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Visual perception of bodily interactions in the primary somatosensory cortex

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Abstract

Brain imaging studies in humans have revealed the existence of a visuo-tactile system, which matches observed touch with felt touch. In this system, the primary somatosensory cortex (SI) appears to play a causal role in the visual processing of tactile events. Whether this visuo-tactile mechanism for touch in SI applies to the sight of 'any' touch, or whether it is restricted to the domain of body-related tactile experiences remains unresolved. To address this issue, repetitive transcranial magnetic stimulation (rTMS) was used to determine whether activity in SI is strictly related to the visual processing of human body-part interactions, or is also involved in processing the contact between inanimate objects, or between human body-parts and objects. The results show that rTMS over SI selectively impaired the processing of a contralateral visual stimulus depicting a human body-part being touched by a human agent, while it did not affect the visual perception of contact between objects, or between human body-parts and objects. Correlation analysis shows that this effect was associated with the intensity and embodiment of the observed touched. This result suggests that SI is more suited to represent social touch, contributing to our understanding of the effect of interpersonal tactile interactions between people.

Introduction

Brain imaging studies in humans have revealed the existence of a visuo-tactile system, which matches observed touch with felt touch – the observation of touch experienced by others, even in the absence of direct tactile experience, is able to activate the same neural circuitry that is normally involved in the real experience of touch, such as the primary (SI) and secondary (SII) somatosensory cortices (Keysers *et al.*, 2004; Blakemore *et al.*, 2005; Schaefer *et al.*, 2005; Ebisch *et al.*, 2008). Reminiscent of the theory of mental simulation of motor acts based on the mirror-neuron system (Gallese, 2005; Grafton, 2009), it has been proposed that this visuo-tactile mirroring mechanism may allow people to understand another person's tactile experience through simulation of the observed tactile events in the observer's somatosensory network (Keysers *et al.*, 2010).

Recently, we have shown that somatosensory areas are causally involved in the visual processing of touch. Stroke patients with a lesion centred in the post-central gyrus showed selective impairment in the processing of visual stimuli depicting tactile events, in spite of a spared ability to process visual stimuli that do not comprise a tactile component (Bolognini *et al.*, 2011a). Moreover, in healthy subjects the disruption of SI, but not SII, activity, by transcranial magnetic stimulation (TMS) selectively impaired visual perception of touch (Bolognini *et al.*, 2011b).

Whether the mirroring mechanism for touch in SI applies to the sight of 'any' touch, or whether it exclusively pertains to the domain of human touch remains unresolved. In everyday life, the experience of touch is not entirely restricted to human interactions; rather, we frequently observe events that involve contact between the body and an object (e.g. hair-brushing) or between inanimate objects (e.g. an accident between cars). To date, brain imaging studies have provided controversial results regarding the involvement of SI in touch observation. There is evidence suggesting that the activation of a visuo-tactile mirroring mechanism might underpin an abstract notion of touch; in this view, biological as well as inanimate stimuli are able to activate a shared neural circuitry for touch by vision (Ebisch *et al.*, 2008). On the other hand, there is evidence suggesting that somatosensory cortices are preferentially activated by the sight of *social* touch (i.e. tactile interactions between persons) and, more generally, when the target of the action is biological, rather than inanimate (Tai *et al.*, 2004; Blakemore *et al.*, 2005).

Here, we investigated whether the mirror activation of SI is restricted to the visual processing of human body-parts contact, or whether it can also play a role in processing contact between inanimate objects (Experiment 1), or between human body-parts and objects

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(Experiment 2). We addressed this issue using TMS, as this technique allows us to investigate causality in the brain–behaviour relationship, by temporarily interacting with the activity of neurons in cortical areas that are beneath the magnetic field administered by a coil positioned over the scalp (Wassermann *et al.*, 2008; Bolognini and Ro, 2010).

Experiment 1 – Human-to-Human and Object-to-Object Touch

Materials and methods

Participants

Twelve healthy participants took part in the study (11 right-handed; ten females; mean age – 23 ± 4 years). All participants gave written informed consent. They were naïve to the experimental procedure and to the purpose of the study. None of the participants had neurological, psychiatric or other relevant medical problems, nor any contraindication to TMS (Rossi *et al.* 2009). The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (*BMJ* 1991; 302: 1194) and was approved by the ethical committee at the University of Milano-Bicocca.

