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Publisher: Psychology Press  
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## Social Neuroscience

Publication details, including instructions for authors and subscription information:  
<http://www.informaworld.com/smpp/title~content=t741771143>

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Matteo Candidi<sup>ab</sup>, Cosimo Urgesi<sup>c</sup>, Silvio Ionta<sup>d</sup>, Salvatore M. Aglioti<sup>ab</sup>

<sup>a</sup> Università di Roma "La Sapienza", Rome, Italy

<sup>b</sup> IRCCS Fondazione Santa Lucia, Rome, Italy

<sup>c</sup> IRCCS "E. Medea", Pordenone, Italy

<sup>d</sup> ITAB, Università di Chieti "G. D'Annunzio", Chieti Scalo, Italy

First Published on: 16 October 2007

To cite this Article: Candidi, Matteo, Urgesi, Cosimo, Ionta, Silvio and Aglioti, Salvatore M. (2007) 'Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions', Social

Neuroscience, 1 - 13

To link to this article: DOI: 10.1080/17470910701676269

URL: <http://dx.doi.org/10.1080/17470910701676269>

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# Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions

**Matteo Candidi**

*Università di Roma “La Sapienza” and IRCCS Fondazione Santa Lucia, Rome, Italy*

**Cosimo Urgesi**

*IRCCS “E. Medea”, Pordenone, Italy*

**Silvio Ionta**

*ITAB, Università di Chieti “G. D’Annunzio”, Chieti Scalo, Italy*

**Salvatore M Aglioti**

*Università di Roma “La Sapienza” and IRCCS Fondazione Santa Lucia, Rome, Italy*

Single-pulse transcranial magnetic stimulation (TMS) studies show that action observation facilitates the onlooker’s cortico-spinal system supporting the notion of motor mirroring. Repetitive transcranial magnetic stimulation (rTMS) over ventral premotor cortex (vPMc) impairs visual discrimination of body actions. Although studies suggest that the action observation–execution matching system may map only actions that belong to the observer’s motor repertoire, we demonstrated comparable motor and premotor facilitation during observation of biomechanically possible as well as impossible actions. It has also been shown that seeing impossible body movements activates the extrastriate body area (EBA). Using event-related rTMS, we sought to determine whether vPMc and EBA are actively involved in the visual discrimination of actions performed through biomechanically possible or impossible kinematics and of their biomechanical plausibility. Stimulation of vPMc impaired discrimination of possible actions while leaving intact the discrimination of biomechanically impossible actions and of biomechanical plausibility. No effect of EBA rTMS on any type of action processing was found. Thus, vPMc is crucial for discrimination of the goal of actions that can be actually performed suggesting that this area is involved in the visual processing of goal-directed actions.

## INTRODUCTION

Humans are naturally accurate in perceiving and understanding body actions performed by other individuals. Studies report that repetitive transcranial magnetic stimulation (rTMS) of ventral

premotor cortex (vPMc) impairs visual discrimination of static (Urgesi, Candidi, Ionta, & Aglioti, 2007) and dynamic displays (Pobric & Hamilton, 2006) of bodily actions. These results supports the notion that action understanding requires motor representations (Rizzolatti & Craighero, 2004).

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Correspondence should be addressed to: Matteo Candidi, Department of Psychology, University of Rome “La Sapienza”, Via dei Marsi 78, I-00185, Roma, Italy. E-mail: [matteo.candidi@uniroma1.it](mailto:matteo.candidi@uniroma1.it)

This research was supported by Ministero Italiano Università e Ricerca (MIUR), University of Rome “La Sapienza” and Fondazione Santa Lucia, Italy.

vPMc is a crucial node of the fronto-parietal mirror-neuron system that matches action observation and action execution. Behavioral, neurophysiological, and neuropsychological studies suggest that action execution and observation are represented in commensurable formats and share the same neural underpinnings (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Buccino et al., 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Grezes & Decety, 2001; Prinz, 2002; Saygin, Wilson, Dronkers, & Bates, 2004; Wohlschläger & Bekkering, 2002). Importantly, mere action observation influences motor representations and plays an important role in learning new movements (Celnik et al., 2006; Stefan et al., 2005). The motor mapping of visually perceived actions, however, seems to occur only for actions that can be practiced and learned. fMRI studies, for example, compared neural activity during observation of learned and non-learned complex dance movements and found that the former condition induced higher premotor and parietal mirror activation than the latter (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005, 2006). In a similar vein, observation of human biting actions but not dog barking activates the frontal node of the mirror-neuron system thus indicating that specific motor mapping contingent upon observation occurs only for actions that belong to the observer's behavioral repertoire (Buccino et al., 2004). According to this view, actions that do not belong to the observers' motor repertoire would elicit only visual mapping in posterior areas. However, humans may perceive and understand actions they cannot perform and that therefore are not part of their own motor repertoire. Recent TMS (Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005) and neuroimaging studies (Costantini et al., 2005) reported a comparable motor and premotor activation during observation of biomechanically possible and impossible ab/adduction index finger movements. Based on the notion that one can mirror only actions that can be performed, motor activation during observation of biomechanically impossible movements was not expected. It is worth noting that the biomechanically impossible index finger movements observed in our studies (Costantini et al., 2005; Romani et al., 2005) consisted in an exaggeration of the correspondent possible movements and thus can be conceptually conceived as possible. Therefore, it is plausible that premotor and motor representations of observed actions do not include the mapping of the exact kinematics

