

Don't Do It! Cortical Inhibition and Self-attribution during Action Observation

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Abstract

■ Numerous studies suggest that both self-generated and observed actions of others activate overlapping neural networks, implying a shared, agent-neutral representation of self and other. Contrary to the shared representation hypothesis, we recently showed that the human motor system is not neutral with respect to the agent of an observed action [Schütz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. Self and other in the human motor system. *Current Biology*, 16, 1830–1834, 2006]. Observation of actions attributed to another agent facilitated the motor system, whereas observation of identical actions linked to the self did not. Here we investigate whether the absence of motor facilitation for observing one's own actions reflects a specific process of cortical inhibition associated

with self-representation. We analyzed the duration of the silent period induced by transcranial magnetic stimulation of the motor cortex in active muscles as an indicator of motor inhibition. We manipulated whether an observed action was attributed to another agent, or to the subjects themselves, using a manipulation of body ownership on the basis of the rubber hand illusion. Observation of actions linked to the self led to longer silent periods than observation of a static hand, but the opposite effect occurred when observing identical actions attributed to another agent. This finding suggests a specific inhibition of the motor system associated with self-representation. Cortical suppression for actions linked to the self might prevent inappropriate perseveration within the motor system. ■

INTRODUCTION

The ability to recognize and distinguish ourselves from other persons is a fundamental component of our social behavior. The brain normally attributes bodily states and actions to the self or to another agent without difficulty or conscious effort. Traditional epistemology suggested that the private nature of somatic and efferent information formed the basis of a sense of self: I can feel my pain and understand my actions because they involve my body, but I cannot feel your pain or know your intentions because they involve your body (cf. Bernecker & Dretske, 2000).

From a neuroscientific point of view, however, the ability to recognize one's own actions appears problematic and poorly understood. In particular, the recent discovery of shared representations of action (SRA; de Vignemont & Haggard, in press), such as those provided by mirror neurons (cf. Gallese, Arbib, Fadiga, & Rizzolatti, 1996; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) suggests that action attribution is a key computa-

tional problem for the sensorimotor systems of the brain. The properties of mirror neurons suggest that both self-generated and observed actions activate overlapping neural networks (for an overview, see Rizzolatti & Craighero, 2004). For instance, transcranial magnetic stimulation (TMS) studies showed that observing the action of another person increased the amplitude of motor-evoked potentials (MEPs) in muscles normally involved in executing the particular action (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Strafella & Paus, 2000; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Action observation thus triggers a somatotopically specific “mirror” modulation of corticospinal excitability (Fadiga, Craighero, & Olivier, 2005), mapping an observed movement onto a motor representation of the same action in the observer (Rizzolatti, Fogassi, & Gallese, 2001). Such a “mirror matching mechanism” implies a shared, agent-neutral representation of self and other (Jeannerod & Pacherie, 2004; Decety & Chaminade, 2003; Jeannerod, 2001a, 2001b). This shared representation hypothesis raises the specific question of action attribution, and the more *general* question of how we distinguish self and other, given that the brain represents others' actions in the same way as it represents one's own (cf. Jeannerod & Pacherie, 2004). If action representations are indeed

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shared, as the hypothesis argues, then errors in assigning actions to the respective agent should occur. Problems of action attribution indeed do occur when one's own and others' actions are carried out at the same time and lead to similar perceptual effects as, for instance, when subjects may see either their own or another person's movements (cf. Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005; Farrer & Frith, 2002; Van den Bos & Jeannerod, 2002; Daprati et al., 1997). In such cases, action attribution processes cannot rely on the subjective experience of intending the action (cf. Haggard, 2005; Jeannerod, 2003), the motor commands (cf. Blakemore, Wolpert, & Frith, 2002; Wolpert, 1997), or morphological differences between the agents' respective bodies.

In line with "mirror theories" of social cognition, most studies have tended to emphasize commonality between self and other rather than distinctions in the neural responses to observation of one's own or another's. We recently showed, however, that the human motor system is *not* neutral with respect to attribution of an observed action (Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006). Instead, observation of our own actions and others' actions influence the motor system in qualitatively different ways. This finding indicates social sensitivity in the human motor system and also suggests that a sense of self might be embedded in primary sensorimotor representations. We used an established method, on the basis of the rubber hand illusion (RHI; Botvinick & Cohen, 1998), for manipulating the subject's sense of ownership over a hand which, in fact, belonged to another person. We then compared motor facilitation to TMS when the subject observed actions of the other person's hand that were or were not illusorily attributed to himself or herself. We found a significant interaction between the agent to whom the hand was attributed, and whether TMS was delivered just after an observed action or when viewing the static hand. Specifically, observing actions facilitated the MEP only when preceding multisensory stimulation linked the observed hand to another person, but not when it was linked to the self. Action attribution therefore modulated motor processes of action observation, contrary to the hypothesis of social equivalence or mirroring. In fact, the pattern of results showed a slight, but nonsignificant, inhibition of the MEP induced by actions attributed to the self. This had not been predicted, but raises the intriguing possibility that self-representation involves motor cortical inhibition.

The Present Study

The present study focused specifically on the putative process of cortical motor inhibition when observing actions linked to the self. We again used the RHI to manipulate the sense of body ownership. Thus, a hand which, in fact, belonged to the experimenter could be attributed either to the self or to another person. The

attribution of a body part can be varied, while keeping morphological, visual perspective, and kinesthetic cues constant. When the observed hand then performs an action, this action will therefore be attributed to the self or to another.

Several studies have suggested that action observation and inhibition are necessarily linked. If the brain's motor system, indeed, resonates to observed actions, some inhibitory mechanism is required to prevent us from imitating all the time, and indeed, for imitating ourselves (Baldissera, Cavallari, Craighero, & Fadiga, 2001; Brass, Zysset, & von Cramon, 2001; Fadiga et al., 1995). However, few studies have investigated this inhibitory aspect of action representation, and those that have done so focused on spinal rather than cortical levels (Baldissera et al., 2001). Our previous study showed clear effects of action attribution on corticospinal excitability and a nonsignificant numerical trend for inhibition of cortical responses when viewing actions attributed to the self. The present study aimed first to investigate whether cortical inhibition is, indeed, part of the mechanism for regulating cortical excitability during action observation, and second to investigate whether inhibition during action observation is agent-specific, and thus, linked to the process of action attribution.

The nature of inhibitory components within the action control system is not well understood (cf. Stuss & Knight, 2002). Further, inhibition is normally difficult to study because it produces no measurable output and can thus not easily be quantified. However, a valuable neurophysiological measure of inhibition in sensorimotor systems is the duration of the *silent period* (SP) induced by TMS in voluntarily contracted muscles. The SP refers to the suppression of background electromyographic (EMG) activity recorded from contracted muscles after single-pulse TMS to the primary motor cortex (M1). Typically, SP follows the MEP elicited by TMS. There is widespread agreement that SP and MEP reflect physiologically distinct mechanisms (e.g., Wassermann et al., 1993; Cantello, Gianelli, Civardi, & Mutani, 1992; Triggs et al., 1992), although the relation between them remains poorly understood (for an overview, see Hallett, 1995). Importantly, however, the SP acts as an indicator of inhibitory processes (Werhahn, Kunesch, Noachtar, Benecke, & Classen, 1999) and especially its late part has been proven to reflect a cortical origin (e.g., Cruccu, Inghilleri, Berardelli, Romaniello, & Manfredi, 1997; Brasil-Neto et al., 1995; Schnitzler & Benecke, 1994; Cantello et al., 1992; Triggs et al., 1992). Neuropharmacological studies suggest that SP is mediated by GABA_B receptors (e.g., Werhahn et al., 1999; Ziemann, Lonnecker, Steinhoff, & Paulus, 1996). Thus, the duration of the SP can be used as an index of GABAergic inhibitory activity of putative local interneurons and corticospinal neurons within the primary motor cortex. The longer the SP duration, the stronger is the inhibition provided by this circuit (Siebner & Rothwell, 2003; Hallett, 1995).

