during actual execution of the observed actions. By contrast, no motor facilitation was observed for ADM, which has only a little role in the execution of the observed actions, mostly limited to postural adjustments of the hand. The motor facilitation during observation of implied body actions suggests that the human motor system is involved in the extrapolation of action information from static images of body postures. That mapping of implied actions is related also to motor regions is in keeping with a recent event-related potential study that shows a specific cortical signature of observing implied action snapshots. This signature consists in a long-lasting positivity that was higher for the more dynamic stimuli, and its source was also in premotor and motor cortices and not only in cortical regions concerned with visual motion (e.g., V5/MT, EBA, or STS; Proverbio et al. 2009).

Although single-pulse TMS cannot establish the specific cortical correlates of motor activations during action observation, mirror muscular facilitation seems to be linked to the activation of the frontal node of the mirror network that matches observed and performed actions (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004). Neuroimaging studies demonstrate that the motor and premotor areas are activated by viewing dynamic full (Rizzolatti et al. 1996; Decety et al. 1997; Grafton et al. 1997; Iacoboni et al. 1999; Buccino et al. 2001; Costantini et al. 2005; Gazzola and Keysers 2009; Kilner et al. 2009) and point-light displays (Saygin et al. 2004) of body actions. Crucially, repetitive TMS of ventral premotor cortex disrupted motor facilitation during observation of biomechanically possible actions, but not impossible actions (Avenanti et al. 2007), thus hinting at the primary role of the ventral premotor cortex in mediating activation of the motor system during observation of actions that belong to the observer's motor repertoire. The ventral premotor cortex may be also

involved in the perception of static images implying actions. A recent functional magnetic resonance imaging study in monkeys (Nelissen et al. 2005) has detected multiple representations of observed actions in the ventral premotor cortex, with patches activated only by full action displays and other patches activated also by mimicked actions or by static presentation of manipulable objects. In a similar vein, activation of human motor and premotor cortex was higher during observation of static pictures of goal-directed actions (Johnson-Frey et al. 2003), suggesting that mere observation of the action goal is enough to trigger mirror motor activation. However, by showing motor activation during observation of static snapshots of mimicked actions, we have demonstrated that the motor mapping of implied body actions is independent of the presentation of the target object (Urgesi, Moro, et al. 2006). Furthermore, repetitive TMS of ventral premotor cortex impaired the visual discrimination of static images implying biomechanically possible body actions (Urgesi, Calvo-Merino, et al. 2007; Urgesi, Candidi, et al. 2007), but not impossible body actions (Candidi et al. 2008). Thus, the frontal node of the mirror motor system seems to play a crucial role in the discrimination of action information extrapolated from static body postures.

The involvement of motor representations in the perception of static body postures that imply action is also in keeping with the behavioral studies that have investigated the interferential effects exerted by the passive viewing of incongruent as compared with congruent actions on movement executions. Indeed, the correct execution of an observer's actual movement can be influenced not only by viewing congruent or incongruent dynamic action sequences (Brass et al. 2000, 2001; Stürmer et al. 2000; Kilner et al. 2003), but also by single static frames suggesting congruent or incongruent actions (Craighero et al. 1996, 1999, 2002; Brass et al. 2000; Vogt et al. 2003). Thus, viewing a static image depicting moving bodies or body parts automatically activates action-related neural representations.

The Time Course of Motor Mirroring during Observation of Implied Actions

Studies indicate that the time course of motor activation triggered by action observation seems to parallel the dynamics of movement execution (Baldissera et al. 2001; Gangitano et al. 2001, 2004; Borroni et al. 2005; Montagna et al. 2005). In a previous single-pulse TMS study, the facilitation of the cortical representation of the FDI muscle during observation of reaching to grasp actions was maximal during presentation of the snapshots with maximal finger aperture, thus in the initial stages of the hand closing phase (Gangitano et al. 2001). In a similar vein, a clear temporal modulation of amplitude of MEPs recorded from 2 hand muscles (flexor digitorum superficialis and FDI) was also found during observation of videos showing a hand reaching, grasping, and holding a sphere (Montagna et al. 2005). It is relevant that FDI facilitation was found not only during observation of the finger closing phase but also during observation of the hand closure and active object holding phase, that is, when the action was still ongoing (Montagna et al. 2005). By presenting in isolation static snapshots representing different phases of precision grasp movements (Urgesi, Moro, et al. 2006), we have previously found that facilitation of the FDI muscle responses was present during observation of the middle postures of a mimicked

grasping action, when the hand had maximal grasp aperture. In contrast, FDI facilitation was absent not only during observation of a resting, relaxed hand but also during observation of a maximal finger closure hand, which suggests the movement has been completed. The temporal modulation of corticospinal excitability during actual and implied action observation is reminiscent of the firing properties of mirror neurons in the monkey's ventral premotor cortex, some of which discharge maximally during observation of the last phases of grasping (Umiltà et al. 2001), others stop firing when the target object has been achieved, whereas others continue to discharge also during the active holding phase (Gallese et al. 1996). Previous studies, however, could not establish whether the temporal modulation of motor facilitation reflects the reading of finger configuration and muscular contractions in the different postures or the anticipatory simulation of future phases of the observed action.