and the pattern of muscles' activations, but the general meaning of actions. Indeed, the functional significance of finger movements is not changed by the biomechanical extension of joint limits. In this vein, activation of the motor system during observation of biomechanically impossible movements may reflect the representation of the actions' meaning and goal. By contrast, observation of completely new movements that cannot be represented in terms of meaningfulness or goal-directedness, for example non-*species*-specific movements (Buccino et al., 2004) or dance patterns exceedingly complex for naïve observers (Calvo-Merino et al., 2005), do not engage the motor system. In a previous fMRI study we reported that impossible movements engender higher activations of parietal and temporo-occipital cortex than possible movements (Costantini et al., 2005). Thus, premotor and motor responses to impossible movements may reflect modulatory signals from parietal and temporal areas. It is worth noting that the temporo-occipital activity found in this study was close to the location of the so-called extrastriate body area (EBA), a cortical region that is selectively activated by viewing images, silhouettes or even stick drawings of static and moving body or body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). Neural activity in EBA has been proved to be crucial for visual perception of human body parts (Urgesi, Berlucchi, & Aglioti, 2004). Moreover, rTMS of EBA impairs visuo-perceptive discrimination of body morphology but does not affect the discrimination of the action being performed (Urgesi et al., 2007). The role of the EBA in processing body movements, however, is still debated (Astafiev, Stanley, Shulman, & Corbetta, 2004; Peelen & Downing, 2005). The EBA is also activated during perception of point-light displays, which suggests the perception of body actions despite the absence of body-form cues (Downing et al., 2001; Grossman & Blake, 2002), as well as during presentation of static body images both implying and not implying motion (Downing et al., 2001; Peelen, Wigget, & Downing, 2006). It has been reported that observation of distorted hand postures enhances the activation of extrastriate visual areas (Avikainen, Liuhanen, Schürmann, & Hari, 2003). Similarly, the EBA seems to be more activated by incoherent body movements while superior temporal and premotor activations are higher during observation of coherent action sequences (Downing, Peelen, Wigget, & Tew, 2006). These results would suggest that EBA

may be involved in the extrapolation of body-form cues even when extrapolating from images unrelated to normal motor functioning. In contrast, temporal and premotor activations may modulate the motor system. Imaging studies, however, cannot establish whether neural activations of cortical areas are crucial for task execution or merely epiphenomenal.

In the present study, we used event-related rTMS to investigate the role played by vPMc and EBA in visual discriminations of biomechanically possible and impossible body actions. In particular, we tested whether neural activations of vPMc and EBA reflect their active involvement in perceiving movements that cannot be performed or are merely epiphenomenal to activations occurring elsewhere in the brain. Rapid rTMS allowed us to transiently disrupt neuronal efficiency by introducing “noise” in the pattern of activity necessary to task execution (Pascual-Leone, Walsh, & Rothwell, 2000). If the targeted area is actively involved in the task being performed, rTMS is expected to impair performance. rTMS was delivered to left and right vPMc and EBA while healthy participants observed snapshots of biomechanically possible or impossible body actions. Participants were asked to match a tachistoscopically presented sample to one of two probes showed in free viewing. The matching and nonmatching stimuli were: (i) two different possible actions (possible action discrimination); (ii) two different impossible actions (impossible action discrimination); or (iii) the same action performed with biomechanically possible and impossible kinematics (biomechanical plausibility discrimination). The biomechanical plausibility action discrimination task allowed us to test whether mapping of observed body actions in vPMc and EBA includes the actions’ goal, their motor kinematics, or both. Indeed, while the discrimination between possible and impossible actions may be based on differences in either movement kinematics or goal, the discrimination of the biomechanical plausibility may rely only on kinematic differences (i.e., possible and impossible actions shared the same goal).

## EXPERIMENTAL PROCEDURES

### Participants

Thirty-two healthy individuals were recruited for the experiment. Based on a random assignment

procedure, 16 participants (1 man) underwent left hemisphere stimulations and the other 16 (4 men) right hemisphere stimulations. A standard handedness inventory (Briggs & Nebes, 1975) allowed us to ascertain that all participants were right-handed. Participants were native Italian speakers with normal or corrected-to-normal visual acuity in both eyes. None of the participants had neurological, psychiatric, or other medical problems or had any contraindication to TMS (Wasserman, 1997). Participants were naïve as to the purposes of the experiment, and information about the experimental hypothesis was provided only after the experimental tests were completed. Participants gave their written informed consent and were paid €15 for their participation in the study. The procedures were approved by the ethics committee of Fondazione Santa Lucia (Rome) and they were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No participant complained of any discomfort or presented any adverse effects during rTMS.

