Report

Sharing Social Touch in the Primary Somatosensory Cortex

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Summary

Touch has an emotional and communicative meaning, and it plays a crucial role in social perception and empathy. The intuitive link between others' somatosensations and our sense of touch becomes ostensible in mirror-touch synesthesia, a condition in which the view of a touch on another person's body elicits conscious tactile sensations on the observer's own body [1]. This peculiar phenomenon may implicate normal social mirror mechanisms [2]. Here, we show that mirror-touch interference effects, synesthesia-like sensations, and even phantom touches can be induced in nonsynesthetes by priming the primary somatosensory cortex (SI) directly or indirectly via the posterior parietal cortex. These results were obtained by means of facilitatory paired-pulse transcranial magnetic stimulation (ppTMS) contingent upon the observation of touch. For these vicarious effects, the SI is engaged at 150 ms from the onset of the visual touch. Intriguingly, individual differences in empathic abilities, assessed with the Interpersonal Reactivity Index [3], drive the activity of the SI when nonsynesthetes witness others' tactile sensations. This evidence implies that, under normal conditions, touch observation activates the SI below the threshold for perceptual awareness [4]; through the visual-dependent tuning of SI activity by ppTMS, what is seen becomes felt, namely, mirror-touch synesthesia. On a broader perspective, the visual responsivity of the SI may allow an automatic and unconscious transference of the sensation that another person is experiencing onto oneself, and, in turn, the empathic sharing of somatosensations [2].

Results and Discussion

Induction and Chronometry of Mirror-Touch Synesthesia

Viewing touch may vicariously activate a putative *tactile mirror* system, comprising the somatosensory cortices (SI and SII) and areas of the mirror motor system [2, 4, 5]. In people with mirror-touch synesthesia, this system appears to be overactive, such that observing other's touch triggers a conscious tactile sensation on the synesthetes' body [4]. Keysers et al. [2] speculate that SI activity may be what discriminates mirror-touch synesthetes from nonsynesthetes, a hypothesis recently questioned by neuroimaging data [6]. Hence, the

causal contribution of the SI to mirror-touch synesthesia, and in turn to social touch, still needs convincing empirical support. This issue was addressed by assessing whether mirror-touch synesthetic responses can be induced in nonsynesthetes by facilitating visual responses of the SI via paired-pulse transcranial magnetic stimulation (ppTMS). Previously, we have provided compelling evidence that somatosensory areas contribute to mirror-touch synesthesia by using transcranial direct current stimulation (tDCS) [7]. However, tDCS lacks of focality, at variance of TMS [8], so the specific role of the SI is still unsolved. Moreover, tDCS induced "subthreshold" synesthesia-like effects, which manifested themselves only at a reaction times level [7].

ppTMS utilizes two TMS pulses, a conditioning pulse followed, at a very short interval, by a test pulse, applied to the same or to two different areas, to prime intracortical circuits in the stimulated area or in functionally connected areas [9, 10]. Applying this to the study of mirror-touch synesthesia, we aimed to uncover the mechanisms of intracortical facilitation within the SI responsible for this phenomenon. Mirror-touch responses by ppTMS in nonsynesthetes were assessed with a visual-tactile spatial congruity task, developed to objectively measure mirror-touch synesthesia [11].

In experiment 1, nonsynesthetes underwent the visual-tactile congruity task in a baseline session and while receiving ppTMS to the SI of the right hemisphere (see Figure 1 and the Supplemental Experimental Procedures available online). The chronometry of the vicarious SI activity was assessed by application of ppTMS to the SI at different interstimulus intervals (ISIs; 50, 150, 250, and 350 ms) from the onset of the visual touch, following previous magnetoencephalography evidence [12]. A repeated-measures ANOVA (rmANOVA) on error rate showed a significant *session* by *side* by *stimulus* interaction ($F_{4,52} = 3.93$, $p = 0.01$). SI ppTMS at 150 ms from the visual touch increased errors in incongruent vision-touch trials, inducing the typical response pattern that features mirror-touch synesthesia [11] (Figure 2A). This interference effect occurred only when the visual touch was contralateral (left sided) to the ppTMS side (right SI) and the actual touch was on the participant's right hand (ipsilateral to ppTMS) ($p_{Bonf} < 0.01$ as compared to baseline and other ISIs). This side specificity may be attributed to the fact that visual stimuli in the left hemifield are related to right hemisphere processing, which was facilitated by ppTMS [7, 13, 14]. SI stimulation at the other ISIs did not increase errors in any condition (all p values ≥ 0.3).