To date, few studies have used the SP duration to study cognitive top-down modulation of inhibitory sensorimotor circuits. If self-representation is, indeed, associated with cortical motor inhibition, we might expect longer SP durations when observing actions attributed to the self than identical actions attributed to another person.

METHODS

Participants

Fifteen healthy subjects (mean age = 24.73 ± 4.17 years, 6 men, 1 left-handed), free from any contraindication to TMS (Wassermann, 1998), participated with ethical committee approval on the basis of informed consent. No adverse events occurred due to the TMS applied during the study.

EMG and TMS Recordings

EMG activity was recorded in both the subject and the experimenter, from the right first dorsal interosseus (FDI). Disposable Ag/AgCl surface electrodes were placed over the muscle belly (active electrode) and over the associated tendon (reference electrode). A ground electrode was placed on the dorsal surface of the right wrist. EMG was amplified, digitized at 5 kHz, and band-pass filtered between 10 and 1000 Hz by a CED 1902 Signal Conditioner (Cambridge Electronic Design, Cambridge, UK).

A figure-of-eight focal coil interconnected to a Magstim 200 (Magstim, Whitland, UK) was placed over the left M1. The intersection of the coil was placed tangentially to the scalp with the handle pointing backward and laterally at a 45° angle away from the midline. In this way, the current induced in the neural tissue was directed approximately perpendicular to the line of the central sulcus, optimal for trans-synaptic activation of the corticospinal pathways (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). Using a slightly suprathreshold stimulus intensity, the coil was moved over the left hemisphere to determine the optimal position from which maximal amplitude MEPs were elicited in the resting FDI muscle (motor hot spot). The optimal position of the coil was then marked on the scalp to ensure that motor hot spot was stimulated throughout the experiment.

Before recording sessions, participants were trained to maintain an isometric tonic contraction (20% of maximal force) of the FDI muscle by adjusting their visually seen EMG activity on screen accordingly. To ensure that subjects maintained the required isometric contraction throughout the experiment, we placed a rubber band over subject's right hand (cf. Figure 1) so that the subject contracted the FDI against the band to maintain the unseen index fingertip in contact with a small tactile marker located on the tabletop. In this way, the FDI

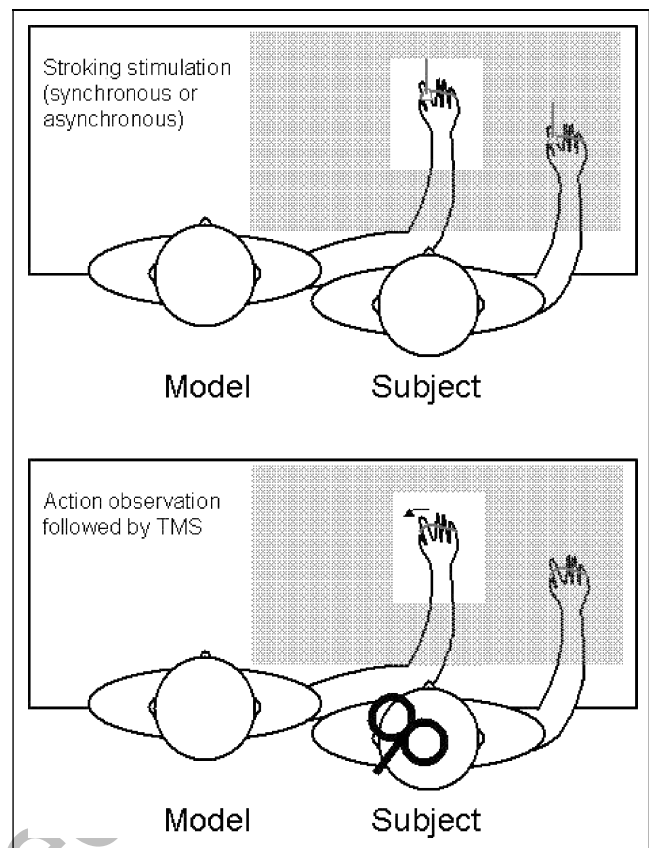


Figure 1. Experimental setup. A rubber band was placed over the subject's right hand to ensure that each subject could maintain an isometric contraction of their index finger throughout the experiment. The model experimenter wore an identical rubber band. In hand action trials, the model experimenter performed a maximal abduction of her index finger. See text for more details.

muscle was constantly in tension. This tonic muscle precontraction was necessary to elicit an SP during TMS trials (Cantello et al., 1992). Subject's EMG activity was constantly monitored by an experimenter. If subjects varied their EMG levels or experienced fatigue, the experiment was briefly interrupted and the contraction adjusted. In 50% of the trials chosen at random, a magnetic pulse was delivered, and MEPs and SP were recorded.

We defined the minimal stimulation intensity required to produce stable MEPs of about 1 mV in five out of five consecutive trials during a voluntary isotonic contraction of the FDI muscle (20% of maximal contraction). During the experiment, we set the stimulator output at 130% of this intensity. In this way, a clear TMS-induced EMG response could be obtained in each trial. On average, stimulus intensity was $49.0 \pm 10.3\%$ (range 35–68%) of the stimulator output.

Our interest focused on the SP rather than on the MEP. Amplifier gain was optimized for recording SP and continuously monitoring appropriate background EMG level during FDI contraction. This led, as expected, to clipping of MEP signal peaks (5.9% of all trials). However,

the SP duration could be reliably estimated from these trials, and they were not excluded.

Apparatus and Experimental Procedure

Subjects sat resting their right arm on a table, hidden under a mirrored surface. An experimenter's right arm was positioned in front of the subject's midline, and could be seen via a one-way mirror section mounted within the surface. Tactile stimulation was applied simultaneously to the subject's and the experimenter's index finger by two identical paintbrushes mounted on computer-controlled motors (cf. Figure 1). In the synchronous condition, the two paintbrushes stroked the subject and the experimenter in perfect synchrony, with identical onset time, direction, speed, and duration. In the asynchronous condition, the two paintbrushes moved with different onset times, directions, speeds, and durations, but the total stimulation of the skin was identical. Based on previous studies (Tsakiris & Haggard, 2005; Botvinick & Cohen, 1998), we hypothesized that the subject should attribute the experimenter's hand to their own body in the synchronous but not in the asynchronous condition. The distance between subject's and experimenter's hands was about 34 cm.

Each subject underwent a block with either synchronous or asynchronous visual–tactile stimulation in counterbalanced order. The blocks were separated by a break of about 5 min, during which subjects were asked to leave the room to reduce transfer effects between blocks. Furthermore, the synchronous and asynchronous blocks were each subdivided into two phases. The induction phase involved 3 min of stroking to induce the RHI (cf. Tsakiris & Haggard, 2005). During this phase, subjects simply looked at the experimenter's static hand.

This was followed by an experimental phase of around 9 min in which short epochs of stroking were unpredictably interspersed with action observation trials. On action observation trials, an audio signal was delivered via headphones to the experimenter only. The experimenter abducted her right index finger in response to this signal. Subjects never made any voluntary actions during the experiment. They were only required to maintain the tonic contraction of the FDI muscle (20% maximal) in both induction and experimental phases of the experiment (see above).

Half of the hand action trials, chosen at random, were followed by a single TMS pulse in order to probe how observation of action influenced the duration of the SP. To reduce TMS onset time predictability, TMS pulses were timed to occur approximately 1180, 1280, or 1380 msec after the auditory signal that served as a go-signal for experimenter's finger movement (hand action trials). Further, on static hand trials, TMS was delivered at identical times, but there was no preceding movement of the experimenter's hand. Finally, “catch trials” were included, which involved a period of stroking followed

by an interval that contained neither experimenter action nor TMS. The intertrial interval was typically about 11 sec. The choice of a long intertrial interval was based on both the necessity to maintain the illusion and the fact that prolonged TMS delivered at 0.1 Hz frequency does not induce any change in excitability (Chen et al., 1999). In total, there were four types of experimental trials in each block arranged in a 2×2 factorial design of experimenter hand action (present or absent) and TMS (present or absent). That is, the experimenter performed hand actions, which were or were not followed by a TMS pulse, or the experimenter's hand was at rest and a TMS pulse was or was not delivered. Each type of trial occurred 20 times. The order of the different trial types was randomized, resulting in a total of 80 trials per block.