Simulation of Implied Actions and Predictive Coding of Ongoing Actions

A main point of novelty of the present study is the maximal mirror motor facilitation during observation of start and middle postures of both hand grasp and flick actions. No facilitation was found during observation of end postures, which suggested that the movement was completed. Importantly, there was a great visual similarity between grasp start postures and end flick postures as well as between grasp end postures and flick start postures. Thus, the differential facilitation cannot be ascribed to the reading out of the finger kinematics at different hand apertures. It rather suggests that mirror motor mapping of implied actions is maximal for ongoing, but incomplete actions. This effect may provide a specific neural basis for the forward bias in the recognition memory of moving conspecifics found in representational momentum experiments (Verfaillie and Daems 2002). Our results support and expand the notion that the functional role of motor activation during action perception is based on predictive coding. This process allows an onlooker to understand early the goal of actions and ultimately to read early the intentions of an actor (Blakemore and Frith 2005; Cattaneo et al. 2007; Kilner et al. 2007) as well as to anticipate the future phases of upcoming actions of others (Wilson and Knoblich 2005; Prinz 2006; Schubotz 2007; Schütz-Bosbach and Prinz 2007). In particular, Wilson and Knoblich (2005) have proposed that the motor representations activated during action observation may provide an internal model of the ongoing action by generating top-down expectations and predictions on its deployment in time. This model has 2 implications: 1) the observer's motor system generates predictive representations of others' actions by projecting the course of ongoing movements into the future; 2) predictions about others' actions are fed back into the visual system and exert top-down influence on action perception, thus allowing to complete missing information.

Our results provide compelling evidence for the involvement of mirroring processes in the anticipatory simulation of observed actions. It is worth noting that motor mirror neurons are activated also when the final part of an object grasp action cannot be seen but only inferred (Umiltà et al. 2001). Therefore, motor mirroring may allow one to anticipate the course of ongoing actions and represent hidden information. In a similar vein, the facilitation of the human motor cortex during

observation of grasping actions was suppressed by the artificial introduction of delayed aperture or sudden closure of fingers (Gangitano et al. 2004), suggesting that mirror mapping is affected by the predictability of the sequence of observed movements. Furthermore, motor activation in response to symbolic cues signaling an upcoming movement has been found in both adults (Kilner et al. 2004; Ramnani and Miall 2004) and children (Southgate et al. 2009).

All in all, this evidence hints at the important role of the mirror system in predicting and anticipating the actions of other individuals. The higher motor facilitation during extrapolation of dynamic information about ongoing, but incomplete actions would suggest that motor mirroring may be inherently linked to predicting and anticipating the future behaviors of other individuals. The ability to provide predictive models of the perception of ongoing actions may rely on the previous motor knowledge of the observer. Several neuroimaging studies have shown that the activation of the mirror neuron system areas is modulated by the observer's motor experience (Calvo-Merino et al. 2005, 2006; Cross et al. 2006, 2009; Reithler et al. 2007; Orgs et al. 2008). On the other hand, the importance of motor expertise for action perception abilities has been demonstrated by behavioral investigations of elite athletes, who present superior abilities not only in the execution of complex actions but also in the prediction and anticipation of the behavior of other players (Farrow and Abernethy 2003; Abernethy and Zawi 2007; Abernethy et al. 2008; Weissensteiner et al. 2008). Crucially, the superior predictive abilities of elite basketball players with respect to naïve and expert observers (e.g., coaches or sport journalists) were associated to differential motor activation during observation of the early phases of erroneous versus correct shots (Aglioti et al. 2008). Therefore, motor experience may endow the motor system with the ability to predict and anticipate the actions of others ahead of their realization.

Conclusion

The most novel result of the present study is that mirror motor facilitation is maximal during observation of implied action snapshot stimuli depicting ongoing but incomplete actions. In keeping with self- and other-action predictive coding models (Ramnani and Miall 2004), our study suggests that the frontal node of the observation-execution matching system is preferentially activated by the anticipatory simulation of the deployment of an action in the future. This would indicate that an important function of action mirroring processes is to derive from the observers' motor knowledge specific predictions concerning the future implementation of others' behaviors.

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