The latency of visual activity in the SI, peaking up at 150 ms, is considerably later than the activation of contralateral SI responses by tactile stimuli (≈ 50 ms) [15]. It is also incompatible with a direct feedforward input from primary visual areas; rather, this timing most likely reflects crossmodal feedback influences from multisensory and/or mirror areas [16].

Interestingly, participants were somewhat aware of the increased interference by the sight of touch during SI stimulation, as assessed with an ad hoc questionnaire (Figure 2B). Indeed, they reported an increased difficulty in touch localization due to the sight of touch during SI ppTMS (item 2), compared with the baseline (Z = 2.25, $p_{Bonf} = 0.012$). Moreover, they were less confident that the viewed touch could not be felt

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A Visual-tactile spatial congruity task

B Paired-pulse TMS

Conditioning pulse — 5 ms → Test pulse
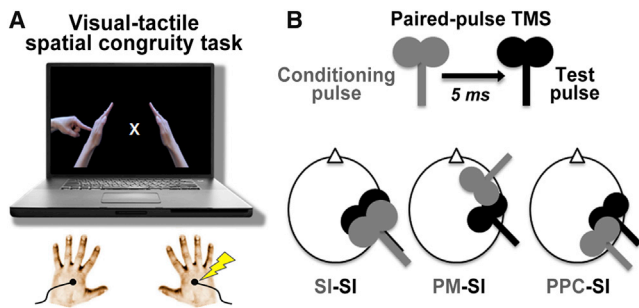
SI-SI   PM-SI   PPC-SI

Figure 1. Visual-Tactile Spatial Congruity Task

(A) An incongruent vision-touch trial of the touch task. In this task, participants viewed a touch to a left or a right hand while simultaneously receiving a tactile stimulus on the same or opposite hand; the participants had to report, as quickly and accurate as possible, which of their own hands was touched, ignoring the viewed touch. A manual response (pressing the corresponding key of the keyboard) was required in experiments 1 and 2, whereas a verbal response was required in experiment 3 (i.e., saying "left" if the tactile stimulus was perceived on the left hand, "right" if it was perceived on the right hand, "none" if no touch was felt). In experiment 3, catch trials with the visual stimulus alone were added, and a control task (no-touch task) was used, showing the hand being approached, but not touched, by the finger; the order of the tasks was randomized across participants.

(B) Schematic representation of the ppTMS paradigms adopted in experiments 1, 2, and 3 (N = 16 in every experiment). A subthreshold (70% of the motor threshold, MT) conditioning TMS pulse (gray coil) was followed by the suprathreshold (130% of the MT) test TMS pulse (black coil) after a delay of 5 ms. This protocol can probe intracortical facilitatory circuits in the SI [10]. In experiments 1 and 3, both pulses were applied to the SI hand area of the right hemisphere. In experiment 2, the conditioning pulse was applied to the SI, PM, or PPC of the right hemisphere, and the test pulse was applied to the right SI (see the Supplemental Experimental Procedures for details).

on their hands (item 1) after SI stimulation (Z = 2.37, p_{Bonf} = 0.024). Instead, SI ppTMS did not change subjective judgments for questions not inquiring specifically about visually induced sensations ("overall difficulty of the tactile task," item 3, Z = 1.78, p = 0.08; "intensity of the viewed touch," item 4, Z = 0.94, p = 0.35).

Crucially, the feeling of being touched by viewing a touch (Spearman correlation, ρ = 0.85, p = 0.0001) correlated with error rate in incongruent vision-touch trials (left-sided visual touch) induced by SI ppTMS at 150 ms.

It is noteworthy that the behavioral effect of SI ppTMS was associated to interindividual differences in emphatic abilities at the Interpersonal Reactivity Index [3] (see Figure S1). The increased errors in incongruent trials by SI ppTMS at 150 ms were positively correlated with the ability to adopt the subjective perspective of others (cognitive empathic subscale "perspective taking" [PT], Pearson's correlation, R = 0.85, p = 0.0001) and to the tendency to have feelings of sympathy and concern for others (affective empathic subscale "empathic concern" [EC], R = 0.61, p = 0.02). Moreover, the subjective feeling of being touched by seeing touches correlated with EC scores (ρ = 0.65, p = 0.0125), whereas visually induced difficulty in touch localization correlated with PT scores (ρ = 0.68, p = 0.008; see items 1 and 2 in Figure 2). No other significant correlation was found (p > 0.08).