To ensure stability of the recordings, that is, to control for changes in corticomotor excitability related to time, fatigue, or TMS per se, we also measured SP durations in each subject in a baseline condition. In this condition, subjects simply fixated on a small cross presented in the midline. During the baseline recording condition, subjects kept their hand in the experimental position with a slight tonic contraction of their index finger. Fifteen pulses were delivered. The baseline condition was repeated at the end of the experiment.

Manipulation of Body Ownership

We measured the RHI both implicitly and explicitly. First, we measured the proprioceptively perceived position of subject's index finger before and after the induction and experimental phase of each block (cf. Tsakiris & Haggard, 2005). A shift that occurred in the felt position of the subject's hand toward the rubber hand after synchronous stroking but not after asynchronous stroking provides an implicit measure of body ownership (Tsakiris & Haggard, 2005). Second, subjects completed an “RHI questionnaire” (Botvinick & Cohen, 1998) after the induction phase and again after the experimental phase. This involved rating agreement on a visual analog scale (from 0 to 10 maximal agreement) with nine statements. The first three statements capture the core of the illusion (Botvinick & Cohen, 1998): (1) “It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched”; (2) “It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand”; (3) “I felt as if the rubber hand were my hand.” Stronger agreement with these statements indicates that subjects experienced a RHI. We expected higher ratings after synchronous than asynchronous visual–tactile stimulation.

Data Analysis

Data were analyzed off-line. Background EMG level prior to TMS and duration of SP induced by TMS were

calculated in each TMS trial. Background EMG level was measured as the average of the rectified EMG signal during the first 100 msec before the TMS pulse. The duration of the SP was measured from the onset of the MEP to the time when the nonrectified EMG activity again reached the prestimulus level (Triggs et al., 1992). To eliminate background noise in determining MEP onset (i.e., SP onset), we used the averages of the EMG signals of each condition and each subject. The end of the SP was determined on each individual trial. Both measurements were made by an experimenter blind to the experimental conditions. A second blind rater independently measured both the onset of the SP on the basis of the averaged EMG signals in each experimental condition and each subject as well as the end of the SP in a randomly selected subset of 40 trials performed by two subjects each. High degree of interrater reliability was found for both SP onset ($r = .83$) and end of SP ($r = .93$).

3.4% of all trials were excluded, either due to technical failure of data recording, or because the end of an SP was not clearly marked by a return of continuous EMG activity, for example, due to muscle relaxation. A one-way ANOVA on percentage of removed trials in each condition (4 experimental, 2 baseline conditions) revealed no significant difference between any of the conditions ($F < 1, p > .6$). Each subject's SP durations and background EMG level were then averaged across repeated trials in each condition, and the averages were used for statistical analysis across subjects.

Measuring cortical silent periods requires a voluntary muscle contraction. However, muscle contraction has a strong and nonlinear effect on the MEP, whereas SP duration is known to be insensitive to changes in EMG level (e.g., Stetkarova, Leis, Stokic, Delapasse, & Tarkka, 1994; Cantello et al., 1992; Triggs et al., 1992). As a result, MEP amplitude would be expected to be less stable and less sensitive to cognitive effects in the present design than in classical action observation experiments (Strafella & Paus, 2000; Fadiga et al., 1995). Nevertheless, we analyzed the MEP data as a function of experimental condition (cf. Figure 4).

SP durations and background EMG level, as well as MEP amplitudes, were analyzed in separate 2×2 ANOVAs with stroking (synchronous, asynchronous) and experimenter action (static hand/hand action) as within-subjects factors. Post hoc comparisons between means were made by means of the Newman-Keuls test. We also performed an ANCOVA by including the pre-TMS EMG level as an additional covariate in the ANOVA on SP durations. Behavioral and subjective indices of RHI were analyzed with the same ANOVA design used for SP, EMG, and MEP measures.

We also computed an effect size index (Cohen's d) for SP duration comparisons. Cohen's d , unlike significance tests, is independent from sample size. The Cohen's d value represents the number of standard

deviations that separate two means and is typically used to compute effect sizes in a between group comparison $[(m_1 - m_2)/\sigma]$. We calculated within-subject effect sizes using a modified d : $t[2(1 - r)/n]^{1/2}$, with t as the test statistic for paired samples and r as the correlation across pairs of means (Morris & De Shon, 2002; Dunlap, Cortina, Vaslow, & Burke, 1996). The SP durations for each experimental condition were transformed into z -scores to reduce correlations between conditions that are due to overall interindividual differences in SP duration and may bias d estimation. Cohen's d effect size indices were computed using the standardized mean SP durations. According to Cohen (1992), the d values for small, medium, and large effects are 0.2, 0.5, and 0.8, respectively.

RESULTS

Proprioceptive Drift and Illusion Questionnaire

We use the term proprioceptive drift to refer to the change in the perceived position of subject's index finger between proprioceptive measures taken before and after stimulation. A positive proprioceptive drift indicates a displacement toward the viewed hand and is used as a quantitative proxy of the RHI.

ANOVA on proprioceptive drift showed the expected significant main effect for stroking condition [$F(1, 14) = 4.939, p = .043$], indicating a larger drift in the synchronous condition (2.4 cm) than in the asynchronous condition (0.2 cm). Furthermore, a significant effect for experimental phase occurred [$F(1, 14) = 5.890, p = .029$], indicating a larger drift after the experimental phase (2.2 cm) than after the induction phase (0.4 cm). However, the interaction between these two factors was not significant ($F < 1, p > .6$). We also specifically tested the drifts during the experimental phase against 0, to assess whether the sense of body ownership was manipulated at the time that SP durations and MEPs were measured. We found a significant drift during the experimental phase in the synchronous stroking block (3.4 cm) [$t(14) = 3.965, p = .01$], but not in the asynchronous block (0.93 cm) [$t(14) = 1.021, p = .32$].

Questionnaire results showed that participants experienced that the experimenter's hand was part of their own body both during the induction and experimental phases on the synchronous block. As expected, asynchronous stroking had no effect. Separate ANOVAs were carried out on responses to three key questionnaire items. For Items 1 to 3, the RHI was stronger after synchronous than asynchronous stroking condition (all $F_s > 5, p_s < .05$). For Items 1 and 3, neither the effect of experimental phase nor the interaction with stroking was significant (all $p_s > .1$). For Item 2, the main effect for experimental phase [$F(1, 14) = 6.089, p = .027$] and the interaction between stroking condition and experimental phase [$F(1, 14) = 6.893, p = .020$] were both

significant. This occurred because of stronger agreement after the experimental phase than the induction phase in the synchronous condition (5.7 vs. 4.4), with the reverse pattern in the asynchronous condition (3.1 vs. 3.4, respectively).

Taken together, both proprioceptive and questionnaire data indicate that the RHI was successfully induced following synchronous stroking in the induction as well as in the experimental phase. The latter indicates that neither action observation nor the delivery of TMS pulses break the illusion.

Duration of Silent Period—Inhibitory Activity in M1

To investigate whether the sense of body ownership affected cortical mechanisms of action observation, we performed an ANOVA on SP duration recorded from the FDI muscle.