Tasks – Human-to-Human Touch and Object-to-Object Touch

Two visual detection tasks were given to subjects. During both tasks, subjects sat at a distance of 45 cm in front of a PC monitor (Samsung SyncMaster 1200NF), and they were shown video clips of the experimental conditions on a dark screen background (luminance 0.01 cd/m^2). In the Human-to-Human Touch task, the video clips depicted the index fingers of two hands (i.e. a left hand in the left hemifield and a right hand in the right hemifield from an egocentric view), presented at 15° of eccentricity from the central fixation point. A left hand and a right hand were also presented below the fingers (see Fig. 1A). During the video clips, in the target trials one index finger moved downward for 1 cm, and touched the hand below; in the catch trials the finger simply approached the hand (by moving downward for 0.5 cm), without actually touching the hand below. In the Object-to-Object Touch task, the video clips depicted two leaves, one in the left hemifield and one in the right hemifield, at 15° of eccentricity from the central fixation point. Two wooden sticks were presented below the leaves, one at each side. The visible outlines of the leaves and of the sticks were broadly of the same size as the fingers and hands of the previous task. Now, during the video clips the target trials showed one leaf moving downward for 1 cm and making contact with the stick, while the catch trial showed the leaf approaching the stick (by moving downward for 0.5 cm), without making any contact with it. In both tasks, the moving visual stimulus exhibited the same direction (vertical) and amount of motion (duration 60 ms) across conditions (see Fig. 1A).

In both tasks, subjects had to look at the fixation point, and to press, with their right index finger, the spacebar on the keyboard to report

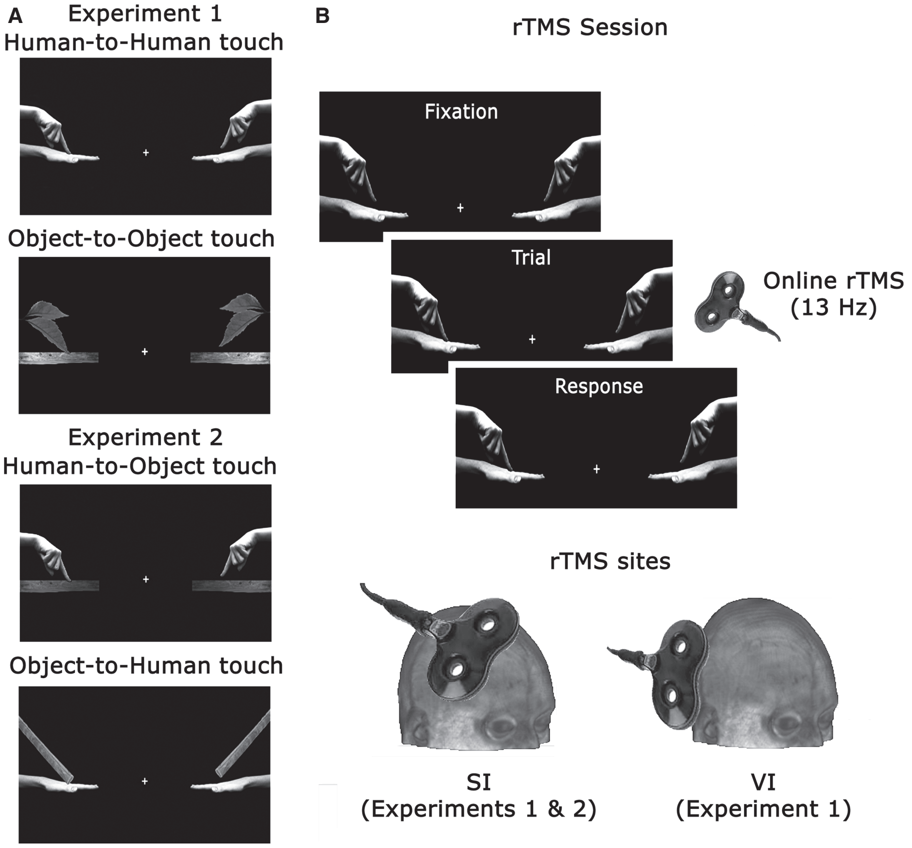

FIG. 1. Schematic representation of the experimental procedure. (A) The types of stimuli used in the visual detection tasks; in each picture, the target trial depicting a left-sided touching stimulus is shown as an example. The visual stimuli exhibited identical motion duration (60 ms) and amplitude across the observed events. (B) Sequence of events in the repetitive transcranial magnetic stimulation (rTMS) session. For example, for the Human-to-Human Touch task – each trial started with the presentation of a central fixation cross. After a delay (> 5 s) the video clip started. At the onset of the clip, rTMS (three TMS pulses at 0, 75 and 150 ms) was delivered over one of the target areas (i.e. right hemisphere – SI, or VI). In each task, subjects were asked to indicate, by pressing the response key, whether the moving visual stimulus touched the stimulus below, while refraining from pressing if the moving visual stimulus approached the stimulus below, but did not touch it.

whether the moving visual stimulus (finger or leaf) had touched the stimulus below (hand or stick, i.e. target trial), regardless of the side on which the stimulus was presented. Furthermore, subjects were instructed to refrain from responding if the moving stimulus simply approached, but did not touch, the stimulus below (catch trial).

In each task, 48 trials were presented – 12 target trials and 12 target-absent trials for each stimulus side (left vs. right). The inter-trial interval varied between 5 and 7 s, to prevent any TMS carry-over effects. The total duration of each task was about 10 min.