In the general population, PT is linked to vicarious somatosensory activity when one is watching others being nonpainfully touched [17, 18], whereas EC might be elicited when one is seeing others in pain [19, 20]. Instead, mirror-touch

synesthetes show higher level of self-reported affective empathy than nonsynesthetes [11]. Interestingly, empathy is not relevant for other types of synesthesia, just for mirror-touch synesthesia [1]. Together with the present results, this evidence suggests that cognitive empathy may be more important for the unconscious simulation of others' tactile sensations, whereas the conscious sharing of touch, which represents the prominent feature of mirror-touch synesthesia, may depend more on affective empathy; this view is further supported by results from experiment 3.

Functional Connectivity in Mirror-Touch Synesthesia

SI has tight functional links with the posterior parietal cortex (PPC) and the premotor cortex (PM); both of these areas contain bimodal neurons responding to visual and tactile stimuli [21–23] and show vicarious activation by the sight of touch [2, 4, 6]. Additionally, synesthesia has been presented as an *anomalous* hyperbinding phenomenon mediated by the parietal cortex [24]. Therefore, the functional interplay with premotor and/or parietal areas may enable the SI to have a role in visual perception of social touch. This hypothesis was tested in experiment 2 by using ppTMS with a twin-coil design to probe intrahemispheric pathways from the PPC and from the PM to the SI in the right hemisphere while nonsynesthetes performed the visual-tactile congruity task (Figure 1). Given the previous results, ppTMS was applied at 150 ms from the visual touch. The advantage of probing intracortical pathways with ppTMS is that the response to the conditioning pulse depends on the state of the pathway at the time the stimulus is applied [25], hence indicating whether the state of connections (effective connectivity [26]) is linked to mirror-touch effects.

The rmANOVA on the error rate showed a significant three-way interaction ($F_{3,39}$ = 5.67, p = 0.003) (Figure 3A). A conditioning pulse over the PPC, followed by a test pulse to the ipsilateral SI, increased errors only in incongruent vision-touch trials, when the visual touch was contralateral to ppTMS, compared with every condition of the baseline and of PM-SI stimulation (p_{Bonf} < 0.001); this effect was analogous to that induced by SI ppTMS (p = 0.9), which also increased errors in the same incongruent vision-touch trials, as compared to baseline and PM-SI stimulation (p_{Bonf} < 0.01). Conversely, facilitation of the SI via the PM did not change accuracy (p > 0.2).

Again, participants reported an increased difficulty in touch localization due to the sight of touch (item 2) and were also less confident about not feeling the viewed touch on their hands (item 1) during ppTMS to the SI (item 1, Z = 2.14, p_{Bonf} = 0.033; item 2, Z = 2.67, p_{Bonf} = 0.048) and to PPC-SI (item 1, Z = 2.20, p_{Bonf} = 0.027; item 2, Z = 1.88, p_{Bonf} = 0.046) compared with baseline (Figure 3B). On the same items, there was no change from baseline due to PM-SI stimulation (p > 0.3). Participants' reports on items 3 and 4 did not change in any session (p > 0.3). The increased errors by SI and PPC-SI stimulations were associated with the post-ppTMS scores on item 1 (SI, ρ = 0.70, p = 0.005; PPC-SI, ρ = 0.64, p = 0.014) and item 2 (SI, ρ = 0.61, p = 0.02; PPC-SI, ρ = 0.55, p = 0.044).