SP durations showed neither a main effect of hand ownership [$F(1, 14) = 1.38, p = .26$], nor of experimenter action [$F(1, 14) = 0.02, p = .884$], but a highly significant interaction between these factors [$F(1, 14) = 12.84, p = .003$].¹

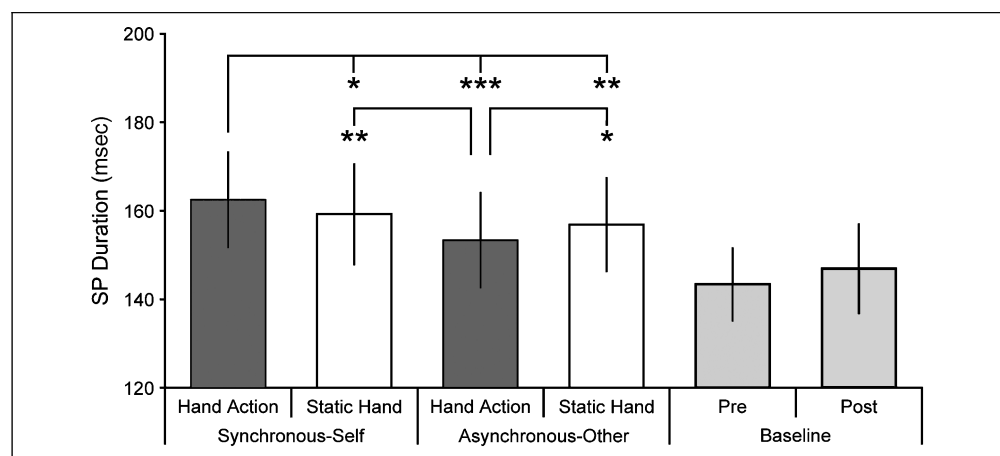
Post hoc analysis showed that in the synchronous stroking condition, mean SP duration (mean \pm SEM: 162 ± 11) was significantly prolonged when subjects viewed hand actions, compared to when subjects observed a static hand ($159 \pm 11, p = .030, d = 0.39$). In the asynchronous stroking condition, however, the effects were reversed: When subjects viewed hand actions, mean SP duration was significantly shorter (153 ± 11) than when subjects observed a static hand ($157 \pm 11, p = .019, d = 0.66$). Furthermore, mean SP duration in the condition synchronous-hand action was significantly longer compared to the condition asynchronous-hand action ($153 \pm 11, p = .0002, d = 1.12$). In contrast, SP duration during the observation of static hand was comparable during synchronous and asynchronous stroking conditions ($p = .09, d = 0.14$). Results are illustrated in

Figures 2 and 3. Note that Figure 2 error bars show the standard error across subjects in each individual condition. This shows quite high individual differences in overall SP duration. In contrast, the *differences* between conditions in SP duration, used for significance testing, showed much lower variability. Thus, numerically small effects were, nevertheless, statistically reliable. For example, when the interaction between body ownership and action observation was defined as a single numerical term, its standard deviation across subjects was noticeably lower (7 msec) than the standard deviation in any of the individual conditions contributing to the interaction (40–44 msec).

In summary, the manipulation of body ownership strongly affected the modulation of the SP contingent upon action observation: When the hand was illusory attributed to the self (synchronous stroking), the observation of index finger adduction–abduction prolonged SP recorded from the FDI muscle, relative to static hand. In contrast, when the hand was attributed to another person (asynchronous stroking), action observation shortened SPs, relative to the observation of a static hand.

Furthermore, this pattern of results was corroborated by a series of controls. First, we compared the two baseline blocks recorded at the beginning and at the end of the experiment. The two blocks did not significantly differ [$t(14) = 0.53, p = .604$], ruling out any unspecific change in corticomotor excitability due to time, fatigue, or TMS per se. Second, in order to compare SP duration in the average of the two baseline blocks with those in the four experimental conditions, we conducted one-way repeated-measures ANOVA with condition as within-subjects factors (average baseline, self-action, self-static, other-action, other-static). The ANOVA revealed a significant effect of condition [$F(4, 56) = 2.96, p = .028$]. Post hoc comparisons with Dunnett tests showed that the conditions other-action and other-static did not significantly differ from the baseline conditions ($p = .38$ and $p = .12$, respectively). The conditions self-action and self-static, however, both

Figure 2. Mean silent-period duration after action observation or during viewing a static hand in each ownership condition. Error bars show standard error across subjects in each condition. See text for statistical description of 2×2 interaction between factors hand action and hand ownership for experimental conditions. Asterisks denote $*p < .005$; $**p < .005$; $***p < .0005$.



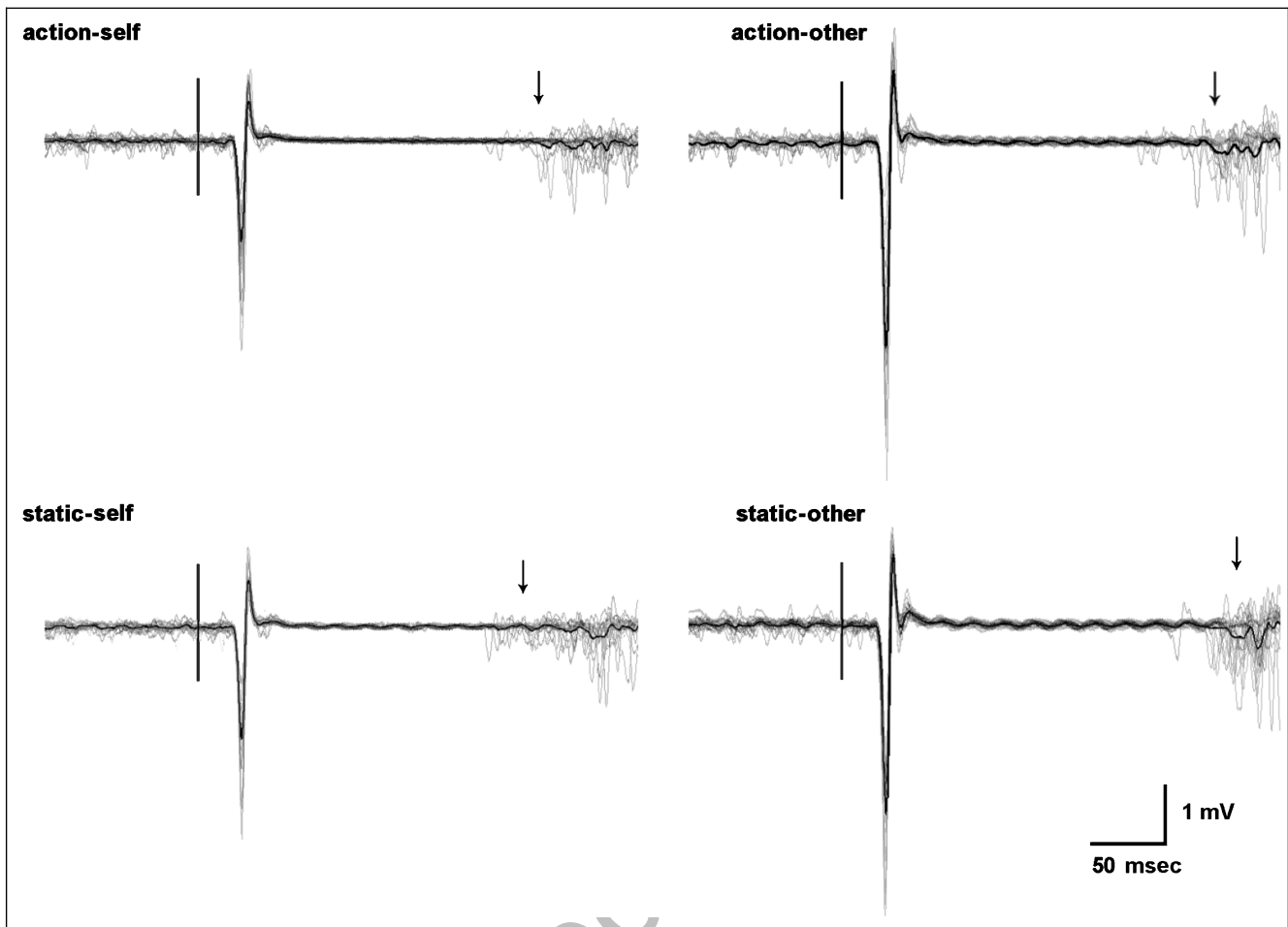


Figure 3. All recorded trials (superimposed gray lines) plus averages (black lines) from one subject showing motor-evoked potentials (MEPs) and silent periods (SPs) from the first dorsal interosseous (FDI) muscle in the conditions used for statistical analysis (see Figure 2). The subject is chosen as representative of the ANOVA interaction in Figure 2. Average SP duration in each trial was measured from the onset of the MEP to return of EMG activity (arrow mark).

showed significant increases over average baseline ($p = .009$ and $p = .042$, respectively). This result indicates that cortical inhibition is modulated by viewing a static hand. This could perhaps reflecting the expectation of the observer that this hand may make a movement, or some more general factor such as the salience of hands relative to inanimate stimuli. In any case, it confirms the importance of using a static hand as a control condition in studies of action observation.