Sequence and timing of the video clips and the TMS pulses were under computer control (E-PRIME software; Psychology Software Tools Inc., Sharpsburg, PA, USA).

TMS protocol

During the TMS session, TMS pulses were delivered using a Super Rapid Transcranial Magnetic Stimulator (Magstim, Whitland, UK) connected with a figure-of-eight coil (double 70 mm diameter), which allowed focal cortical stimulation.

Before the experiment, the individual motor threshold (MT) at rest was determined for each participant by stimulating the hand area of the right primary motor cortex (MI). MT was defined as the minimum intensity that elicited detectable motor twitches in the digits of the resting left hand, i.e. a visible contraction during at least three out of six consecutive TMS pulses. Mean MT was 59% (SD = 7.5%) of the maximal output of the stimulator.

The cortical areas targeted for stimulation were SI and the primary visual cortex (VI) in the right hemisphere. The appropriate location for stimulating the SI hand area was identified by moving the coil approximately 2–4 cm posterior to the motor hotspot, until no detectable motor twitches occurred. To confirm that this location was indeed within the SI hand area, the subject performed a tactile detection task while receiving TMS (the details are reported in Bolognini *et al.*, 2011b). By moving the coil between trials, we were able to determine the position and orientation of the coil at which the TMS most reliably interfered with tactile detection. During TMS, almost every subject reported paraesthesia to the contralateral (left) hand. Nine of the 12 subjects reported a deficit in detecting the contralateral–left tactile stimulus during bilateral stimulation (omissions – 13%). These data provide independent confirmation that the scalp position chosen for the experiment was indeed over the SI hand area.

The coil location corresponding to VI was 2 cm dorsal and 0.6 cm lateral to the calcarine sulcus (Fernandez *et al.*, 2002). After localizing each area over the scalp, the coil was positioned on the appropriate stimulation site during each experimental session and held in place by a mechanical device.

During the repetitive TMS (rTMS) sessions, rTMS was delivered as a train of three pulses at a frequency of 13 Hz (i.e. at 0–75–150 ms with respect to the onset of the video clip, i.e. moving visual stimulus) (see Fig. 1B). This time interval and stimulation parameters were chosen on the basis of the chronometry of tactile processing in SI (Cohen *et al.*, 1991) and that of visual processing in VI, as shown by previous TMS studies (Amassian *et al.*, 1989).

The stimulus intensity used during all the experimental sessions was set at 110% of the individual MT. Participants tolerated the rTMS well and did not report any adverse effects.

Experimental procedure

Throughout the experiment, subjects were comfortably seated in an armchair, in a quiet, dimly illuminated room. The experiment comprised four sessions for each of the two tasks – a training session and three experimental sessions. The training session always preceded the experimental protocol and allowed participants to become familiar with the task.

The experimental sessions consisted of a baseline and two rTMS sessions (SI-rTMS, VI-rTMS). The order of the two tasks and that of the three experimental sessions for each task was counterbalanced across participants. The entire procedure lasted about 2 h.

A questionnaire was administered to measure how participants interpreted the visual stimuli. The items were as follows: (1) 'The tactile stimulation looked like to be very intense'. (2) 'The tactile stimulation looked like to be very unpleasant'. (3) 'The hand being touched could depict my hand'. (4) 'The touching finger could depict my finger'. (5) 'The touched hand and the touching finger belonged to different persons'. Items 1 and 2 were given for both Human-to-Human and Object-to-Object Touch tasks; items 3–5 were given only for the Human-to-Human Touch task. For every item, participants rated their agreement using a five-point Likert scale, + 2 indicating 'strongly agree', −2 'strongly disagree' and 0 'neither agree nor disagree', although intermediate values (± 1) could be used. Values above 0 indicate agreement, whereas values below 0 indicate disagreement.

Statistical analyses

Statistical analysis was performed using STATISTICA for Windows, release 6.0 (StatSoft). A first analysis was conducted on the mean percentage of errors (target omissions plus incorrect responses to the catch trials, i.e. false alarms) through repeated-measures analysis of variance (ANOVA) with Task (Human-to-Human Touch vs. Object-to-Object Touch), Session (Baseline, SI-rTMS, VI-rTMS) and Side (Left- vs. Right-sided stimuli) as main factors.

Then, to separate genuine rTMS effects on perceptual sensitivity from changes in the response criterion, we computed psychophysical indices derived from Signal Detection Theory (Green & Swets, 1966). This psychophysical approach allows us to discern the stimulus-related (i.e. perceptual sensitivity, d') and subject-related (i.e. response bias, c) rTMS influences on visual performance (Green & Swets, 1966). Here changes in sensitivity (d' values) and in the response criterion (c values) were quantified for every experimental condition. Analyses of d' and c values were performed via the same ANOVA model, with Task, Session and Side as main factors. When appropriate, pairwise comparisons were calculated using the Newman–Keuls test. For the significant effects, we measured the effect size in the ANOVAs, by calculating the partial eta squared ($p\eta^2$), which measures the degree of association between an effect and the dependent variable, namely the proportion of the total variance that is attributable to a main factor or to an interaction (Cohen, 1973).