Moreover, PT scores were positively correlated with mirror-touch errors by SI (R = 0.74, p = 0.003) and PPC-SI (R = 0.55, p = 0.04) stimulations. Even the subjective reports in the post-ppTMS assessment were associated with empathy: the visually induced feeling of being touched (item 1) after SI ppTMS correlated with EC scores (ρ = 2.75, p = 0.012), whereas the visually induced difficulty in touch localization (item 2) correlated with PT scores after both SI (ρ = 2.67, p = 0.020) and PPC-SI (ρ = 2.75, p = 0.017) stimulations.
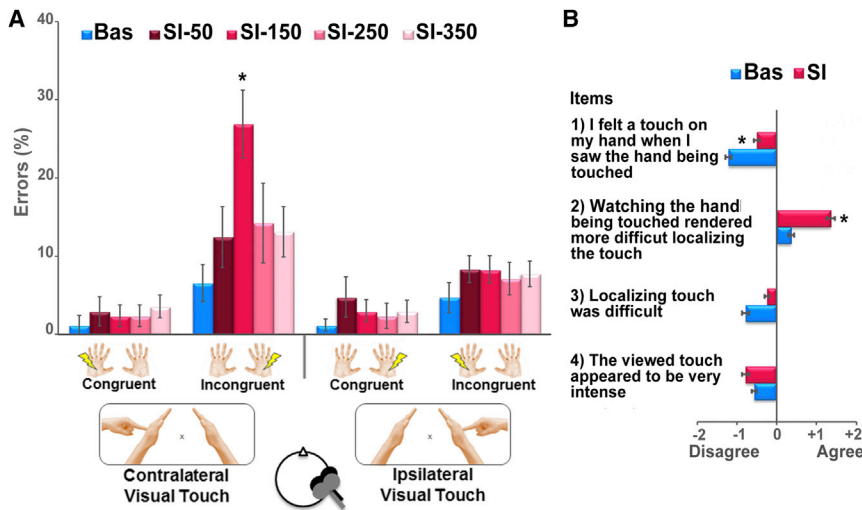
Figure 2. Results from Experiment 1

(A) The effect of SI ppTMS on the mean (±SE) error rate (%) in the visual-tactile spatial congruity task. The bars depict the subjects' performance at baseline (Bas) and during ppTMS of the SI at ISIs of 50, 150, 250, and 350 ms from the visual touch. Here, ipsilateral and contralateral refer to the location of the visual stimulus with respect to the side of ppTMS. The five (*session*: baseline and four ppTMS ISIs) by two (*side*: ipsilateral and contralateral visual touch) by two (*stimulus*: congruent and incongruent vision-touch trials) rmANOVA showed a significant three-way interaction (p = 0.01), explored with Bonferroni corrected post hoc tests; see also Table S1. Note that the difference between congruent and incongruent vision-touch trials that characterized synesthesia [11] emerged only during SI stimulation, selectively when the visual stimulus was contralateral to ppTMS, within a time window of 150–350 ms (p$_{Bonf}$ < 0.05); there was no difference between congruent and incongruent vision-touch trials in baseline or during SI ppTMS at 50 ms (p > 0.3). Anecdotally, two subjects spontaneously told the experimenters to have felt sometimes touches on both hands, although only unilateral touches were given.

(B) Subjective reports of synesthesia-like sensations were assessed with the questionnaire administered after the baseline (Bas) and the ppTMS session (SI). Four judgments (described in the figure) were obtained by means of a five-point Likert scale (score: −2, strongly disagree; −1, disagree; 0, neither agree nor disagree; +1, agree; +2, strongly agree). Values greater than 0 indicate agreement, and hence the presence of mirror-touch synesthesia, whereas values less than 0 indicate disagreement. Comparisons between the baseline and the assessment after SI ppTMS were performed with the Wilcoxon signed-rank test, with the Bonferroni correction applied. See the Supplemental Results for details.
See also Figure S1 and Table S1.

Therefore, aside from a local mechanism within the SI, mirror-touch phenomena can be induced by priming of SI activity via the ipsilateral PPC. Our results speak in favor of an effective connectivity [26] between the PPC and SI, which may be driven by visual input [2]. Indeed, the caudal part of the SI features multisensory receptive fields and direct connections with regions of the PPC containing visual-tactile neurons; these neurons respond both when an animal is touched and when it is observing someone else being touched on the same body part, contributing to the spatial matching between the body of the self and of another [27, 28]. The PPC also constitutes the main source of visual information to the mirror system [2, 29, 30].