Second, we assessed the influence of muscle contraction on SP duration. In our study, the FDI was isometrically contracted. The level of isometric contraction is known to influence TMS measures of cortical excitability. Thus, MEP amplitudes depend strongly on background EMG, although SP duration is reported to be less sensitive (e.g., Taylor, Allen, Butler, & Gandevia, 1997; Flament, Goldsmith, Buckley, & Lemon, 1993). Nevertheless, we investigated whether any variation in background EMG undetected by the monitoring experimenter could have contributed to the observed differences between conditions in SP duration.

To do this, we first analyzed background-rectified FDI EMG activity in the 100 msec prior to TMS using two-way repeated measure ANOVA to detect differences between any conditions. No significant main effects [$F(1, 14) < 2.02$, $p_s > .18$] or interaction were found [$F(1, 14) = 0.50$, $p = .49$]. We also performed an ANCOVA, in which we added the pre-TMS EMG level as an additional covariate to the 2×2 ANOVA of SP duration. The additional covariate did not show any significant relation with SP duration ($p = .64$), and its inclusion did not change either the pattern or significance of the ANOVA results.

Furthermore, we investigated whether our ANOVA results might be an artifact of the (modest) individual differences in overall SP duration. We therefore normalized SP durations in each condition using the average of the each subject's two baseline blocks (condition/averaged baseline). This did not change the pattern or significance of the ANOVA results. In particular, the interaction between ownership and experimenter action in the analysis of normalized SP durations remained highly significant [$F(1, 14) = 8.88$, $p = .0099$].

Corticomotor Excitability

Results of MEPs are shown in Figure 4.

The present results replicated the direction of the interaction found in a previous study (Schütz-Bosbach et al., 2006). Specifically, the MEPs were facilitated more when viewing actions attributed to another than when viewing actions attributed to the self. In this experiment, however, neither the main effects [$F_s(1, 14) < 1.8, p_s > .19$] nor the interaction reached significance [$F(1, 14) = 0.12, p = .73$]. We assume this is because of the lower sensitivity and higher noise of MEP measures at the high amplitudes found with precontraction. Moreover, MEPs in the present study were overall much larger than in Schütz-Bosbach et al. (2006). In the previous study, the MEP amplitude range was 1.37 to 1.59 mV across the experimental conditions. Here MEPs were around twice the previous amplitudes. This general increase in MEP size is caused by the muscle precontraction. Background EMG will inevitably vary randomly across trials, although average EMG levels did not differ significantly between conditions. This random variation would lead to noise in MEP amplitudes, but not in SP durations.

DISCUSSION

We investigated whether observing actions that appeared to be subject's own or another's modulate the excitability of inhibitory mechanisms in the onlookers' motor cortex. To this end, we used an established experimental method, the RHI, to manipulate body ownership. This allowed us to control whether our subjects experienced another person's hand as being part of their own body or as belonging to another person. Both qualitative questionnaire data and quantitative sensorimotor measures confirmed that this manipulation was successful. The model's hand made occasionally index

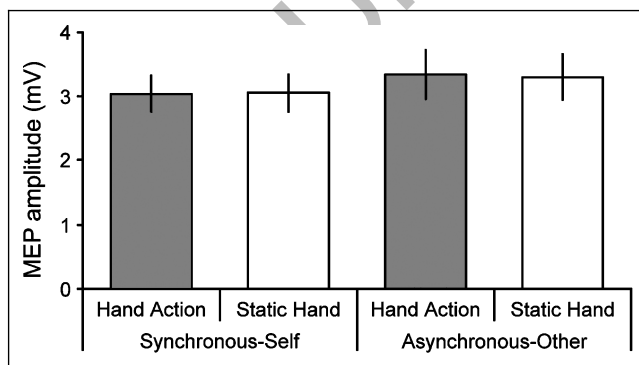


Figure 4. Mean and standard error of motor-evoked potentials (MEPs, mV) after action observation or during viewing a static hand in each ownership condition. 6.5% of trials in the four experimental conditions showed clipping of the MEP signal peaks. These trials were excluded from further analysis. A one-way ANOVA on percentage of removed trials in each condition revealed no significant difference between any of the conditions ($F < 1, p > .8$).

finger movements, observed by the subject. We compared the effects of the observed actions linked either to the self or another agent on the silent period, which can be recorded from voluntarily contracted muscles.

The TMS-induced silent period detectable in surface EMG recordings of voluntarily contracted muscles is regarded as an indicator of cortical motor inhibition, and has been widely used in neurophysiological studies to probe the instantaneous state of inhibitory circuits in the primary motor cortex (Siebner & Rothwell, 2003; Werhahn et al., 1999; Siebner et al., 1998; Ziemann et al., 1996; Hallett, 1995). Lesion and epidural recording studies clearly demonstrate that SP is generated cortically, at least in its later part (e.g., Schnitzler & Benecke, 1994). Evidence of a dose-dependent prolongation of SP after administration of GABA agonists (e.g., Werhahn et al., 1999; Ziemann et al., 1996) has suggested that SP duration reflects GABA_B receptor-mediated inhibitory activity of cortical and corticospinal neurons within the primary motor cortex (e.g., Siebner & Rothwell, 2003; Werhahn et al., 1999).

To our knowledge, however, only one previous study has shown modulation of SP duration according to cognitive context (Stefan, Wycislo, & Classen, 2004). Stefan et al. (2004) showed that directing attention to a target hand significantly increased sensorimotor learning-related changes in the duration of cortical SPs. Here we have used SP duration to measure how action observation and self-representation influence inhibitory intracortical circuits within the motor cortex. We hypothesize that the level of activation of cortical inhibitory circuits varies systematically during cognitive tasks (Eimer & Schlaghecken, 1998), and that SP duration is directly proportional to instantaneous inhibition. We compared the duration of the silent period evoked by TMS over M1 just after observing an action which was attributed to the self or another agent, and while observing the hand being static.

We found that systematic changes in silent period duration occurred as a function of hand ownership and hand action: When subjects observed actions of a hand that appeared to be their own, silent periods were significantly prolonged relative to viewing the same hand remaining static. Conversely, when subjects observed actions of a hand that was clearly not their own, silent periods were significantly reduced relative to viewing the static hand. Neither the RHI nor the presence of an action had any effect on SP as main effects, but their interaction was highly significant. That is, action attribution modulated the effect of action observation on the motor system. Because the SP measure is specifically linked to inhibitory activity in M1, our results clarify the nature of this modulation. Observing an action linked to the self produced motor cortex inhibition, as revealed by long SP durations. Observing other's actions reduced the level of M1 inhibition, thus reducing SP durations.

In a previous study, we measured changes in MEP amplitudes using a similar design (Schütz-Bosbach et al., 2006). That study found a significant increase in corticospinal excitability when viewing others' actions, and a numerical but nonsignificant decrease when viewing actions attributed to the self. The present SP results are broadly consistent with the previous MEP results if one considers that SP duration is directly proportional to the level of cortical inhibition. That is, viewing others' actions increased corticospinal excitability and reduced inhibitory activity in M1, whereas viewing actions linked to the self decreased cortical excitability and increased inhibitory activity in M1. Although it has been argued that action observation implies cortical inhibitory mechanisms (cf. e.g., Baldissera et al., 2001), this assumption has not yet been formally investigated. Our study therefore shows that action observation influences inhibitory circuits in M1, as well as, and perhaps more reliably than corticospinal excitability and further it establishes, for the first time, that the involvement of those inhibitory mechanisms is agent-specific.