### Stimuli and tasks

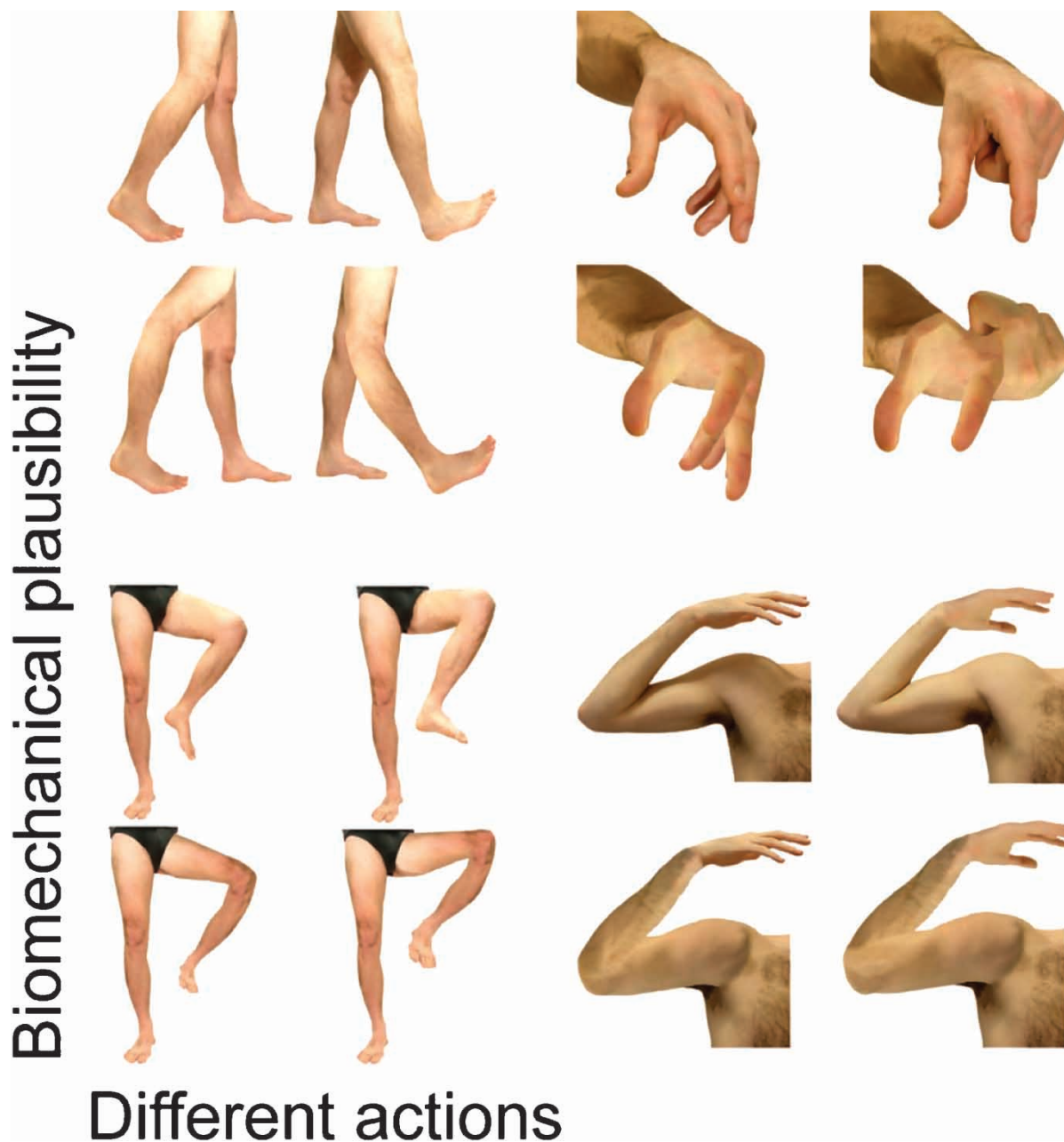
Experimental stimuli were color pictures depicting snapshots of body actions. One male model was videotaped while performing four pairs of different actions. Each pair was composed of two slightly different actions performed with the same limb. Two pairs of actions involved the right upper limb and the other two pairs involved the right lower limb. Pairs of stimuli represented meaningful (precision grip or gross grasping for upper limb and forward or backward walking for lower limb) or meaningless actions (hand approaching the anterior or posterior part of the shoulder for upper limb, and foot moving towards the contralateral knee, either in front of or behind it, for lower limb). To rule out any effect of mere observation of graspable objects (Chao & Martin, 2000) mimicking action stimuli in the absence of any object (i.e., a class of stimuli that has been shown to activate vPMc) were used (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005). Furthermore, since our design required fast stimuli presentation, the sense of acting body was elicited selecting snapshots from the middle phase of each action. We have demonstrated that visual perception of static images implying body actions activates the motor system (Urgesi, Moro, Candidi, & Aglioti, 2006b) and that the visual

discrimination of static images representing body actions is a task adept to investigate the role of vPMc in action perception (Urgesi et al., 2007). The two stimuli of each pair were matched for the instant at which the snapshot was taken, and for perspective, luminance, and crude contours. For each biomechanically possible action we created a stimulus representing the corresponding action performed with a biomechanically impossible kinematic. The biomechanically impossible action stimuli were created by modifying the original action snapshots using Adobe Photoshop software (Adobe Systems Incorporated, San Jose, CA). In the impossible action stimuli the joints were modified so as to violate the biomechanical constraints of the human body, while the general sense of the corresponding possible action was maintained. For example, in the two impossible grasping movements, the index finger (precision grip) or all fingers (gross grasping) approached the thumb on the dorsum of the hand (Figure 1). To balance the laterality of the stimulus set, the eight right-limb possible- and impossible-action images were mirrored to obtain the corresponding left-limb action images. Therefore, 32 different stimuli were used.

Within the same block, participants performed three types of matching-to-sample tasks. In all tasks, participants had to choose which one of two different probe images matched the target image. The matching and non-matching stimuli could depict: (i) two slightly different biomechanically possible actions (possible actions discrimination); (ii) two slightly different biomechanically impossible actions (impossible actions discrimination); or (iii) a biomechanically possible action and the corresponding biomechanically impossible action with the same general meaning (biomechanical plausibility discrimination). All the discriminations regarded actions made by the same model with the same body part. To investigate any differences between possible and impossible action images that might explain differential rTMS modulation, we collected subjective reports on the stimuli from an independent sample of 10 individuals. They were asked to judge each stimulus by marking a vertical, 10 cm visual analog scale (VAS), with 0 cm indicating “*no effect*” and 10 cm “*maximal effect imaginable*”. Subjects rated the following properties of the observed stimuli: (1) quantity of implied motion; (2) unpleasantness; (3) biomechanical plausibility; (4) sense of joint stretch; and (5) painfulness.

## Transcranial magnetic stimulation

Participants wore a tightly fitting bathing cap on which scalp stimulation points were marked. Motor-evoked potentials (MEPs) were recorded from first dorsal interosus (FDI) muscle of the dominant hand. Surface Ag/AgCl electrodes were placed in a belly tendon montage with the active electrode placed over the muscle belly and the reference over the interphalangeal joint. Responses were amplified at a gain of  $1000 \times$  by a Digitimer D360 amplifier (Digitimer, Hertfordshire, UK), bandpass filtered (20 Hz–2.5 kHz), and digitized (sampling rate: 5 kHz) by means of a CED Power 1401 controlled with Spike 2 software (Cambridge Electronic design, Cambridge, UK). The resting motor threshold (rMT), defined as the lowest intensity able to evoke five out of ten MEPs with an amplitude of at least  $50 \mu\text{V}$ , was determined by holding the stimulation coil over the optimal scalp position (i.e., the motor cortex area contralateral to the dominant hand producing the largest MEPs) for the FDI muscle. Moreover, during the experimental sessions, electromyographic signals were continuously recorded from the FDI and the abductor digiti minimi (ADM) muscles of the responding and non-responding hands to control for MEP that could be evoked by stimulation of vPMc (Uozumi, Tamagawa, Hashimoto, & Tsuji, 2004). Off-line visual inspection of data did not show any MEP or any alteration of the electromyographic signal following stimulation of left or right vPMc or EBA. Stimulation sites were identified on each participant’s scalp with Softaxic Navigator system (EMS, Bologna, Italy). Skull landmarks (nasion, inion, and two preauricular points) and about 60 points providing a uniform representation of the scalp were digitized by means of a Fastrak Polhemus digitizer (Polhemus, Colchester, VT). Coordinates in Talairach space (Talairach & Tournoux, 1988) were automatically estimated by the Softaxic Navigator from an MRI-constructed stereotaxic template. The scalp locations that corresponded best to left and right EBA and vPMc coordinates (Costantini et al., 2005; Downing et al., 2001; Urgesi et al., 2004) were identified and marked with a pen. Mean coordinates, in Talairach space (Talairach & Tournoux, 1988), of the targeted stimulation sites in the left hemisphere group were  $x = -53.7 \pm 0.1$ ,  $y = -71.0 \pm 0.0$ ,  $z = 4.0 \pm 0.0$  for EBA, and  $x = -57.1 \pm 0.2$ ,  $y = 11.7 \pm 0.9$ ,