Finally, for each task, the visual analog scale (VAS) subjective ratings were analysed by comparing the mean score vs. 0 using t-tests.

Results

With respect to the errors, the ANOVA revealed a significant effect of Task ($F_{1,11} = 11.84$, $P < 0.01$, $p\eta^2 = 0.52$), as subjects overall committed more errors in the Object-to-Object Touch task (26%) than in the Human-to-Human Touch task (19%). Moreover, the significant Session by Side interaction ($F_{2,22} = 3.58$, $P < 0.05$, $p\eta^2 = 0.25$) showed a significant difference between left-sided (24% of errors) and right-sided (19% of errors, $P < 0.05$) stimuli only when rTMS was delivered on SI. Other effects did not reach significance – Session ($F_{2,22} = 2.37$, $P = 0.1$), Side ($F_{1,11} = 0.04$, $P = 0.8$), Task by Session ($F_{2,22} = 0.71$, $P = 0.5$), Task by Side ($F_{1,11} = 1.27$, $P = 0.3$), Task by Session by Side ($F_{2,22} = 2.52$, $P = 0.1$) (Fig. 2A).

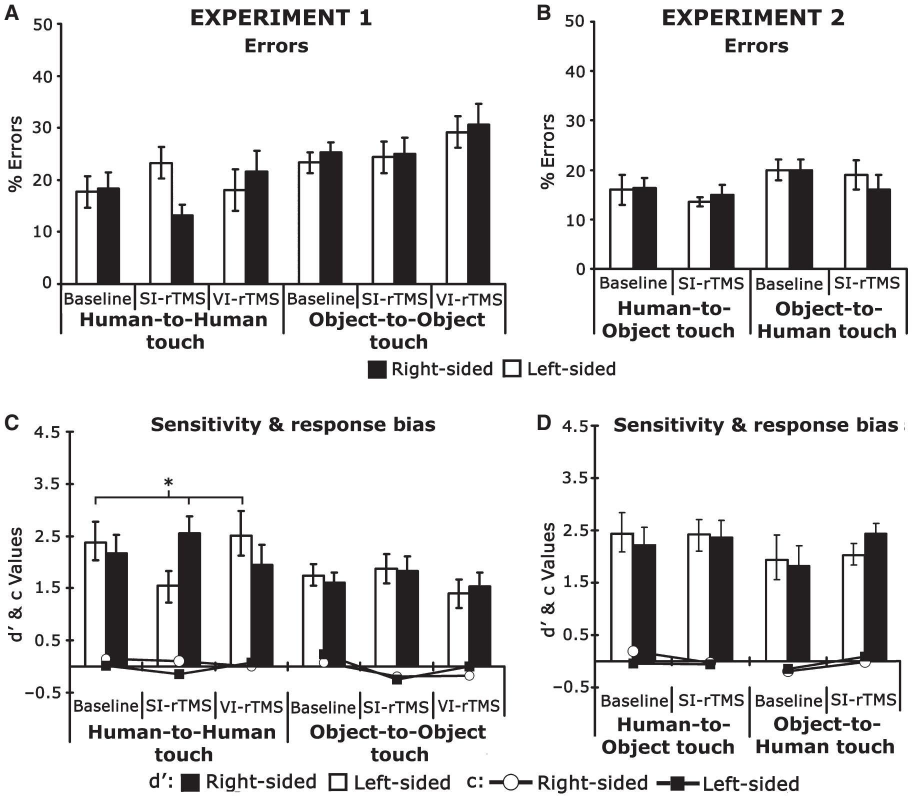

FIG. 2. Repetitive transcranial magnetic stimulation (rTMS) effects on behaviour. (A, B) Mean percentage errors in each experimental condition of Experiments 1 and 2, respectively. (C, D) Mean values of sensitivity (d′) and response criterion (c) in each experimental condition of Experiments 1 and 2, respectively. The asterisk indicates a significant rTMS effect. Error bars depict standard errors.