The absence of main effects of RHI or action observation argues against a number of artifactual explanations. Firstly, the changes in cortical processing cannot simply be due to changes in arousal due to the illusion, or the observed action. Second, this pattern of results is also inconsistent with an interpretation based on multisensory conflict. In the crucial condition where our subjects observed an action which they attributed to themselves, they were, in fact, completely immobile. This might generate a multisensory conflict between visual information that an action had occurred, and somatomotor information that the subject did not move. Could increased cortical inhibition simply be due to such conflicts? Our design included a second type of multisensory conflict, namely, between visual and tactile information during the induction of the RHI itself. If conflict per se increased SP duration, then one might expect a significant main effect of synchronous versus asynchronous stroking. However, this was far from significant in our data. Further, functional imaging studies on conflict between motor intention and visual feedback have not reported suppression of primary motor or premotor areas but rather activations in those areas (Leube, Knoblich, Erb, & Kircher, 2003; Fink et al., 1999). We speculate that cortical inhibition can be a genuine response to observing one's own actions for preventing inappropriate perseveration or entrainment (see below), whereas reduction of cortical inhibition can be a genuine response to observing others' actions.

The finding that observing others' actions can modulate inhibitory circuits in M1 is in line with a previous study (Strafella & Paus, 2000). In that study, observing another person's action reduced short- but not long-interval intracortical motor inhibition as measured by paired-pulse TMS technique (Strafella & Paus, 2000). Because short- and long-interval intracortical inhibition are

thought to be mediated by GABA_A and GABA_B receptors, respectively (e.g., McDonnell, Orekhov, & Ziemann, 2006), the authors concluded that viewing others' actions triggers activity mainly in GABA_A-mediated inhibitory motor circuits (Strafella & Paus, 2000). Given the association between SP and GABA_B circuits, our result suggests that GABA_B circuits may be suppressed by the observation of others' action. Although both long-interval intracortical inhibition and SP duration are thought to probe GABA_B mechanisms, these two measures may also reflect distinct inhibitory mechanisms (McDonnell et al., 2006).

We now discuss the implication of our results for motor representation and for social cognition. First, our results confirm the concept of a "mirror system" resonating with others' actions (Strafella & Paus, 2000; Fadiga et al., 1995). Specifically, we found that observing another person's finger movement leads to a significant modulation of SP in the observer's corresponding muscle, relative to observing a static hand. However, our results are not consistent with the concept of an SRA (de Vignemont and Haggard, in press), in which a single neural code represents both one's own and others' actions. We found that specific corticomotor processing in response to observed actions operated in opposite directions for actions linked to the self and actions linked to others. That is, the motor system clearly distinguishes between self and other. It shows social differentiation, rather than the social equivalence proposed by SRA. We previously reported a socially differentiative effect on MEP facilitation, using a broadly similar design (Schütz-Bosbach et al., 2006). The present result shows an even stronger form of social differentiation in inhibitory sensorimotor networks, with a significant inhibition in the self condition not found previously.

Jeannerod and Pacherie (2004), Jeannerod (2001a, 2001b, 2003), and Fournieret and Jeannerod (1998) have noted that the existence of agent-neutral SRAs necessitates an additional "who system." This system would serve to attribute actions to agents, and thus, form the foundation of all social cognition. The pattern of social equivalence and social differentiation can be used to localize the SRA and the putative "who system" in the brain. Areas involved in SRA should show social equivalence, whereas areas involved in the "who system," or in stages of action understanding subsequent to attribution should show social differentiation. Our result shows therefore that the sensorimotor cortex, and specifically its inhibitory networks, either house the putative "who system," or are located downstream from it. Because the putative "who system" must logically, in turn, be located downstream from the SRA, our results show that SRA may not involve the sensorimotor cortex, in contrast to some previous suggestions (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Fadiga et al., 1995).

Additional evidence for distinctive representations of self and other has also recently been provided by David

et al. (2006). Subjects played a virtual ball-tossing game with two avatars. In the active condition, subjects made an avatar, viewed from a first- or third-person perspective, throwing a ball to another avatar by pressing a button. In the passive condition, they just observed the ball-tossing game and indicated which of the virtual characters threw the ball. When subjects actively controlled an avatar seen in a first-person perspective (i.e., self condition), increased activity was found in medial prefrontal brain regions. However, when subjects passively watched an acting avatar from a third-person perspective (i.e., other condition), increased neural activity was found in temporal–occipital, and in the premotor, inferior frontal, and posterior parietal regions comprising the human mirror system (cf. Rizzolatti & Craighero, 2004). Along similar lines, a recent study by Fourkas, Avenanti, Urgesi, and Aglioti (2006) contrasted first-person imagery and third-person imagery of index finger movements. The authors found greater facilitation of MEPs to TMS recorded from subjects' FDI muscles in third-person imagery, that is, when the imagined action was clearly attributable to another person. Furthermore, Désy and Théoret (2007) recently showed that corticospinal excitability increased more strongly during observation of movements made by a hand having a different skin color to that of the observer than for a same-color hand. These findings are in line with our hypothesis of a specific role of motor resonance in representing *others*, which is not merely parasitic on representation of the self (cf. Schütz-Bosbach et al., 2006).

In apparent contrast with our finding that observing one's own hand movements may induce an inhibition of hand motor representation, Garry, Loftus, and Summers (2005) found that the observation of one's own hand movement through a mirror (so that the moving hand appeared in the place of the nonmoving hand), brought about an increase of excitability of the nonmoving hand motor cortex. It is important to mention that the study by Garry et al. (2005) did not compare corticomotor excitability induced by observation of own and other's action, and so does not demonstrate social equivalence in the motor system. However, the increase of excitability during the observation of self-movement deserves discussion. A number of reasons may account for by the facilitation found in the study of Garry et al., including the fact that participants actively made movements with one hand (which is known to facilitate the ipsilateral motor cortex; see Muellbacher, Facchini, Boroojerdi, & Hallett, 2000; Brasil-Neto, Araújo, & Carneiro, 1999) and the use of a circular coil, which recruits larger populations of cortical neurons and may thus disclose different neural effects in the motor system (see, for example, Tamburin, Manganotti, Zanette, & Fiaschi, 2001). Note that by using a focal coil, Funase, Tabira, Higashi, Liang, and Kasai (2007) found no difference in ipsilateral corticomotor excitability during direct or indirect (i.e., with a mirror) observation of hand movements, suggest-

ing that the excitability change in ipsilateral M1 during observation of self-movements may reflect a transfer of excitability across hemispheres, perhaps related to mechanisms involved in bimanual motor coordination (Muellbacher et al., 2000; Brasil-Neto et al., 1999).

A novel finding of the present study was the significantly increased inhibitory activity in M1 associated with viewing actions related to the self. We discuss two possible functional roles of this inhibition. First, it may play a role in suppressing imitation. Several studies have found that direct imitation of an observed action is a form of prepotent response (Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Meltzoff & Moore, 1990). This raises the question of why people do not imitate all the time (Brass et al., 2001). Voluntary inhibition of motor execution areas has been suggested as a possible answer to this question (Baldissera et al., 2001). We suggest that imitation of one's own current action (i.e., perseveration) poses an even more acute problem than imitation of others. If viewing an action tends to automatically entrain performing the corresponding action, then the voluntary motor system requires a special mechanism to allow discrete movements to be made under visual control, without entraining repetition. We speculate that the increased sensorimotor inhibition in the self-condition of our study may form part of this mechanism.