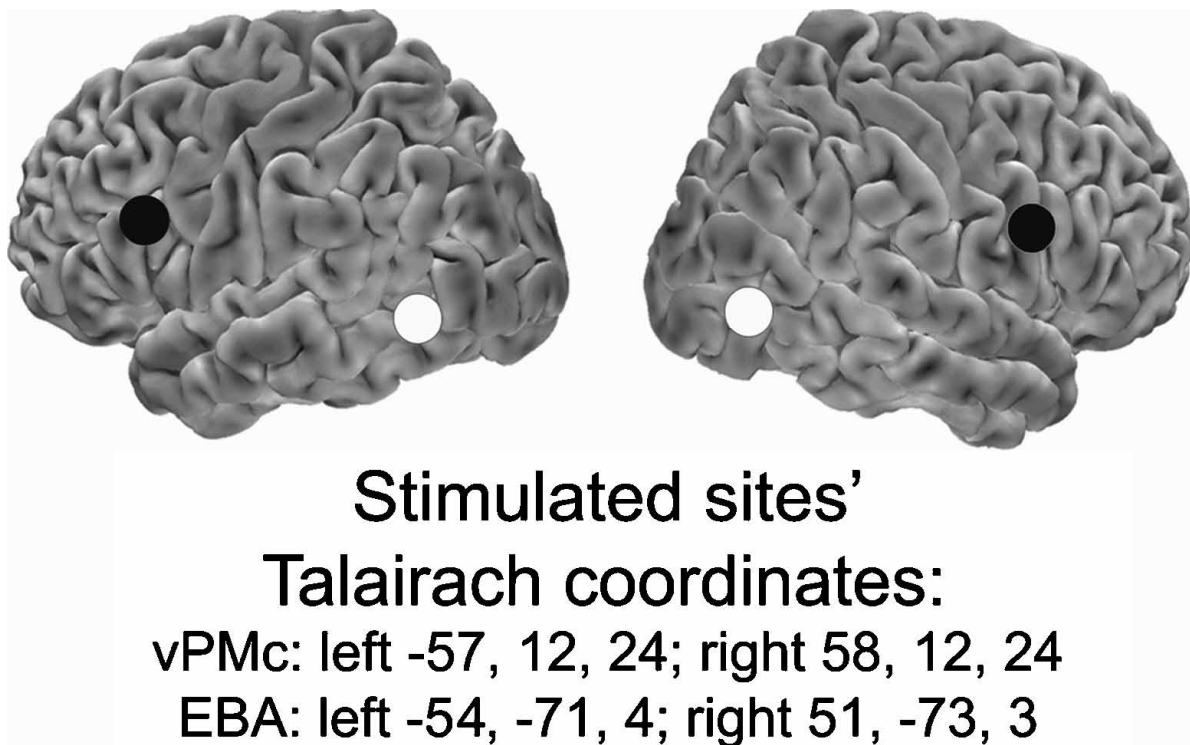


**Figure 1.** Examples of the experimental stimuli. Images represented upper and lower limbs performing meaningful and meaningless actions. All left images were obtained by mirroring the corresponding right ones.

$z = 24.0 \pm 0.0$  for vPMc; mean coordinates of the targeted sites in the right hemisphere group were  $x = 51.7 \pm 0.5$ ,  $y = -72.9 \pm 0.2$ ,  $z = 3.1 \pm 0.6$  for EBA, and  $x = 58.1 \pm 0.3$ ,  $y = 12.0 \pm 0.5$ ,  $z = 24.1 \pm 0.3$  for vPMc (Figure 2).

rTMS was performed by connecting two Magstim Mode 200 stimulators with Bistim module (The Magstim Company, Carmarthenshire, UK), producing a maximum output of 1.75 T at the coil surface (stimulus attenuation, 22%; duration,

1 ms; rise time, 110  $\mu$ s). Two pulses were delivered with an interstimulus interval of 100 ms by means of a 70 mm figure of eight stimulation coil (Magstim polyurethane-coated coil). In keeping with previous studies showing rTMS suppressive effect on EBA (Urgesi et al., 2004) and vPMc (Urgesi et al., 2007), the first TMS pulse was delivered 150 ms after the onset of sample presentation for stimulation of both EBA and vPMc areas. The stimulation timing was consistent with



**Figure 2.** Talairach coordinates of stimulated sites corresponding to left and right vPMc and EBA. For each participant, stereotaxic coordinates corresponding to the target areas were obtained by means of the SofTactic neuronavigation system.

the time course of vPMc activation during visual presentation of moving body parts as revealed by magnetoencephalography studies (Nishitani & Hari, 2000, 2002). Stimulation intensity was 120% of the rMT for both pulses and ranged from 38% to 63% of the maximum stimulator output (mean = 51.8%) for the group of participants receiving right hemisphere stimulations and from 36% to 64% of the maximum stimulator output (mean = 46.5%) for the left hemisphere group. During magnetic stimulation, the coil was held tangential to the scalp, with the handle pointing backward and laterally at a 45° angle from the middle sagittal axis of the participants' head. For sham stimulation, the coil was held sided-up and tangential to the scalp over the vertex of the participants' head. This ensured that no focal magnetic stimulation reached the brain during the sham stimulation and controlled for noise and sensation of the coil against the head. The same intensity and timing of real magnetic stimulation were used for sham stimulation. The coil was held by hand, and its position with respect to the marks was checked continuously. During sham and real stimulation participants wore commercial earplugs to protect their

hearing. None of them reported phosphenes after rTMS of EBA.