Of major interest were the findings from the analysis of perceptual sensitivity (*d′*) (Fig. 2C). First, we found a significant Session by Side interaction ($F_{2,22} = 4.09$, $P < 0.03$, $p\eta^2 = 0.27$), showing a significant difference between left-sided (1.7) and right-sided (2.2, $P < 0.05$) only in the SI-rTMS session. Crucially, the significant Task by Session by Side interaction ($F_{2,22} = 4.62$, $P < 0.02$, $p\eta^2 = 0.42$) highlighted the selectivity of the rTMS interference. Other effects did not reach significance – Task ($F_{1,11} = 3.87$, $P = 0.08$), Session ($F_{2,22} = 0.35$, $P = 0.7$), Side ($F_{1,11} = 0.04$, $P = 0.8$), Task by Session ($F_{2,22} = 0.97$, $P = 0.4$), Task by Side ($F_{1,11} = 1.21$, $P = 0.7$). To explore the Task by Session by Side interaction, we conducted separate two-way ANOVAs for each task, with Session and Side as the main factors. The ANOVA for the Human-to-Human Touch task showed only a significant Session by Side interaction ($F_{2,22} = 7.21$, $P < 0.01$, $p\eta^2 = 0.40$), while the ANOVA for the Object-to-Object Touch task did not show any significant effect ($P > 0.3$). *Post-hoc* comparisons showed a reduction of sensitivity for left-sided stimuli as compared with right-sided stimuli only in the SI-rTMS session ($P < 0.03$). Moreover, left-sided stimuli in the SI-rTMS session (1.55) were significantly different from left-sided stimuli of Baseline (2.38, $P < 0.05$) and VI-rTMS (2.5, $P < 0.3$) sessions. Additionally, for the Human-to-Human Touch task, we conducted a one-way ANOVA on the responses to contralateral, left-sided visual stimuli, which showed a significant effect of Session ($F_{2,22} = 4.58$, $P < 0.02$, $p\eta^2 = 0.3$). *Post-hoc* comparisons showed a decrease of *d′* values during SI-rTMS (1.55), as compared with either the Baseline (2.38, $P < 0.02$) and to the VI-rTMS session (2.5, $P < 0.03$). The one-way ANOVA on the responses to ipsilateral, right-sided visual stimuli did not show a significant effect of Session ($F_{2,22} = 1.49$, $P = 0.2$, $p\eta^2 = 0.12$) (see Fig. 2C).

Analysis of response bias (*c*) did not show any significant effect – Task ($F_{1,11} = 1.94$, $P = 0.2$), Session ($F_{2,22} = 2.01$, $P = 0.2$), Side ($F_{1,11} = 0.01$, $P = 0.9$), Task by Session ($F_{2,22} = 1.15$, $P = 0.3$), Task by Side ($F_{1,11} = 1.62$, $P = 0.2$), Session by Side ($F_{2,22} = 0.12$, $P = 0.9$), Task by Session by Side ($F_{2,22} = 0.12$, $P = 0.8$) (see Fig. 2C).

Subjective reports and correlation analysis

Participants agreed that the Human-to-Human Touch seemed quite intense (0.64, $t_{11} = 2.32$, $P < 0.04$), but disagreed that it was unpleasant (−1.45, $t_{11} = -5.88$, $P < 0.01$). Additionally, they agreed that ‘The touched hand and the touching finger belonged to different persons’ (1.36, $t_{11} = 3.75$, $P < 0.01$), and consequently they disagreed that the touching index depicted their own finger (−0.58, $t_{11} = -3.02$, $P < 0.01$); and finally they agreed that the hand being touched could represent their own hand (0.75, $t_{11} = 2.32$, $P < 0.04$).

Subjects did not rate the Object-to-Object Touch as intense (−1.27, $t_{11} = -4.66$, $P < 0.01$) or as unpleasant (−1.55, $t_{11} = -7.45$, $P < 0.01$).

To assess whether the SI-rTMS-induced interference was associated with the subjective reports, Pearson’s correlation analyses were performed between the SI-rTMS effect, namely the difference between *d′* values for left-sided stimuli in the Baseline and in the SI-rTMS session (i.e. SI-rTMS minus Baseline, with negative values indicating a decrease of sensitivity during the stimulation of SI) and VAS ratings of intensity, pleasant and self-related touch. The SI-rTMS-induced interference was significantly correlated with VAS intensity ($r = -0.65$, $P < 0.02$) and with the report that the touched hand could represent the participant’s own hand ($r = -0.77$, $P < 0.03$). No other significant correlation was found (VAS unpleasantness, $P = 0.2$; touching finger representing the participant's own finger, $P = 0.2$; hands belonging to different persons, $P = 0.6$).

Experiment 2 – Human-to-Object and Object-to-Human Touch

Materials and methods

Participants, stimuli and procedure, and statistical analyses

Twelve participants (right-handed = 11; mean age = 25 ± 3 years; 11 females), selected using the same criteria of Experiment 1, entered Experiment 2.

The tasks, the experimental setting and the statistical analysis were the same as those of Experiment 1, the only difference relating to the visual stimuli. In the Human-to-Object Touch task, the video clips depicted the right or the left index finger moving downward and touching the stick below, or simply approaching the stick, without touching it (target and catch trials, respectively). In the Object-to-Human Touch task, the video clips shows the left or the right stick moving downward and touching the hand below, or approaching without touching it (target and catch trials, respectively) (see Fig. 1A).

