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Report

Somatic and Motor Components of Action Simulation

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Summary

Seminal studies in monkeys report that the viewing of actions performed by other individuals activates frontal and parietal cortical areas typically involved in action planning and execution [1–3]. That mirroring actions might rely on both motor and somatosensory components is suggested by reports that action observation and execution increase neural activity in motor [4–13] and in somatosensory areas [8–10, 14–17]. This occurs not only during observation of naturalistic movements [4–17] but also during the viewing of biomechanically impossible movements that tap the afferent component of action, possibly by eliciting strong somatic feelings in the onlooker [18, 19]. Although somatosensory feedback is inherently linked to action execution [20], information on the possible causative role of frontal and parietal cortices in simulating motor and sensory action components is lacking. By combining low-frequency repetitive and single-pulse transcranial magnetic stimulation, we found that virtual lesions of ventral premotor cortex (vPMc) and primary somatosensory cortex (S1) suppressed mirror motor facilitation contingent upon observation of possible and impossible movements, respectively. In contrast, virtual lesions of primary motor cortex did not influence mirror motor facilitation. The reported double dissociation suggests that vPMc and S1 play an active, differential role in simulating efferent and afferent components of observed actions.

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Results

In the present study, we investigated the contribution of premotor, motor, and sensory regions recruited during action observation in mapping different types of observed actions onto the corticospinal system. By comparing human body movements that clearly differed in their biomechanical plausibility and in the amount of sensory feedback evoked in the onlooker (see Supplemental Data available online), we explored the role of frontoparietal regions in simulating the efferent (motor) and afferent (somatic) components of observed action.

In three experiments, we recorded motor-evoked potentials (MEPs) to single-pulse transcranial magnetic stimulation (spTMS) over the left primary motor cortex (M1) from two muscles of the right hand, namely the first dorsal interosseus (FDI, in the region of the index finger) and the abductor digiti minimi (ADM, in the region of the little finger). MEPs were collected during the observation of different video clips depicting the dorsal view of a static hand ("static") (1) or a right index finger performing abduction-adduction movements with angular displacements well within (biomechanically "possible") (2) or well beyond (biomechanically "impossible") (3) those allowed by the metacarpophalangeal joint in physiological conditions (see Movie S1). Dynamic video clips were chosen on the basis of the results of a preliminary psychophysical study in which 23 subjects not participating in the TMS experiments judged the biomechanically impossible movements as evoking strong somatic feelings (e.g., sensation of joint stretch or pain) (see Supplemental Data for details). Impossible movements seemed more linked to the afferent components of action than did possible movements (Table S1). Subjective reports collected at the end of each TMS experiment confirmed that aversive somatic feelings were triggered by the observation of biomechanically impossible movements (Table S2).

In each experiment, MEPs to spTMS during observation of the three types of video clips (static, possible, and impossible) were recorded in two counterbalanced separate sessions hereafter called "in-win" and "out-win." In the in-win sessions, all MEPs were recorded immediately after 15 min of 1 Hz repetitive TMS (rTMS). This low-frequency rTMS protocol should disrupt functions related to the targeted area for at least 7–8 min [21–23]. Because spTMS lasted about 6 min, all the in-win-session MEPs were recorded within the inhibitory window created by rTMS. In the out-win (outside the inhibition window, baseline) sessions, MEPs were recorded before rTMS (in about half of the subjects) or at least 1.5 hr after rTMS so it could be ensured that all interferential effects had faded away (in the remaining subjects, Figure S1).

Comparison of the amplitude of MEPs in the in-win and out-win sessions allowed us to assess the causative role of the stimulated areas in mapping the observed movements onto the onlooker's corticospinal system.

Inhibitory rTMS was delivered over three cortical areas supposed to be part of the action simulation system, namely the ventral premotor cortex (vPMc, in experiment 1) [4–10, 19, 24–26], the primary somatosensory cortex (S1, in experiment 2) [8–10, 14–17], and the primary motor cortex (M1, in experiment 3) [13–15, 19].

One major result of the present study is that the mirror corticospinal motor responses contingent upon observation of others' abduction-adduction finger movements performed within (biomechanically possible) or beyond (biomechanically impossible) the constraints of the metacarpophalangeal joint were differentially affected by inhibition of neural activity in the different targeted areas.