### Procedure

Each participant was tested in one experimental session lasting approximately 2 hours. Participants completed two practice blocks, followed immediately by the experimental blocks.

Possible- and impossible-actions discrimination as well as biomechanical-plausibility discrimination trials were randomly delivered within the same 24-trials blocks (8 trials per task).

Two blocks of 24 trials (16 trials per task) were performed for each stimulation site (EBA, vPMc, sham), for a total of 144 matching-to-sample trials. Within each block, half of the sample stimuli were images of possible actions and the other half were impossible actions. Given that the different discriminations were randomly requested in the same block, participants could not anticipate the type of discrimination performance required in that particular trial from viewing the sample stimulus. It is worth noting that the same sample stimuli were presented in the biomechanical plausibility as in

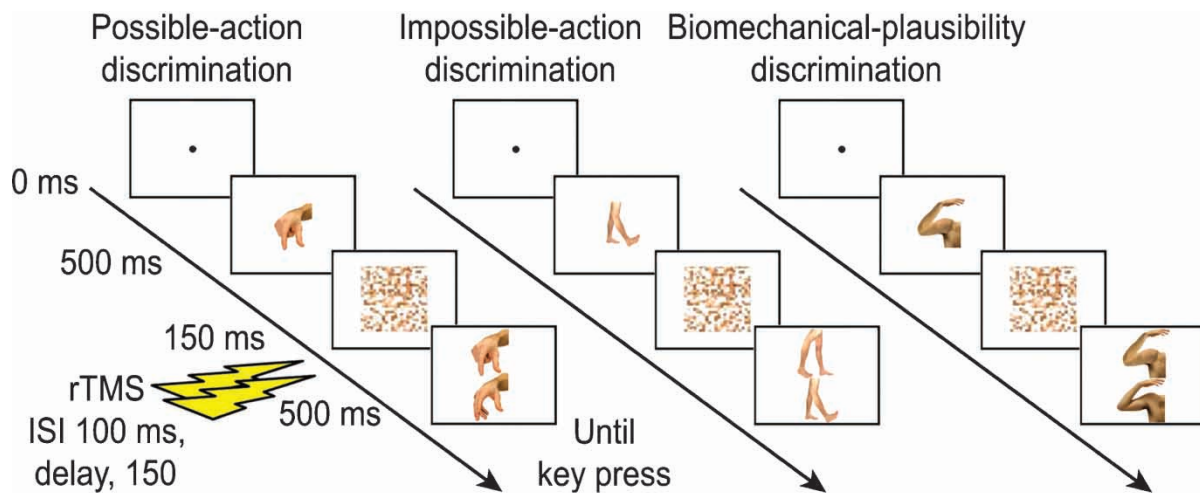
the possible and the impossible action discrimination tasks. Thus, any differential effect of vPMC and EBA stimulations in the different tasks cannot be due to low-level visual differences in the stimuli, but rather to the type of discrimination implicitly induced by the stimuli. A short rest was allowed before proceeding to a different block. Each individual performed twice all the three stimulation conditions according to an across-participants counterbalanced sequence. Each trial started with the presentation of a central fixation point (lasting 500 ms) aimed at minimizing eye movements. Then the sample stimulus was presented for 150 ms at the center of the monitor. Image persistence was limited by presenting a random-dot mask (9.1 × 9.1° in size) for 500 ms. This was obtained by scrambling the corresponding sample stimulus by means of a custom-made image segmentation software. Immediately after the disappearance of the mask, the two probe stimuli appeared and remained on the screen until a response was made. Participants were asked to respond as quickly as possible by using their index or middle finger to press the left or the right key of a custom-made response box (Figure 3).

Each key corresponded to one of the two positions on the screen on which the probe stimuli were presented; the positions of the probe stimuli were randomized in each trial. To rule out purely motor effects of rTMS on the speed of response, the responding hand was ipsilateral to the side of stimulation. Thus, the left hand was used in the group receiving left hemisphere stimulations and the right hand in the group receiving right hemi-

sphere stimulation. Reaction times (RTs) and accuracy of response were automatically recorded and stored for analysis.

## Data analysis

Individual mean RTs and response accuracy were calculated for each experimental condition (16 trials per cell). Only RTs for correct responses were considered; moreover, RTs that fell below or above three standard deviations from each individual mean were identified for each cell and removed as outliers (0.47% and 0.51% for left and right hemisphere groups, respectively). Mean normalized and raw accuracy and RTs for all EBA, vPMC, and sham stimulation conditions are reported in Table 1 and Table 2. Along with its capability to selectively interfere with neural activity, TMS may introduce some biasing non-specific effects. Touch and noise sensation of the coil over the head may unspecifically influence performance (Blanke et al., 2005; Sawaki, Okita, Fujiwara, & Mizuno, 1999; Terao et al., 1997). Furthermore our experimental design tested two different samples of subjects for the left and right hemisphere, respectively. Thus, to compare the specific effect of rTMS for each task in each individual, RTs and accuracy raw values for left and right EBA and vPMC stimulation conditions were normalized on the sham stimulation condition. This procedure allowed us to test the specific effect of rTMS interference independently from tasks difficulty and interindividual differences in



**Figure 3.** Procedure examples of possible, impossible and biomechanical plausibility discriminations. Repetitive transcranial magnetic stimulation (rTMS) was applied with a delay of 150 ms after sample presentation. On each trial, a 10-Hz dual-pulse train lasting 200 ms was delivered during mask presentation.