The TMS procedure was identical to Experiment 1, but now only SI cortex was stimulated. Mean individual MT at rest was 58% (SD = 7.8%) of the maximal output of the stimulator. Analyses of errors, sensitivity and response bias were performed via a 2 (Task – Human-to-Object, Object-to-Human) by 2 (Session – Baseline, SI-rTMS) by 2 (Side – Left-, Right-sided stimuli) ANOVA.

The questionnaire for Experiment 2 comprised the following items: (1) 'The tactile stimulation looked like to be very intense'. (2) 'The tactile stimulation looked like to be very unpleasant'. (3) 'The hand being touched could depict my hand'. (4) 'The touching finger could depict my finger'. Items 1 and 2 were given for both Human-to-Object and Object-to-Human Touch tasks, item 3 was given for the Object-to-human Touch task, and item 4 was given for the Human-to-object Touch task. For every item, participants rated their agreement using a five-point scale (see Experiment 1).

Results

Analysis of the errors revealed a significant effect of Task ($F_{1,11} = 7.88$, $P < 0.02$, $p\eta^2 = 0.71$), showing that subjects made more errors in the Human-to-Object Touch task (19%) than in the Object-to-Human Touch task (15%) (Fig. 2B). The main effect of Session ($F_{1,11} = 6.76$, $P < 0.02$, $p\eta^2 = 0.31$) showed that the errors were slightly higher in the Baseline (18%) as compared with the SI-rTMS session (16%). Other effects did not reach significance – Side ($F_{1,11} = 0.06$, $P = 0.8$), Task by Session ($F_{1,11} = 0.03$, $P = 0.9$), Task by Side ($F_{1,11} = 0.95$, $P = 0.4$), Session by Side ($F_{1,11} = 0.26$, $P = 0.6$), Task by Session by Side ($F_{1,11} = 1.29$, $P = 0.3$) (Fig. 2B).

Sensitivity analysis did not show any significant main effect – Task ($F_{1,11} = 2.67$, $P = 0.1$), Session ($F_{1,11} = 4.67$, $P = 0.07$), Side ($F_{1,11} = 0.01$, $P = 0.9$), Task by Session ($F_{1,11} = 0.58$, $P = 0.5$), Task by Side ($F_{1,11} = 1.33$, $P = 0.3$), Session by Side ($F_{1,11} = 1.71$, $P = 0.2$), Task by Session by Side ($F_{1,11} = 0.16$, $P = 0.7$).

Similarly, analysis of the response bias did not show any significant main effect – Task ($F_{1,11} = 1.94$, $P = 0.2$), Session ($F_{1,11} = 0.15$, $P = 0.7$), Side ($F_{1,11} = 0.56$, $P = 0.5$), Task by Session ($F_{1,11} = 3.07$, $P = 0.1$), Task by Side ($F_{1,11} = 0.77$, $P = 0.4$), Session by Side ($F_{1,11} = 0.93$, $P = 0.4$), Task by Session by Side ($F_{1,11} = 0.39$, $P = 0.5$) (Fig. 2D).

To control for whether the four tasks differed for the level of difficulty, we analysed the d' values of the baseline session via a three-way ANOVA with Experiment as between-subjects factor, and Task and Side as within-subjects factors. No significant effect emerged ($P > 0.09$), suggesting that the four tasks were equally sensitive.

Subjective reports

Participants disagreed that the Human-to-Object Touch was unpleasant (−0.72, $t_{11} = -2.18$, $P < 0.05$) and that the touching index finger could depict their own finger (−1.18, $t_{11} = -3.13$, $P < 0.01$); their scores did not differ from 0 with respect to VAS intensity (−0.27, $t_{11} = -0.55$, $P = 0.5$).

The Object-to-Human Touch was not rated as intense (0.5, $t_{11} = 2.17$, $P = 0.07$) nor as unpleasant (−0.64, $t_{11} = -2.05$, $P = 0.07$), but participants agreed that the touched hand could represent their own hand (0.72, $t_{11} = 2.66$, $P < 0.02$).

Discussion

The aim of the present study was to uncover the selectivity of the causal involvement of SI in the visual processing of tactile events, with respect to the type of observed touching and touched stimuli. In particular, in the first experiment we compared the effect of rTMS interference of SI and VI on the ability to detect visual stimuli depicting a touch between body-parts (i.e. an index finger touching the back of a hand) and between objects (i.e. a leaf touching a wooden stick). rTMS delivered to SI selectively reduced visual perceptual sensitivity (i.e. decreased d' values) for detecting contralateral visual events comprising a tactile component. The SI-rTMS interference was selective in two ways – it was specific for the task, namely for discrimination of human bodily touch, as well as for the side of the touching stimuli, as it affected only the perception of the contralateral (left-sided) stimuli. Moreover, the SI disruption was evident only at the perceptual level (as assessed by d'), as no significant change in the response criterion or in the error rate emerged in the SI-rTMS session.