Virtual Lesion of vPMc Disrupts Motor Mapping of Biomechanically Possible Actions

The vPMc has been viewed as the core frontal region of the action mirror system [4–10], and recent event-related rTMS studies have demonstrated its causal role in action perception [24, 25] and imitation [26]. Therefore, in the first experiment, we applied rTMS over the left vPMc (Figure 1) at the scalp location that corresponded most closely to the activations found during action observation [5–10, 19]. Raw MEP amplitudes were analyzed by means of a three-way repeated-measures analysis of variance (ANOVA) with muscle (FDI, ADM), session (out-win, in-win) and condition (static, possible, impossible) as within-subjects factors (see Supplemental Data for further analysis). We found a significant triple interaction, muscle × session × condition ($F [2, 24] = 4.66$, $p = 0.019$). To further investigate this interaction, we performed two separate two-way repeated-measure ANOVAs, one for each muscle, with session (out-win, in-win) and condition (static, possible, impossible) as within-subjects factors. We found a significant main effect of session for MEPs recorded from both the FDI ($F [1, 12] = 18.36$, $p = 0.001$) and the ADM muscles ($F [1, 12] = 43.37$, $p < 0.0001$), with reduced MEP amplitudes after rTMS (~60% of the out-win, baseline session) (Figure 1 and Figure S2). Thus, rTMS over vPMc elicited a strong reduction of corticospinal excitability, comparable to that obtained after rTMS over more dorsal premotor sites [27–29]. MEPs recorded from the FDI muscle differed in the different conditions ($F [2, 24] = 12.08$, $p = 0.0002$) because the amplitude during observation of impossible ($p = 0.007$) and possible ($p = 0.029$) movements was higher than it was during observation of static-hand clips. Observation of possible and impossible movements did not differ from one another ($p = 0.29$). Crucially, we found a significant session × condition interaction ($F [2, 24] = 7.97$, $p = 0.002$) only for the MEPs recorded from FDI. Post-hoc analysis revealed that in the out-win baseline session (blue dots in Figure 1), observation of possible and impossible movements elicited higher MEPs with respect to the static condition ($p = 0.0002$ and $p = 0.0003$, respectively); possible and impossible conditions were comparable ($p = 0.58$) in the out-win session. In contrast, in the in-win session (histograms in Figure 1), the impossible condition elicited higher MEP amplitudes than did the static ($p = 0.041$) and possible conditions ($p = 0.034$), which in turn did not differ from one another ($p = 0.61$).

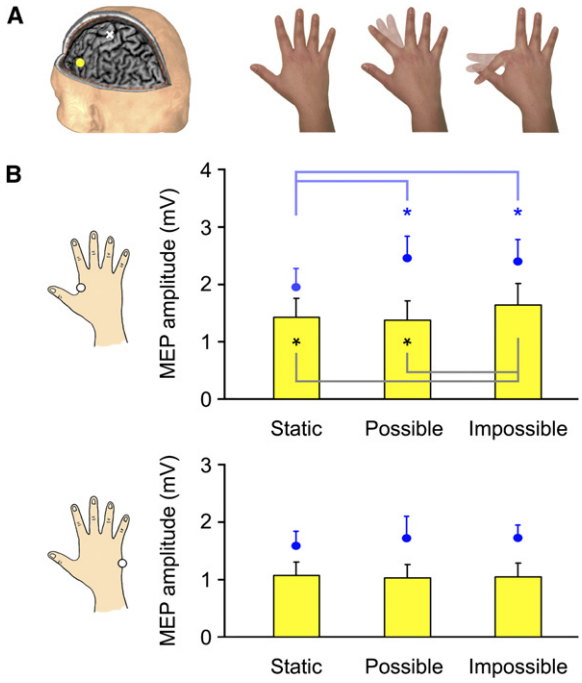

Figure 1. Results from Experiment 1, in which rTMS Was Delivered over the Left vPMc

(A) Stimulation sites on a cortical model and schematic depiction of the visual stimuli. The white cross represents M1, and the yellow blob represents vPMC. Scalp location corresponding to the pars opercularis of the inferior frontal gyrus was targeted for each observer by means of neuronavigation. Mean coordinates, in Talairach space, of this site were $x = -58 \pm 0.5$, $y = 14 \pm 0.6$, and $z = 24 \pm 0.2$. Mean coordinates of left M1 (optimal scalp position, the site of spTMS) were $x = -30 \pm 1.5$, $y = -18 \pm 2.0$, and $z = 65 \pm 0.9$.