Second, attribution of action to the self appears to engage a set of inhibitory processes reminiscent of sensory suppression. Activity in primate and human somatosensory cortex evoked by afferent signals is reduced during voluntary action (Kakigi et al., 1995; Chapman, 1994; Jiang, Chapman, & Lamarre, 1991; Chapin & Woodward, 1982). Computational models of motor control suggest that sensory suppression reflects attribution of stimuli either to external events or to one's own movement (Blakemore, Wolpert, & Frith, 1998; Claxton, 1975; Weiskrantz, Elliot, & Darlington, 1971) and it has been suggested that a deficient mechanism may account for abnormalities in awareness and control of action (e.g., delusions of control experiences associated with schizophrenia) (Blakemore et al., 2002; Frith, Blakemore, & Wolpert, 2000). Moreover, perseveration as a common symptom which may result from lesions in frontal brain regions can be conceptualized as inappropriate imitation of one's own previous action. Also, patients suffering from the Tourette's syndrome regularly exhibit motor tics, which are well-formed actions performed under inappropriate or unusual circumstances (cf. Miller & Cummings, 2006). It is a common observation that such tics are often produced in groups rather than singly. That is, the Tourette's patient who coughs, swears, and so forth will often do so in a series of several repeated actions. We suggest that this can be seen as repeated imitation of one's own previous action. Indeed, TMS studies have found decreased neuronal inhibition and a reduced cortical silent period in the primary motor area

in Tourette's syndrome (Ziemann, Paulus, & Rothenberger, 1997). Furthermore, a body part specific compulsion to execute the imagined movements was reported following parietal lesions (Schwöbel, Boronat, & Branch-Coslett, 2002).

Our study did not focus on sensory processes, but on the level of excitation/inhibition in MI, with which SI has functional local interconnections (Classen et al., 2004). We found that merely observing an apparently voluntary action increased sensorimotor cortical inhibition. Thus, observation-evoked inhibition for one's own actions might involve a motor parallel to sensory suppression. Previous studies showed that the preparation of motor commands is sufficient for sensory suppression, even in the absence of actual movement (Voss, Ingram, Haggard, & Wolpert, 2006). We speculate that mere *attribution* of observed actions to the self, in the absence of any motor command, may partially recruit similar inhibitory circuits.

UNCITED REFERENCES

Cantello et al., 1991
Rossini et al., 1994

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Note

1. We conducted a further analysis in which we measured the SP duration from the onset of TMS delivery to return of EMG activity (see Methods). This analysis yielded the same pattern of results. In particular the interaction between hand ownership and action remained highly significant [$F(1, 14) = 9.66, p = .0077$]. Again, no main effect of ownership [$F(1, 14) = 1.48, p = .24$] or action [$F(1, 14) = 0.03, p = .85$] was found.

REFERENCES

- Avenanti, A., Bolognini, N., Maravita, A., & Aglioti, S. M. (2007). Somatic and motor components of action simulation. *Current Biology, 18*, 2129–2135.
- Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2002). Lateralization in motor facilitation during action observation: A TMS study. *Experimental Brain Research, 144*, 127–131.
- Baldissera, F., Cavallari, P., Craighero, L., & Fadiga, L. (2001). Modulation of spinal excitability during observation of hand actions in humans. *European Journal of Neuroscience, 13*, 190–194.
- Bernecker, S., & Dretske, F. (2000). *Knowledge: Readings in contemporary epistemology*. Oxford: Oxford University Press.
- Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception and Performance, 32*, 210–225.
- Blakemore, S.-J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience, 1*, 635–640.
- Blakemore, S.-J., Wolpert, D. M., & Frith, C. D. (2002). Abnormalities in the awareness of action. *Trends in Cognitive Sciences, 6*, 237–242.
- Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature, 391*, 756.
- Brasil-Neto, J. P., Araújo, V. P., & Carneiro, C. R. (1999). Postexercise facilitation of motor evoked potentials elicited by ipsilateral voluntary contraction. *Muscle & Nerve, 22*, 1710–1712.
- Brasil-Neto, J. P., Cammarota, A., Valls-Solé, J., Pascual-Leone, A., Hallett, M., & Cohen, L. G. (1995). Role of intracortical mechanisms in the late part of the silent period to transcranial stimulation of the human motor cortex. *Acta Neurologica Scandinavica, 92*, 383–386.
- Brasil-Neto, J. P., Cohen, L. G., Panizza, M., Nilsson, J., Roth, B. J., & Hallett, M. (1992). Optimal focal transcranial magnetic activation of the human motor cortex: Effects of coil orientation, shape of the induced current pulse, and stimulus intensity. *Journal of Clinical Neurophysiology, 9*, 132–136.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition, 44*, 124–143.
- Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *Neuroimage, 14*, 1416–1423.
- Cantello, R., Gianelli, M., Bettucci, D., Civardi, C., De Angelis, M. S., & Mutani, R. (1991). Parkinson's disease rigidity. Magnetic motor evoked potentials in a small hand muscle. *Neurology, 41*, 1449–1456.
- Cantello, R., Gianelli, M., Civardi, C., & Mutani, R. (1992). Magnetic brain stimulation. The silent period after motor evoked potential. *Neurology, 42*, 1951–1959.
- Chapin, J. K., & Woodward, D. J. (1982). Somatic sensory transmission to the cortex during movement: Gating of single cell responses to touch. *Experimental Neurology, 78*, 654–669.
- Chapman, C. E. (1994). Active versus passive touch: Factors influencing the transmission of somatosensory signals to primary somatosensory cortex. *Canadian Journal of Physiology and Pharmacology, 72*, 558–570.
- Classen, J., Wolters, A., Stefan, K., Wycislo, M., Sandbrink, F., Schmidt, A., et al. (2004). Paired associative stimulation. *Supplements to Clinical Neurophysiology, 57*, 563–569.
- Claxton, G. (1975). Why can't we tickle ourselves? *Perceptual and Motor Skills, 41*, 335–338.
- Cohen, J. (1992). A power primer. *Psychological Bulletin, 112*, 155–159.
- Cruccu, G., Inghilleri, M., Berardelli, A., Romaniello, A., & Manfredi, M. (1997). Cortical mechanisms mediating the inhibitory period after magnetic stimulation of the facial motor area. *Muscle & Nerve, 20*, 418–424.
- Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., et al. (1997). Looking for the agent: An investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition, 65*, 71–86.
- David, N., Bewernick, B. H., Cohen, M. X., Newen, A., Lux, S., Fink, G. R., et al. (2006). Neural representations of self and other: Visual-spatial perspective taking and