Notably, the SI-rTMS interference correlated with the intensity, but not with the unpleasantness, of the observed touch (i.e. the more intense the touch was rated, the greater was the visual impairment induced by SI stimulation), and with the report that the touched hand could represent the participant's own hand (i.e. more the touched hand was rated as depicting the participant's own hand, the greater was the SI interference). Moreover, subjects interpreted the touching and touched hands as belonging to different persons, hence representing an interpersonal (social) touch. These findings are in line with previous evidence suggesting the existence of specific relationships between the sensory qualities of the bodily touch, the embodiment of the observed sensations and the visual recruitment of somatosensory areas (e.g. Blakemore *et al.*, 2005; Bufalari *et al.*, 2007; Ebisch *et al.*, 2008).

With respect to the effect of VI stimulation, the interference induced in this area did not affect visual processing of human bodily touch or object contact, in line with evidence showing that biological and non-biological moving stimuli are preferentially processed outside VI (Walsh *et al.*, 1998; Proverbio *et al.*, 2009).

The second experiment further explored the role of SI in the visual processing of tactile interactions between body-parts and objects. There was no SI-rTMS disruption of visual perception in the Human-to-Object Touch task or in the Object-to-Human Touch task.

Overall, the present findings indicate that SI is causally involved in the visual processing of signals pertaining only to the domain of body-parts contact, suggesting that an important factor for the mirror activation of SI is that the recipient of the touched and the touching agent are both actually capable of feeling touch. This in turn suggests that the visuo-tactile mirroring mechanism of SI does not apply to the sight of 'any' touch, but rather is strongly restricted to the sight of body-related experiences.

In broad agreement with this, previous studies have shown a preferential activation of SI when viewing a human touch, as compared with the sight of a no-touch event (Schaefer *et al.*, 2005; Bolognini *et al.*, 2011b), or with the view of an object being touched (Blakemore *et al.*, 2005). Ebisch *et al.* (2008) showed a significant difference in the mirror activation of SI by the sight of intentional touch by a human agent, as compared with accidental touch by an inanimate agent. Moreover, SI activity was positively correlated with the degree of intentionality of the observed touch, as rated by the observers. However, the authors did not observe any difference in SI between animate (i.e. a hand touched the back of another hand) and inanimate (i.e. a hand touched a wooden chair) intentional touch, at odds with our findings. On the other hand, equal overlapping activation for different tactile experiences, namely intentional and accidental touch between human body-parts and/or objects, emerged in the bilateral SII (Keysers *et al.*, 2004). This evidence has led to the proposal that the mirror activity in SI might specifically reflect an automatic simulation of the proprioceptive aspects of the observed touch when intentionality is assumed by the observer; instead, SII activation by the sight of touch seems to underpin an abstract notion of touch (Ebisch *et al.*, 2008).

The selectivity of SI activity for touch observation is also in line with evidence in people with mirror-touch synaesthesia, the phenomenon by which watching touch to another person triggers consciously reported tactile experiences on their own body. By using a visuo-tactile interference task, it was shown that the synaesthetes were slower to report a real touch when there was simultaneously felt synaesthetic touch in another location. This effect was restricted to the sight of touch to a human body, being absent if bodies were replaced by objects, consistent with the subjective reports of synaesthetes that observed touch to an object is normally not felt (Banissy & Ward, 2007).

Other psychophysical studies have shown that seeing a body-part, but not an object, can increase the accuracy with which one can localize a tactile stimulus on that body part. It has been proposed that viewing a body-part induces a top-down visual modulation of SI activity corresponding to the viewed body-part (Kennett *et al.*, 2001). Because the sense of touch has a close and interactive relationship with higher cognitive representations of the human body (Cardini *et al.*, 2010; Serino & Haggard, 2010), the sight of body-parts touching each other's, at variance with the sight of object contact, may amplify the mirror recruitment of SI.

We did not find any effect of rTMS interference over SI for the visual processing of human-to-object and/or object-to-human contacts. Different factors may explain this null result. First, there is an 'intensity coding' effect (Keysers *et al.*, 2010) – the touching inanimate stimulus we used, i.e. a wooden stick, may be not enough intense to trigger SI activity, as suggested by participants' reports (see VAS intensity). Indeed, for objects touching the body, activations in SI appears stronger when the visual stimulus suggests intense pain, such as when a needle is shown penetrating a hand deeply as opposed to pricking it, or if participants imagine that they are in a painful situation themselves (Bufalari *et al.*, 2007; Keysers *et al.*, 2010). The intensity of observed tactile stimulus can also modulate the intensity of the synaesthesic experience – touching the face with a knife tip or finger elicits a stronger synaesthetic sensation than using a feather (Holle *et al.*, 2011).