(B) MEP amplitudes recorded from FDI and ADM are reported in the upper and lower part of the figure, respectively. In the out-win baseline session (blue dots), observation of possible and impossible index-finger movements brought about a facilitation of the FDI muscle. In the in-win session (columns), only impossible movements facilitated the FDI muscle. Error bars indicate the standard error of the mean (SEM). Asterisks indicate significant post-hoc comparisons ($p < 0.05$).

No effect of condition or interaction was found for MEPs recorded from the ADM muscle.

The mirror facilitations in the two sessions were directly compared by the normalization of MEP amplitude during action observation with MEP amplitude during static (possible/static and impossible/static). Importantly, although there was no significant difference between out-win (mean ± standard deviation [SD]: 132% ± 39%) and in-win (118% ± 27%; $t [12] = 0.94$, $p = 0.37$) sessions for the FDI MEP facilitation to biomechanically impossible movements, MEP facilitation to possible movements was strongly suppressed in the in-win session (96% ± 13%) and was significantly different from MEP facilitation in the out-win session (132% ± 35%, $t [12] = 3.67$, $p = 0.003$; see also Figure S3 and Supplemental Data).

In sum, the observation of index-finger movements brought about a MEP amplitude increase that was specific for the muscle that would be involved in the actual execution of the same action, thus indicating that the mirror motor mapping occurred according to somatotopic rules. Moreover, the increase of MEPs was

comparable for possible and impossible movements [18]. By using inhibitory low-frequency rTMS, we demonstrated that a generalized reduction of excitability of hand corticospinal representations can be obtained not only after dorsal premotor [27–29] but also after vPMc stimulation. Crucially, vPMc inhibition induced a dramatic change in the motor modulation induced by the different visual stimuli. In particular, vPMc inhibition mainly suppressed MEP facilitation contingent upon the observation of biologically possible body movements, without significantly changing the facilitation elicited during the observation of impossible movements (see also Figure S3). This strongly suggests that mirror corticospinal responses to the observation of others' possible body movements is linked to neural activity in vPMc. Conversely, this area does not seem crucially involved in mapping biomechanically impossible actions.

Virtual Lesion of S1 Disrupts Motor Mapping of Biomechanically Impossible Actions

Classical views of S1 focus on its involvement in coding afferent signals originating from the body. Recent studies, however, indicate that the somatosensory cortices play an important role in mapping others' painful and tactile sensory states [30–32]. Neurophysiological studies have found that somatosensory processing is modulated by the observation of others' actions [15–17]; this finding is corroborated by monkey [14] and human neuroimaging evidence [9, 10] that hand representations in the somatic cortices are recruited also during the observation of hand movements and even more so during observation of an object-grasping hand [9, 10]. Listening to the sound of hand actions induced an increase of the blood-oxygenation-level dependent (BOLD) signal in the somatic cortices that was positively correlated with the listeners' ability to take the perspective of another individual [8]; these findings suggest that we simulate both motor and sensory features of others' actions. Importantly, neural clusters in this region, as well as in other parietal sensorimotor areas, were activated even more strongly during observation of biomechanically impossible movements, which, as indicated by subjective reports, evoked abnormal somatic feelings in the observers [19]. Note also that a high degree of functional coupling between vPMc and S1 was found during the execution of movements without proprioceptive feedback in subjects who had undergone ischemic nerve block [20]. In light of this, in the second experiment, we applied rTMS over the left S1 (Figure 2).

The three-way repeated-measure ANOVA on MEP amplitudes showed a significant triple interaction ($F [2, 24] = 8.98$, $p = 0.001$). To investigate the interaction, we carried out two separate two-way ANOVAs for each muscle separately. For the FDI muscle, the ANOVA showed significant main effect of condition ($F [2, 24] = 6.61$, $p = 0.0005$), with slightly higher MEP amplitude for possible ($p = 0.064$) and impossible conditions ($p = 0.052$) than for the static condition. No significant effect of session was found (Figure S2). This might be in keeping with a study that showed that 1 Hz rTMS over anterior parietal sites does not induce overall changes in corticospinal excitability [27]. Crucially, however, we found a significant session × condition interaction ($F [2, 24] = 10.76$, $p = 0.0005$). Post-hoc comparisons