Phantom Touches by the Sight of Touch, but Not by the Sight of Action

Experiment 3 aimed to ensure that mirror-touch effects were not merely driven by attentional capture due to the moving hand by adopting a control (no-touch) task showing the hand being approached, but not touched, by the index finger. Moreover, to ascertain that mirror-touch errors were not affected by the hand being used to respond, we now required a verbal response. Finally, the number of trials was increased, and a pure visual condition (catch trials, CTs) was added. In this experiment, ppTMS was delivered to the right SI at 150 ms. The rmANOVA showed a significant four-way interaction (F$_{2,26}$ = 11.01, p = 0.0003): SI stimulation induced mirror-touch errors in incongruent vision-touch trials only during the view of touches (p$_{Bonf}$ < 0.0001 for all comparisons) (Figure 4). Moreover, when the contralateral visual stimulus was presented alone (CT), subjects occasionally reported having felt a tactile stimulus on their own hand during SI ppTMS, as compared to ipsilateral CT during SI stimulation (p$_{Bonf}$ = 0.001) and to ipsilateral and contralateral CT of the baseline (p < 0.02). These phantom touches were localized by the 86% participants on their own left hand, indicating that the viewed left-sided touch on

a left hand was remapped on the observer's own left hand. This effect cannot be explained by paresthesia because ppTMS was delivered 150 ms after the visual touch [15]. The absence of SI effects during the sight of moving, but not touching, hands supports the selectivity of the vicarious activity of the SI by touch observation (touch task), rather than by action observation (no-touch task).

A trend for an increased effort in tactile localization due to the sight of touch emerged during SI ppTMS (0.29), compared to baseline (−0.07, Z = 1.89, p = 0.056), and this effect tends to be associated with the error rate during SI ppTMS (ρ = 0.51, p = 0.06). Subjective reports on other items of the questionnaire did not change after SI ppTMS (p > 0.1). For the no-touch task, subjective reports (assessed with ad hoc items about the observed movement) were not influenced by SI ppTMS (p > 0.6) (see Table S2).

PT scores were still associated with mirror-touch errors by SI ppTMS (R = 0.57, p = 0.032), while EC scores correlated with ppTMS-induced phantom touches (R = 0.64, p = 0.014). In this experiment, subjective reports in the post-ppTMS assessment did not correlate with empathy in both tasks (p > 0.07).

Conclusions

Contingent upon touch observation, priming of short-latency facilitatory intracortical circuits in the SI, directly or via its effective connections with the ipsilateral PPC, determines the emergence of a behavioral pattern in the visual-tactile spatial congruity task that is considered a marker of mirror-touch synesthesia [11], further supported by changes in subjective tactile sensations related to touch observation. When the visual touch is presented alone, without any real touch, phantom touches can even emerge by enhancing the vicarious activity of the SI, which allows an anatomical remapping of the phantom touch on the observer's hand. These synesthesia-like effects are differentially linked to cognitive and affective
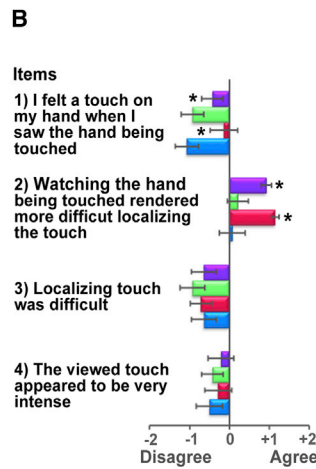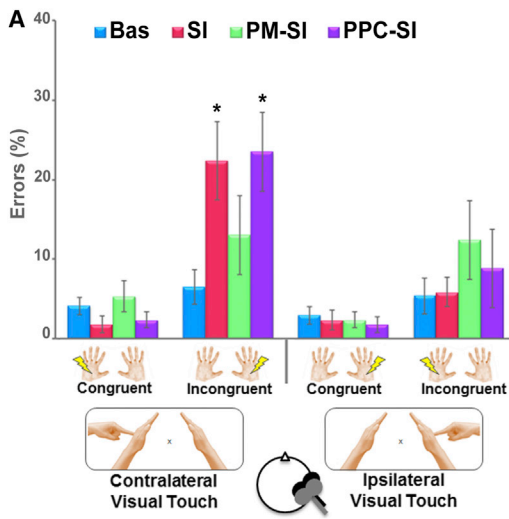
Figure 3. Results from Experiment 2