**TABLE 1**  
Normalized RTs and accuracy of response means ( $\pm$  MSE) of EBA and vPMc stimulation conditions

	<i>Left</i>		<i>Right</i>	
	<i>EBA</i>	<i>vPMc</i>	<i>EBA</i>	<i>vPMc</i>
<i>Normalized RTs (sham%)</i>				
Possible action	98.27 (3.25)	101.52 (3.06)	97.30 (2.80)	105.57 (3.55)
Impossible action	100.02 (3.93)	93.44 (3.37)	97.85 (3.04)	104.98 (4.85)
Biomechanical plausibility	100.01 (3.11)	96.96 (2.31)	101.29 (2.16)	101.37 (3.25)
<i>Normalized accuracy of response (sham%)</i>				
Possible action	99.62 (5.22)	101.66 (3.96)	101.60 (3.09)	100.54 (3.21)
Impossible action	105.44 (5.07)	98.42 (4.28)	102.38 (6.07)	96.46 (4.46)
Biomechanical plausibility	99.95 (6.84)	100.15 (5.37)	101.55 (5.52)	100.35 (5.66)

the absolute level of performance. Individual normalized accuracy and RTs were entered in two separate mixed-model ANOVAs, with Group (left, right hemisphere) as between-subjects factor and Task (possible actions, impossible actions, and biomechanical plausibility discriminations) and Stimulated site (EBA, vPMc) as within-subjects variable. Duncan's tests were used for post hoc analysis. The subjective reports of the independent group of individuals for the possible and the impossible body actions stimuli were compared by means of dependent-sample *t*-tests (two tailed).

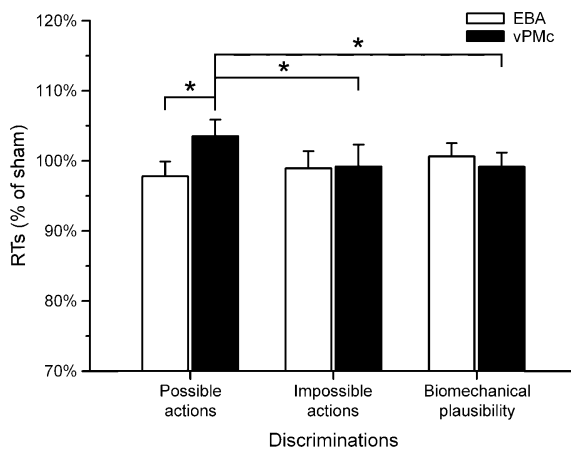
## RESULTS

Analysis on RTs showed that the main effects of Group,  $F(1, 30) = 1.21$ ,  $p = .280$ , Task,  $F(2, 60) = 0.22$ ,  $p = .807$ , and Stimulated site,  $F(1, 30) = 0.54$ ,  $p = .467$ , were nonsignificant, thus ruling out any non-specific effects of rTMS involving group, task, or stimulated site. Crucially, however, the interaction between Task and Stimulated site was significant,  $F(2, 60) = 4.62$ ,  $p = .014$  (Figure 4).

Post hoc comparisons revealed that normalized RTs during discrimination of possible actions were increased after stimulation of vPMc ( $103.55\% \pm 2.33\%$ ) with respect to stimulation of EBA ( $97.78\% \pm 2.11\%$ ,  $p = .004$ ). In contrast, no significant difference was observed between the effects of vPMc and EBA rTMS for impossible actions discrimination ( $99.21\% \pm 3.08\%$  vs.  $98.94\% \pm 2.45\%$ ,  $p = .886$ ) and for biomechanical plausibility discrimination ( $99.16\% \pm 2.00\%$  vs.  $100.65\% \pm 1.86\%$ ,  $p = .433$ ). Furthermore, the interferential effect of vPMc rTMS on discrimination of possible actions was significantly higher than the effect of vPMc rTMS on impossible actions ( $p = .022$ ) and biomechanical plausibility discriminations ( $p = .025$ ), which in turn did not differ from one another ( $p = .980$ ). In contrast, while the effect of EBA rTMS on discrimination of impossible actions was significantly lower than that of vPMc rTMS on discrimination of possible actions ( $p = .020$ ), no differential effect in the three discrimination tasks was obtained after EBA rTMS (all  $ps > .153$ ). No other pairwise comparison was significant. Furthermore no other two-way interactions nor the three-way

**TABLE 2**  
Raw RTs and accuracy of response means ( $\pm$  MSE) of all experimental conditions

	<i>Left</i>			<i>Right</i>		
	<i>Sham</i>	<i>EBA</i>	<i>vPMc</i>	<i>Sham</i>	<i>EBA</i>	<i>vPMc</i>
<i>Raw RTs (ms)</i>						
Possible action	796.96 (94.18)	755.26 (70.65)	806.67 (100.41)	799.11 (45.96)	778.60 (51.13)	840.73 (51.46)
Impossible action	890.69 (132.05)	851.87 (96.12)	798.96 (90.97)	843.23 (57.94)	815.50 (51.54)	878.09 (64.47)
Biomechanical plausibility	846.00 (111.65)	814.49 (85.30)	818.86 (110.02)	811.56 (54.51)	817.61 (53.77)	815.27 (54.91)
<i>Raw accuracy of response(% of total)</i>						
Possible action	85.94 (3.05)	83.60 (2.27)	85.94 (2.39)	79.30 (2.53)	79.69 (1.76)	79.30 (2.84)
Impossible action	79.30 (1.78)	82.81 (3.20)	77.34 (2.67)	73.05 (2.72)	73.05 (2.90)	69.14 (2.38)
Biomechanical plausibility	84.77 (3.65)	82.03 (3.27)	82.81 (2.94)	78.91 (2.85)	78.52 (3.12)	77.34 (2.61)



**Figure 4.** Normalized RTs (mean  $\pm$  MSE) of the interaction Task  $\times$  Stimulated site. The interferential effect of rTMS was only observed for left and right vPMc (black columns) stimulation during biomechanically possible action discrimination.