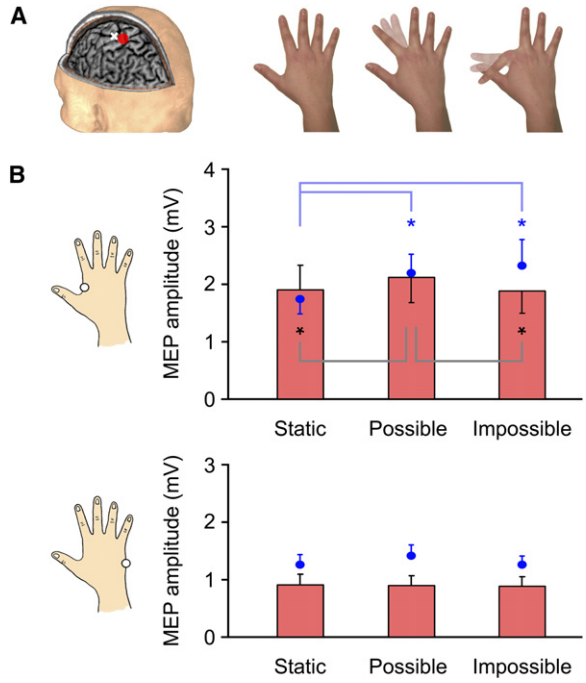

Figure 2. Results from Experiment 2, in which rTMS Was Delivered over the Left S1

(A) Stimulation sites on a cortical model and schematic depiction of the visual stimuli. We targeted scalp location corresponding to S1 for each observer by moving the coil 3 cm back with respect to the optimal scalp position (M1). By means of neuronavigation, we localized this site in Talairach space. Mean coordinates of S1 (red blob) were $x = -33 \pm 1.3$, $y = -33 \pm 1.4$, and $z = 66 \pm 0.7$. Mean coordinates of M1 (white cross) were $x = -33 \pm 1.3$, $y = -21 \pm 2.1$, and $z = 65 \pm 0.7$. (B) In the out-win baseline session (blue dots), observation of possible and impossible index-finger movements brought about a facilitation of the FDI muscle. In the in-win session (columns), only possible movements facilitated the FDI muscle. Error bars indicate SEM. Asterisks indicate significant post-hoc comparisons ($p < 0.05$).

showed the following: In the out-win session (blue dots in Figure 2), MEP amplitude during observation of possible and impossible movements was comparable ($p = 0.17$) and was higher than during observation of static stimuli ($p = 0.0005$; $p = 0.0002$); this indicates that in the out-win session, the corticospinal facilitation was similar for the two types of observed actions. In the in-win session (histograms in Figure 2), MEP amplitude was significantly higher during observation of possible than impossible and static conditions ($p = 0.043$; $p = 0.024$), which in turn did not differ from one another ($p = 0.88$). Finally, the MEP amplitude for impossible movements were higher in the out-win than in the in-win session ($p = 0.0007$). No modulation of MEPs recorded from the ADM muscle was found, further confirming that the corticospinal mapping of biomechanically possible and impossible movements follows somatotopic rules (Figure 2).

The analysis of mirror MEP facilitations (movement/static ratio) in the FDI muscle confirms that although there was no significant difference between out-win and in-win FDI MEP facilitation to possible movements (131% ± 26% versus 118% ± 36%, $t [12] = 1.07$, $p = 0.31$), MEP facilitation to biomechanically impossible movements was significantly reduced in the in-win

(107% ± 25%) compared to the out-win session (139% ± 29%, t [12] = 7.66, p = 0.000006). This pattern of results clearly indicates that rTMS over S1 selectively reduced the corticospinal mapping of impossible actions (see also Figure S3). In sum, experiment 2 indicates that interfering with neural activity in S1 by means of rTMS selectively disrupts the corticospinal mapping of biomechanically impossible movements.

Virtual Lesion of M1 Does Not Affect Motor Mapping of Biomechanically Possible and Impossible Actions

Far from being an area concerned with the mere issuing of output signals to subcortical motor structures, M1 might be involved causatively in complex functions such as for example motor imagery [33, 34]. It is thus entirely plausible that this area also plays a role in the action simulation induced by action observation [13–15, 19]. In view of this, in a third experiment, we applied rTMS directly over M1 and tested its effect on the MEP amplitude during observation of the same stimuli used in experiments 1 and 2. This experiment also allowed us to explore whether the effects of rTMS conditioning over vPMc (experiment 1) or S1 (experiment 2) were related to the current spreading to M1.