- agency in a virtual ball-tossing game. *Journal of Cognitive Neuroscience*, *18*, 898–910.
- de Vignemont, F., & Haggard, P. (in press). Shared representations of actions. *Social Neuroscience*.
- Decety, J., & Chaminade, T. (2003). When the self represents the other: A new cognitive neuroscience view on psychological identification. *Consciousness and Cognition*, *12*, 577–596.
- Désy, M.-C., & Théoret, H. (2007). Modulation of motor cortex excitability by physical similarity with an observed hand action. *PLoS ONE*, *2*, e971.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.
- Dunlap, W. P., Cortina, J. M., Vaslow, J. B., & Burke, M. J. (1996). Meta-analysis of experiments with matched groups or repeated measures designs. *Psychological Methods*, *1*, 170–177.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1737–1747.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, *15*, 213–218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs. another person as being the cause of an action: The neural correlates of the experience of agency. *Neuroimage*, *15*, 596–603.
- Fink, G. R., Marshall, J. C., Halligan, P. W., Frith, C. D., Driver, J., Frackowiak, R. S., et al. (1999). The neural consequences of conflict between intention and the senses. *Brain*, *122*, 497–512.
- Flament, D., Goldsmith, P., Buckley, C. J., & Lemon, R. N. (1993). Task dependence of responses in first dorsal interosseous muscle to magnetic brain stimulation in man. *Journal of Physiology*, *464*, 361–378.
- Fourkas, A. D., Avenanti, A., Urgesi, C., & Aglioti, S. M. (2006). Corticospinal facilitation during first and third person imagery. *Experimental Brain Research*, *168*, 143–151.
- Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, *36*, 1133–1140.
- Frith, C. D., Blakemore, S.-J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *355*, 1771–1788.
- Funase, K., Tabira, T., Higashi, T., Liang, N., & Kasai, T. (2007). Increased corticospinal excitability during direct observation of self-movement and in direct observation with a mirror box. *Neuroscience Letters*, *419*, 108–112.
- Gallese, V., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Garry, M. I., Loftus, A., & Summers, J. J. (2005). Mirror, mirror on the wall: Viewing a mirror reflection of unilateral hand movements facilitates ipsilateral M1 excitability. *Experimental Brain Research*, *163*, 118–122.
- Haggard, P. (2005). Conscious intention and motor cognition. *Trends in Cognitive Sciences*, *9*, 290–295.
- Hallett, M. (1995). Transcranial magnetic stimulation. Negative effects. *Advances in Neurology*, *67*, 107–113.
- Jeannerod, M. (2001a). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage*, *14*, S103–S109.
- Jeannerod, M. (2001b). Simulation of action as a unifying concept for motor cognition. In S. H. Johnson (Ed.), *Cognitive neuroscience. Perspectives on the problem of intention and action*. Cambridge: MIT Press.
- Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioral and Brain Research*, *142*, 1–15.
- Jeannerod, M., & Pacherie, E. (2004). Agency, simulation and self-identification. *Mind and Language*, *19*, 113–146.
- Jiang, W., Chapman, C. E., & Lamarre, Y. (1991). Modulation of the cutaneous responsiveness of neurones in the primary somatosensory cortex during conditioned arm movements in the monkey. *Experimental Brain Research*, *84*, 342–354.
- Kakigi, R., Koyama, S., Hoshiyama, M., Watanabe, S., Shimojo, M., & Kitamura, Y. (1995). Gating of somatosensory evoked responses during active finger movements magnetoencephalographic studies. *Journal of the Neurological Sciences*, *128*, 195–204.
- Leube, D. T., Knoblich, G., Erb, M., & Kircher, T. T. (2003). Observing one's hand become anarchic: An fMRI study of action identification. *Consciousness & Cognition*, *12*, 597–608.
- McDonnell, M. N., Orekhov, Y., & Ziemann, U. (2006). The role of GABA(B) receptors in intracortical inhibition in the human motor cortex. *Experimental Brain Research*, *173*, 86–93.
- Meltzoff, A. N., & Moore, M. K. (1990). A new foundation for cognitive development in infancy: The birth of the representational infant. In E. K. Scholnick, K. Nelson, S. Gelman, & P. H. Miller (Eds.), *Conceptual development: Piaget's legacy* (pp. 53–78). Mahwah, NJ: Erlbaum.
- Miller, B. L., & Cummings, J. L. (2006). *The human frontal lobes: Functions and disorders*. New York: Guilford Press.
- Mills, K. R., Boniface, S. J., & Schubert, M. (1992). Magnetic brain stimulation with a double coil: The importance of coil orientation. *Electroencephalography and Clinical Neurophysiology*, *85*, 17–21.
- Morris, S. B., & De Shon, R. P. (2002). Combining effect size estimates in meta-analysis with repeated measures and independent-groups designs. *Psychological Methods*, *7*, 105–125.
- Muellbacher, W., Facchini, S., Boroojerdi, B., & Hallett, M. (2000). Changes in motor cortex excitability during ipsilateral hand muscle activation in humans. *Clinical Neurophysiology*, *111*, 344–349.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.
- Romani, M., Cesari, P., Urgesi, C., Facchini, S., & Aglioti, S. M. (2005). Motor facilitation of the human cortico-spinal system during observation of bio-mechanically impossible movements. *Neuroimage*, *26*, 755–763.
- Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., et al. (1994). Noninvasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basis principles and procedures for routine clinical application: Report of an IFCN committee. *Electroencephalography and Clinical Neurophysiology*, *91*, 79–92.
- Schnitzler, A., & Benecke, R. (1994). The silent period after transcranial magnetic stimulation is of exclusive cortical

- origin: Evidence from isolated cortical ischemic lesions in man. *Neuroscience Letters*, *180*, 41–45.
- Schütz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology*, *16*, 1830–1834.
- Schwöbel, J., Boronat, C. B., & Branch-Coslett, H. (2002). The man who executed “imagined” movements: Evidence for dissociable components of the body schema. *Brain and Cognition*, *50*, 1–16.
- Siebner, H. R., & Rothwell, J. (2003). Transcranial magnetic stimulation: New insights into representational cortical plasticity. *Experimental Brain Research*, *148*, 1–16.
- Stefan, K., Wycislo, M., & Classen, J. (2004). Modulation of associative human motor cortical plasticity by attention. *Journal of Neurophysiology*, *92*, 66–72.
- Stetkarova, I., Leis, A. A., Stokic, D. S., Delapasse, J. S., & Tarkka, I. M. (1994). Characteristics of the silent period after transcranial magnetic stimulation. *American Journal of Physical Medicine and Rehabilitation*, *73*, 98–102.
- Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: A transcranial magnetic stimulation study. *NeuroReport*, *11*, 2289–2292.
- Stuss, D. T., & Knight, R. T. (2002). *Principles of frontal lobe function*. New York: Oxford University Press.
- Tamburin, S., Manganotti, P., Zanette, G., & Fiaschi, A. (2001). Cutaneomotor integration in human hand motor areas: Somatotopic effect and interaction of afferents. *Experimental Brain Research*, *141*, 232–241.
- Taylor, J. L., Allen, G. M., Butler, J. E., & Gandevia, S. C. (1997). Effect of contraction strength on responses in biceps brachii and adductor pollicis to transcranial magnetic stimulation. *Experimental Brain Research*, *117*, 472–478.
- Triggs, W. J., Macdonell, R. A., Cros, D., Chiappa, K. H., Shahani, B. T., & Day, B. J. (1992). Motor inhibition and excitation are independent effects of magnetic cortical stimulation. *Annals of Neurology*, *32*, 345–351.
- Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 80–91.
- Tsakiris, M., Haggard, P., Franck, N., Mainy, N., & Sirigu, A. (2005). A specific role for efferent information in self-recognition. *Cognition*, *96*, 215–231.
- Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. M. (2006). Motor facilitation during action observation: Topographic mapping of the target muscle and influence of the onlooker’s posture. *European Journal of Neuroscience*, *23*, 2522–2530.
- Van den Bos, E., & Jeannerod, M. (2002). Sense of body and sense of action both contribute to self recognition. *Cognition*, *85*, 177–187.
- Voss, M., Ingram, J. N., Haggard, P., & Wolpert, D. M. (2006). Sensorimotor attenuation by central motor command signals in the absence of movement. *Nature Neuroscience*, *9*, 26–27.
- Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation: Report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5–7, 1996. *Electroencephalography and Clinical Neurophysiology*, *108*, 1–16.
- Wassermann, E. M., Pascual-Leone, A., Valls-Sole, J., Toro, C., Cohen, L. G., & Hallett, M. (1993). Topography of the inhibitory and excitatory responses to transcranial magnetic stimulation in a hand muscle. *Electroencephalography and Clinical Neurophysiology*, *89*, 424–433.
- Weiskrantz, L., Elliot, J., & Darlington, C. (1971). Preliminary observations of tickling oneself. *Nature*, *230*, 598–599.
- Werhahn, K. J., Kunesch, E., Noachtar, S., Benecke, R., & Classen, J. (1999). Differential effects on motor cortical inhibition induced by blockade of GABA uptake in humans. *Journal of Physiology*, *517*, 591–597.
- Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences*, *1*, 209–216.
- Ziemann, U., Lonnecker, S., Steinhoff, B. J., & Paulus, W. (1996). Effects of antiepileptic drugs on motor cortex excitability in humans: A transcranial magnetic stimulation study. *Annals of Neurology*, *40*, 367–378.
- Ziemann, U., Paulus, W., & Rothenberger, A. (1997). Decreased motor inhibition in Tourette’s disorder: Evidence from transcranial magnetic stimulation. *American Journal of Psychiatry*, *154*, 1277–1284.