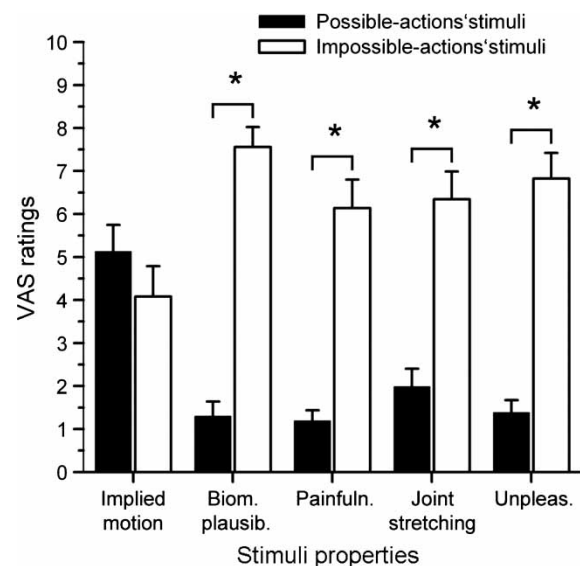
interactions reached significance. Given that the interaction Group by Stimulated area failed to reach significance threshold,  $F(1, 30) = 3.14$ ,  $p = .087$ , stimulation of both left and right vPMc impaired discrimination of possible but not impossible actions. This would suggest that no hemispheric difference exists in processing of body actions. In a similar vein, the nonsignificant effects of the interaction Group by Task,  $F(2, 60) = 0.21$ ,  $p = .809$ , and of the three-way interaction,  $F(2, 60) = 2.58$ ,  $p = .084$ , indicate that left and right hemisphere rTMS produced a similar pattern of results in all conditions, thus ruling out any spurious effect due to between-groups differences. The mixed-model ANOVA on normalized accuracy, did not disclose any significant effect. In particular the nonsignificant effect of the interaction Task by Stimulated site,  $F(2, 60) = 1.69$ ,  $p = .194$ , rules out that rTMS modulations on RTs may be explained by speed-accuracy trade-off effects. Thus, interferential stimulation of vPMc induced slower responses for visuo-perceptive discrimination of possible but not impossible body actions, without affecting response accuracy. No effect of interferential stimulation of EBA was observed (see Tables 1 and 2).

Subjective reports about different properties of the stimuli used in the TMS study showed that the motion implied by the observed stimuli significantly differed from zero for both possible (implied motion,  $t(9) = 8.23$ ,  $p = .000$ ) and impossible actions stimuli (implied motion,  $t(9) = 5.79$ ,  $p = .000$ ). These results suggest that both possible and impossible stimuli induced the

perception of implied motion and were perceived as part of an action sequence. More importantly, no differences in the amount of implied motion attributed to possible and impossible action stimuli ( $5.12 \text{ cm} \pm 0.62 \text{ cm}$  vs.  $4.08 \text{ cm} \pm 0.70 \text{ cm}$ ),  $t(9) = 1.84$ ,  $p = .099$ . Conversely possible and impossible stimuli were differentially rated for unpleasantness ( $1.38 \text{ cm} \pm 0.29 \text{ cm}$  vs.  $6.82 \text{ cm} \pm 0.60 \text{ cm}$ ),  $t(9) = -8.03$ ,  $p = .000$ , biomechanical plausibility ( $1.29 \text{ cm} \pm 0.35 \text{ cm}$  vs.  $7.56 \text{ cm} \pm 0.47 \text{ cm}$ ),  $t(9) = -10.13$ ,  $p = .000$ , joint stretching ( $1.98 \text{ cm} \pm 0.42 \text{ cm}$  vs.  $6.34 \text{ cm} \pm 0.65 \text{ cm}$ ),  $t(9) = -6.06$ ,  $p = .000$ , and painfulness ( $1.19 \text{ cm} \pm 0.25 \text{ cm}$  vs.  $6.14 \text{ cm} \pm 0.66 \text{ cm}$ ),  $t(9) = -7.53$ ,  $p = .000$  (Figure 5).

## DISCUSSION

The present study sought to determine the role played by left and right vPMc and EBA in the discrimination of biomechanically possible and impossible actions. We asked participants to perform a matching-to-sample task that required the discrimination between two different possible actions, two impossible actions, and between the same action performed with biomechanically possible and impossible kinematics. In different blocks, rapid event-related rTMS trains of two



**Figure 5.** Subjective VAS ratings of the different properties of the experimental stimuli. While biomechanically possible and impossible actions were comparable for implied motion, the latter induced higher sense of biomechanically implausibility, painfulness, joint stretching and unpleasantness with respect to the former.

pulses were applied 150 ms after sample presentation over left and right vPMc and EBA. Magnetic stimulation had no effect on accuracy of response but selectively impaired RTs for possible actions discrimination when applied over both left and right vPMc. No effect of left and right vPMc and EBA rTMS was observed for either discrimination of impossible actions or for discrimination of the biomechanical plausibility of actions.

### Visual processing of body actions in premotor cortex

Passive observation of actions activates premotor areas (Keysers & Gazzola, 2006; Rizzolatti & Craighero, 2004), suggesting that action observation triggers the simulative mapping of observed actions onto the observer's motor representations. Recent studies reported that vPMc rTMS impairs discrimination of static (Urgesi et al., 2007) and dynamic (Pobric & Hamilton, 2006) displays of actions. In keeping with previous studies (Pobric & Hamilton, 2006; Urgesi et al., 2007), our results indicate that vPMc neural activity is actively involved in visual perception of biomechanically possible actions. This suggests that motor and premotor areas may be specifically involved in visual processing of action-related features of the visible body parts even when the task does not explicitly require the motor simulation of the observed movements. This may be in keeping with the fact that motor activation during action observation seems to topographically map the moving body part (Buccino et al., 2001; Fadiga, Craighero, & Olivier, 2005; Urgesi, Candidi, Romani, Fabbro, & Aglioti, 2006a). Mapping observed actions onto the onlooker's motor representations may provide the visual system with a fine-grained description of the moving body; motor representations of the acting bodies may thus feed back into visual cortices and refine perception of body forms (Wilson & Knoblich, 2005). Indeed, monitoring our own body postures and actions reinforces the representation of postures and actions of other people's bodies (Reed & Farah, 1995). Furthermore, self-produced limb movements activate EBA (Astafiev et al., 2004), suggesting a functional link between the motor system and the body's visual representations. The interaction between visual and motor body-related areas

may subserve the sophisticated human ability to process actions performed by conspecifics.