A three-way ANOVA on MEP amplitudes showed no significant triple interaction. There was a significant main effect of session (F [1, 12] = 11.68, p = 0.005). This effect was accounted for by the lower MEP amplitude recorded in the in-win session (~75% of the MEP amplitude in the out-win session, see Figure S1), in keeping with previous reports of reduced motor excitability after 1 Hz rTMS [21, 28, 35]. There was also significant main effect of muscle (F [1, 12] = 7.13, p = 0.020), with higher amplitudes for MEPs recorded from the FDI than ADM muscle. The nonsignificant interaction muscle × session suggests that 1 Hz rTMS affected the two muscles in the same way.

There was a significant main effect of condition (F [1, 12] = 9.85, p = 0.0008) and, more importantly, a significant muscle × condition interaction (F [1, 12] = 6.43, p = 0.006). This interaction was accounted for by the higher MEP amplitude recorded from the FDI during observation of both possible and impossible finger movements with respect to static hand observation (p = 0.001 and p = 0.003). Possible and impossible movements did not differ from one another (p = 0.37) (Figure 3); moreover, no modulation in the ADM muscle was found. Analysis of MEP facilitations in the FDI muscles confirmed that mirror corticospinal responses were comparable in the two sessions for both possible (out-win: 136 ± 45%, in-win: 127 ± 44%, t [12] = 0.92, p = 0.37) and impossible (out-win: 130 ± 57%, in-win: 129 ± 44%, t [12] = 0.12, p = 0.91, see also Figure S3) movements.

These results indicate that although rTMS over M1 was effective in provoking a general reduction of hand-muscle motor excitability, it did not alter the pattern of corticospinal mirror facilitation contingent upon observation of biomechanically possible and impossible finger movements (Figure 1, Figure S3). This finding indicates that M1 is not involved actively in the MEP facilitation induced by action observation [11, 12, 36–40] and suggests that observational action-related corticospinal mapping reflects the functional contribution of other nodes of the action mirror system.

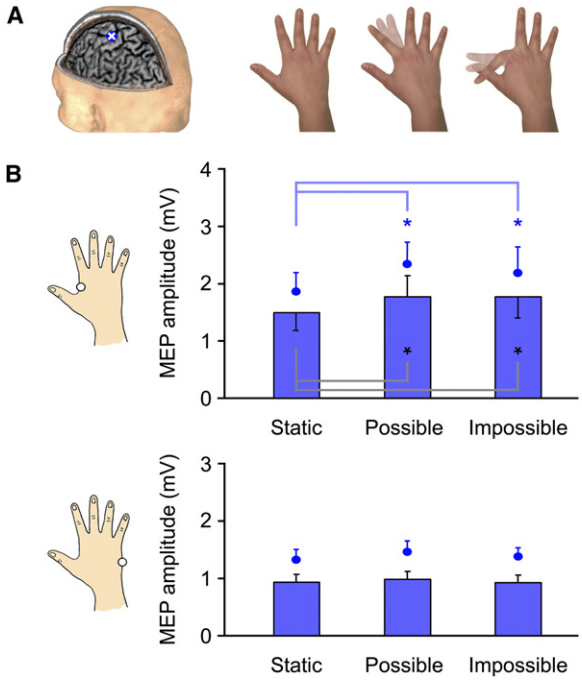

Figure 3. Results from Experiment 3, in which rTMS Was Delivered over the Left M1

(A) Stimulation site on a cortical model and schematic depiction of the visual stimuli. Scalp location corresponding to the left M1 was stimulated in each subject by using the optimal scalp position for evoking MEPs. By means of neuronavigation we localized this site in Talairach space. Mean coordinates of M1 (white cross and blue blob) were: x = −32 ± 1.4, y = −20 ± 2.5, z = 64 ± 0.7.

(B) In both the out-win baseline (blue dots) and the in-win (columns) sessions, observation of possible and impossible index-finger movements brought about a facilitation of the FDI muscle. Error bars indicate SEM. Asterisks indicate significant post-hoc comparisons (p < 0.05).