Second, SI is more active when viewing hands manipulating objects (e.g. grasping a cup) (Pierno *et al.*, 2009); given the role of SI in haptic exploration, it has been proposed that SI might be particularly important for inferring the properties of objects from the way we see other people manipulate them (Keysers *et al.*, 2010). In this view, in our study the sight of an index finger merely touching a neutral object, without any goal-directed action, might be not sufficient to trigger a mirror engagement of SI.

Finally, the sight of a touch between human body-parts may also amplify the somatosensory activation, as compared with a touch between a body-part and an object, because SI would respond to both the observed touching and touched hands.

On a broader perspective, the somatosensory mirror system seems highly malleable, and susceptible to factors such as intensity of the stimuli, passive vs. active stimulation, intentionality, self-oriented experience, perspective-taking and attention (Fitzgibbon *et al.*, 2011). Such modulatory factors may determine the visual recruitment of SI by touch observation.

Our second finding was the lateralization of the SI-rTMS disruptive effect, which was specific for the processing of a contralateral (to the rTMS site) bodily touch. There are two explanations for this side-effect. The first rests on the assumption that visual stimuli presented in the left hemifield should be related to contralateral, right hemisphere processing; this hemifield effect should be independent of the type (left or right) of viewed hands. The alternative interpretation is related more to 'mirroring' theories, as our left hemifield stimuli depicted a left hand (egocentric perspective) being touched by a left index finger (allocentric perspective), as also confirmed by subjective reports. In this view, the side-specific rTMS effect might suggest a 'resonance' with the experience of the person being touched. Indeed, the SI-rTMS effect correlated with the interpretation of the touched hand as depicting the observer's own hand. Moreover, each hemisphere is more strongly activated when viewing actions conducted by a model's contralateral hand than when viewing actions conducted by an ipsilateral hand (Aziz-Zadeh *et al.* 2002), and mirror activations by the sight of touch are somatotopically organized, following the sensory homunculus magnification in SI (Blakemore *et al.*, 2005; Schaefer, *et al.* 2009). Even in synaesthesic patients there is often an anatomical mapping in which, for instance, the observed touch to a left cheek is felt on their left cheek and activates the right SI (Blakemore *et al.*, 2005; Holle *et al.*, 2011). Through this anatomical mapping, SI may convey a simulation of the precise body location at which the touch occurred, hence providing somatotopically specific representations of other people's somatosensations. Our experimental design does not allow us to discern whether it is the view of the contralateral left-sided touch, the view of left hands or the combination of both factors (i.e. left hands in the left hemifield) that determines the lateralization of the rTMS-SI effect.

From a neurophysiological perspective, SI exhibits properties that may be relevant for visual functions related to tactile events. First, some SI neurons code for arbitrary visual–tactile associations. Animal studies have shown that SI neurons in monkeys may fire both in response to a tactile stimulus and in response to a visual stimulus that may have previously been associated with the tactile stimulus (Zhou & Fuster, 1997, 2000). This evidence suggests that the mirror activation of SI may involve a local mechanism within SI. On the other hand, the caudal part of SI features multimodal receptive fields and direct connections with multisensory regions of the posterior parietal cortex (PPC) that contain bimodal neurons that combine visual and somatosensory information. These visuo-tactile neurons respond both when the animal is touched and when observing touch to someone else on the same body part, contributing to spatial matching between the bodies of the self and others in both action recognition and imitation (Ishida *et al.*, 2010; Keysers *et al.*, 2010; Macaluso & Maravita, 2010). As parietal areas are thought to constitute the main source of crossmodal information for the mirror system (e.g. Keysers *et al.*, 2010), the connectivity between SI and PPC may provide a potential substrate for the visual activation of SI by touch observation. Recent neuropsychological evidence from our lab supports this view – the sight of touch seems to affect visual perception through intra-hemispheric interactions between the visual input and the tactile input within PPC, with the tactile input probably provided by SI through a simulation process (Bolognini *et al.*, 2011a).

Conclusions

The present rTMS study shows that SI is causally involved in visual perception of a human body-part being touched by a human agent, suggesting simulation of observed somatosensory events based on the possibility of simulating specific body-related experiences. If simulation processes in SI reflect only the perception of bodily interactions, SI is probably better suited to represent social touch. In this perspective, by matching observed and felt touch, SI may contribute to our capacity to understand the effect of human intentional tactile stimulations on another person, perhaps allowing us to more easily 'resonate' with the body-related experiences of both the touched person and the human agent. However, the intensity of the perceived touch and the presence of a goal-directed action in the observed stimuli probably contribute to SI activity. Thus, to activate a shared neural circuitry for touch by vision in SI, for the brain it matters what is being touched and who is touching.

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Abbreviations

MI, primary motor cortex; MT, motor threshold; PPC, posterior parietal cortex; rTMS, repetitive transcranial magnetic stimulation; SI, primary somatosensory cortex; SII, secondary somatosensory cortex; VAS, visual analog scale; VI, primary visual cortex.

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