### Neural representations of biomechanically impossible actions

The present study significantly expands previous evidences (Pobric & Hamilton, 2006; Urgesi et al., 2007) by testing whether vPMc is also involved in visual discrimination of movements that cannot be performed. We show that vPMc plays a crucial role only in visuo-perceptive discriminations of biomechanically possible actions, but does not play any causative role in processing pictures of actions that cannot be performed. This suggests that premotor representations of actions only occur for movements that belong to the observer's motor repertoire. This is in keeping with studies showing that activations of mirror neurons system areas are modulated by motor expertise (Calvo-Merino et al., 2005, 2006; Cross, Hamilton, & Grafton, 2006). Similarly, it has been shown that purely motoric learning of specific actions improves their visuo-perceptual discrimination (Casile & Giese, 2006). Furthermore, Buccino et al. (2004) reported that only gestures belonging to the *species*-specific motor repertoire activate the motor system, whereas actions that are typical of other species seem to engender predominantly visual activations. The notion that only doable movements activate observers' motor and premotor cortices has been re-examined by the finding of comparable activations of motor and premotor cortices during observation of impossible movements (Costantini et al., 2005; Romani et al., 2005). Motor activation during observation of biomechanically impossible actions (Costantini et al., 2005; Romani et al., 2005) may reflect the fact that the cortico-spinal motor system does not map the specific kinematics of the observed actions but their general meaning. To test this hypothesis we explored the active involvement of vPMc in a task requiring the discrimination between the meaning of two actions executed with biomechanically impossible kinematics. If vPMc codes the goal of an action regardless of its motor kinematics, this area should play a role independently from the biomechanical plausibility of the observed action. In contrast, our results clearly show that activations of vPMc are not necessary for visual perception of the general meaning of actions that, although conceptually possible, are biomechanically impossible and thus cannot be

performed. Thus, motor representation of observed actions does not seem to be constant with respect to kinematics of the movement. Another result of the present study is that vPMc does not seem to play any causative role in the discrimination of actions' biomechanical plausibility. It is worth noting here that this task required the discrimination of two actions that shared the same goal but were performed with either biomechanically possible or impossible kinematics. Interfering with vPMc activity did not affect performance during the biomechanical plausibility discrimination which may suggest that the motor representations of observed actions are not used for the visual perception of action kinematics. Therefore, neural activation of vPMc is not necessary for the discrimination of actions with different kinematics but sharing the same goal. In contrast, vPMc activity is crucial for discriminating the goal of different actions that are performed with biomechanically possible kinematics. This may indicate that the premotor cortex is likely to code a combination of goals and kinematics that allow the representation of actions as goal-directed movements (Rizzolatti et al., 2004). This is in line with imaging and single-unit electrophysiological data showing that premotor cortices may be the neural substrate of actions' goal representation (Johnson-Frey et al., 2003; Rizzolatti et al., 1988).

### **Processing of body actions in extrastriate body area**

The present study shows that, although impossible movements may trigger premotor cortices activations (Costantini et al., 2005), vPMc has no crucial role in perceptual representations of impossible actions. Motor activation during observation of biomechanically impossible movements may reflect modulatory signals from other cortical structures such as temporal and parietal areas (Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004). Indeed, observation of biomechanically impossible movements engenders higher activations of temporal and parietal areas as compared to observation of possible movements (Costantini et al., 2005). EBA response to acting bodies is enhanced by observation of incoherent sequences of body movements with strong configural changes of the body posture while neural activations of vPMc and of superior temporal sulcus are higher during observation of

coherent sequences of body movements (Downing et al., 2006). This suggests that EBA and vPMc play different roles in processing acting bodies: EBA may be involved in the static representation of human bodies' postures and in detecting visual discrepancies in the postural configurations of body images. Enhanced extrastriate activation during observation of impossible movements (Costantini et al., 2005), distorted body postures (Avikainen et al., 2003), and visuo-proprioceptive discrepancies (Dohle, Kleiser, Seitz, & Freund, 2004) may reflect general novelty or emotive salience of the stimuli. Neuroimaging studies, however, cannot establish whether changes of metabolic activity related to a given task is crucial rather than epiphenomenal. In contrast, using rTMS allows the investigation of the active role played by EBA in processing possible and impossible body actions. Previous rTMS studies have shown that interference with neural activity of EBA impairs discrimination performances based on the categorization of morphological details of the human body parts, but does not affect action discrimination (Urgesi et al., 2004, 2007). Here we demonstrate that EBA is not actively involved in discriminating two different possible actions performed by the same person, thus suggesting that the role of EBA in body perception is not causally related to the processing of action-related cues. Furthermore, the present study shows that EBA does not play any crucial role in discriminating impossible body actions as well as their biomechanical plausibility. EBA activity has been proved selective for images of the human body and its single parts (Downing et al., 2001, 2006) and premotor cortices have been demonstrated to be insensitive to observation of actions performed by nonbiological agents like robots (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). In view of this, one may wonder whether the lack of influence of EBA and vPMc on the perception of impossible body postures may be due to the fact that our stimuli were not coded as "body" or "bodily actions". However, the possible and impossible action stimuli used in our study induced the perception of comparable amount of implied motion and were perceived as parts of actions. Subjective ratings indicated that impossible actions stimuli induced higher joint stretching sensations, lower biomechanical plausibility, higher unpleasantness and higher painfulness in comparison with possible actions stimuli. That impossible action stimuli were perceived as body

parts in action rules out that the lack of effects of vPMC and EBA rTMS is due to an inappropriate coding of these stimuli. Our data show that EBA is not crucially involved in the visual discrimination of impossible body movements. The suggestion is made that this area may be part of a wide parieto-temporal network related to the multi-sensorial coding of afferent components of actions (Costantini et al., 2005). Indeed, enhanced neural activity in EBA during observation of impossible body postures may derive from sensorimotor feedback signals that modulate body form perception (Astafiev et al., 2004). Future studies are needed to better understand the functional links between extrastriate visual representation of acting bodies and sensorimotor representations in fronto-parietal areas.

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