Discussion

Classically, efferent and afferent components during action execution have been linked to motor and somatosensory areas [41]. However, direct evidence for the purported differential role of afferent and efferent components in action simulation is lacking. Indeed, although viewing others' bodily movements likely elicits resonance not only with motor but also with sensory components of action [8–10, 13–17, 19], most of the studies performed so far focused on the efferent (motor) components of action simulation. In the present study, we explored the causative role played by motor, premotor, and sensory areas in the resonant mapping of efferent and afferent components of observed actions. We used a TMS paradigm derived from the combination of a virtual-lesion (1 Hz rTMS) and a correlational (spTMS) approach [22, 23]. The paradigm was applied while the experimental subjects observed either possible or biomechanically impossible finger movements that seem to tap the afferent component of action by eliciting somatic feelings in the onlooker.

Results indicate that observation of the two types of finger movements elicits comparable mirror corticospinal facilitation specific to the muscle involved in the observed movement [18]. Notably, however, the virtual-lesion

approach suggests that different neural substrates might selectively underlie the simulation of efferent and afferent components of observed actions. The inhibition of neural activity in the vPMc disrupted mirror responses to the observation of biomechanically possible finger movements, whereas the inhibition of S1 reduced mirror responses to biomechanically impossible movements. The inhibition of M1 brought about a general reduction of excitability but did not affect the corticospinal mapping of any types of movements.

The reported double dissociation highlights the active contribution of vPMc and S1 to the corticospinal mapping of human possible and biomechanically impossible finger movements, respectively. Moreover, the results suggest that simulation of possible and impossible movements relies on at least partially separate cortical systems, which specifically represent somatosensory and motor properties of observed actions. The notion of separate simulation of afferent and efferent components of observed actions has relevance for the ability to predict others' actions in that action-related perception is linked to an inherently anticipatory process [40, 42]. Moreover, the fine tuning of afferent and efferent components of action is also crucial for correct ownership attribution and sense of agency [43].

It is important to note that the pattern of changes in corticospinal excitability after rTMS over vPMc, S1, and M1 assured that repetitive stimulation was effective: rTMS over premotor and motor areas elicited a strong reduction of corticospinal excitability in both muscles [21, 27–29]; in contrast, rTMS over S1 did not affect corticospinal excitability [27]. There are at least two reasons why the results we obtained with the virtual-lesion approach cannot be accounted for by nonspecific changes in the reactivity of the motor system induced by rTMS. First, rTMS to vPMc and S1 selectively impaired corticospinal mapping of one type of movement, leaving the other unaffected. Second, rTMS to M1 brought about a general reduction of corticospinal excitability but did not change the amount of mirror motor facilitation. Remarkably, the finding that mirror motor facilitation was not affected by inhibition of M1 also suggests that the functional contribution of M1 to the MEP changes reported in the present and in previous action observation studies is not crucial [11, 12, 18, 36–40].

The vPMc Is Involved Actively in Mirroring the Efferent Components of Observed Actions

The human vPMc plays an important role not only in understanding the goal and the intention behind an observed action [4, 7] but also in encoding more basic processes, such as kinematics and motor features of observed actions [4, 11, 26]. The notion of resonant mapping of motor properties of action has been supported by the consistent action-observation-related increase of MEP amplitude that (1) was present for both transitive and intransitive actions [11, 12], (2) was specific for the muscles involved in the observed movements [36–40], and (3) was temporally coupled with the kinematics of observed actions [36, 44]. Although spTMS indicates that kinematics and motor features of observed actions are encoded into the observer's motor system, this approach alone cannot provide information about the specific corticocortical or corticospinal contribution to the action-observation-related MEP facilitation [12, 23].

Evidence from H reflex [38, 44, 45] and paired-pulse TMS [38, 39] studies suggests that mirror MEP facilitation was due mainly to a cortical modulation. However, up until now, the suggestion that the MEP change effect is linked to computations performed in premotor areas has been based on indirect evidence [11, 12]. The present study provides the first direct evidence that the vPMc plays a causative role in the MEP facilitation contingent upon action observation. Moreover, the active involvement of the vPMc in the simulation of the efferent components of observed actions demonstrates a specific role for this area not only in relatively complex action perception tasks [24, 25] but also in the basic motor encoding of others' possible actions.

Importantly, results indicate that S1 is not involved in the corticospinal mapping of biomechanically possible movements. It should be noted that observation of our possible actions does not evoke salient tactile, proprioceptive, or painful components in the onlookers. In contrast, observation of actions that imply the use of objects (e.g., hammering) might increase the salience of the somatic component of the action. Viewing touch modulates somatosensory cortices [30–32], and the vision of goal-directed hand actions activates S1 more strongly than do hand movements not directed at objects [9]. Therefore, it is entirely plausible that the somatosensory mapping of possible actions with conspicuous afferent properties can be disclosed also through the use of TMS.

The Somatic Cortex Plays a Causative Role in Mapping the Afferent Components of Observed Actions

Studies of expert dancers [46] and pianists [47] show that their motor mirror system is activated preferentially when they view actions belonging to their specific domain of expertise. Moreover, that neural activity in the human vPMc was found during observation of dogs biting but not dogs barking might suggest that only actions belonging to the observers' behavioral repertoire are mapped in the frontal node of their action mirror system [5]. The findings of these studies seem to contradict fMRI [19] and TMS ([18], present study) evidence that neural activity in premotor and motor areas and MEP facilitation are comparable when possible or biomechanically impossible finger movements are observed (see Supplemental Discussion). Interestingly, recent studies indicate that even the actions that do not belong in the observer's motor repertoire might be encoded into the action mirror system as long as the goal of the action is familiar to the observer [9, 10]. For example, observation of a robotic arm grasping an object might induce frontoparietal mirror activity comparable to that induced by human grasping [9]; moreover, mirror responses to the vision of human hand actions were found in aplasic subjects born without hands or arms as well as in typically developed individuals [10]. It should be noted that although the finger movements shown in our study are biomechanically impossible, they derive from an exaggeration of corresponding physiological movements and thus share a number of features with them,

including the visual appearance of the hand, the movement dynamics, the predictability, and even the goal [18, 19, 36, 42]. Therefore, it is in principle plausible that premotor areas map the action properties shared by possible and impossible movements [19, 42].

Investigation of the effect of observing biomechanically impossible actions might be crucial for the exploration of the somatosensory component of action simulation in that visual observation of these movements (1) elicits somatic sensations in the onlooker, ranging from aversion to the sensation of joint stretch or pain, and (2) selectively activates a large sensorimotor parietal network, including S1, thus suggesting that visual action observation recruits multimodal sensory networks where somatic and visual properties of action simulation are merged [19]. Another entirely novel result of the present study is that virtual lesions of S1, but not of vPMc or M1, disrupt corticospinal mapping of biomechanically impossible movements, indicating that mirroring this type of movement might be linked mainly to computations that take place in S1 and likely also in parietal multimodal regions [19]. The present findings that the viewing of biomechanically impossible movements evoked a range of aversive somatic feelings in the onlookers, and the crucial role of S1 in the specific mirroring of this type of movement would suggest that afferent components of observed actions are encoded primarily in parietal somatosensory areas rather than in the frontal node of the mirror system (see further discussion in Supplemental Data).

Neurophysiological and neuroimaging studies indicate that primary sensorimotor cortices might be activated by action perception [8–10, 13–17, 19]. Moreover, recent studies demonstrate that seeing innocuous or painful sensory stimuli delivered to others specifically modulates the onlookers' somatosensory cortices [30–32]. It is thus plausible that S1 might encode somatic states evoked by biomechanically impossible body movements. Moreover, this area is involved in mapping kinesthesia [48, 49]. Thus, biologically impossible actions might automatically activate kinesthetic representations of the movement-related violation of biomechanical constraints in multisensory parietal areas and S1 alike [19]. This somatic representation might be subsequently mapped onto the corticospinal system [18] and the frontal node of the mirror system [19] for the derivation of the motor properties of the observed action.

Conclusion

The combination of correlational and causative approaches used in the present research allowed us to demonstrate the specific role and functional connectivity of frontoparietal systems in the corticospinal mapping of observed actions. Note that in addition to affecting a given target area, rTMS might also influence remote interconnected brain areas [23, 27–29]. Thus, it is entirely possible that rTMS over vPMc or S1 modulated activity in other frontoparietal and somatomotor areas and/or that these areas contributed to the observed effects (see further discussion in Supplemental Data). At any rate, the scenario emerging from our study suggests that vPMc and S1 play a crucial role in matching others' possible and biomechanically impossible body movements onto our motor system, whereas the primary motor cortex is involved less directly in such mirror mapping. These findings suggest that separate cortical areas deal preferentially with afferent and efferent components of others' action.

Supplemental Data

Supplemental Results, Supplemental Discussion, Experimental Procedures, three figures, two tables, and one movie are available at http://www.current-biology.com/cgi/content/full/17/24/2129/DC1/.

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