(A) Mean (±SE) error rate (%) in the visual-tactile spatial congruity task in baseline (Bas), and during the ppTMS of the SI, PM-SI, and PPC-SI of the right hemisphere (ISI = 150 ms from the visual touch). Only the schematic representation of the ppTMS of the SI is reported below the graphs; see Figure 1 for the other conditions. The four (*session*: baseline, ppTMS of the SI, PPC-SI, and PM-SI) by two (*side*) by two (*stimulus*) rmANOVA showed a significant three-way interaction (p = 0.01). Congruent and incongruent vision-touch trials, with the visual stimulus contralateral to ppTMS, were different during SI and PPC-SI stimulations ($p_{Bonf} < 0.0001$), but not in the baseline (p = 0.9); when the visual stimulus was ipsilateral to ppTMS, congruent and incongruent vision-touch trials never differ each other (p > 0.2).
(B) Subjective reports of synesthesia-like sensations assessed after the baseline and each ppTMS session. See the legend to Figure 2 and the Supplemental Information for details.
See also Table S1.

empathy. It is noteworthy that real synesthetic sensations are unusual, unexpected, and somewhat unknown experience for nonsynesthetes, especially in an experimental setting in which the participant is asked to perform a task without being explicitly instructed to pay attention to these sensations; instead, for synesthetes, the synesthetic percept is a common experience, present from birth. Therefore, even if SI ppTMS is able to induce mirror-touch synesthesia, such novel sensation may not be promptly recognized by nonsynesthetes, and thus be unambiguously reported (a similar argument applies to phosphene perception by occipital TMS [31]).

This evidence indicates that ppTMS of the SI, by inducing pulse-dependent tuning, might increase intracortical coherence activity of the tactile mirror system during touch observation, in a time-dependent way [32]; this, in turn, impairs the ability to discriminate visual touch from actual touch and can cause phantom touches. Previously, tDCS of the SI was shown to induce only a slowdown of responses in incongruent vision-touch trials [7]. This is most likely because tDCS does not stimulate axons and causes them to discharge action potentials, as ppTMS does [33, 34]. Rather, tDCS most likely targets neuronal signaling by modulating the resting membrane threshold [8], suggesting that the present ppTMS effects are not simply due to a change in excitability.

Hence, the SI appears to be endorsed with specialized mechanisms for the sharing of touch during human interactions, which work in concert with empathy. Touch observation may promote an automatic, usually unconscious, stimulation of others' tactile sensations in the SI, as it occurs in the mirror motor system during action observation [30]. The functional
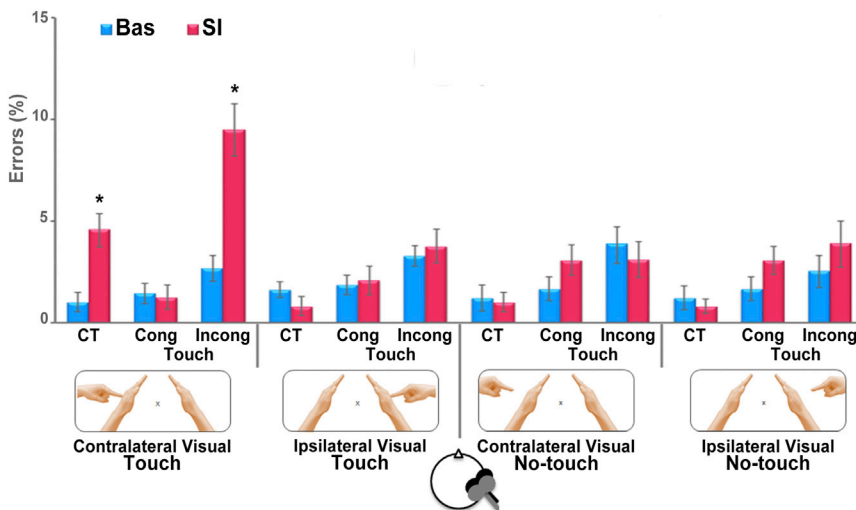

Figure 4. Results from Experiment 3

The effect of SI ppTMS on the mean (±SE) error rate (%) in the touch and no-touch visual-tactile congruity tasks. The bars depict the subjects' performance at baseline (Bas) and during ppTMS of the SI (ISI = 150 ms from the visual touch). The two (*task*: *touch* and *no-touch*) by two (*session*: baseline and SI ppTMS) by two (*side*) by three (*stimulus*: catch trial [CT], congruent, and incongruent vision-touch trials) rmANOVA showed a significant four-way interaction (p = 0.01), which was explored by separate rmANOVA for each task, followed by Bonferroni-corrected post hoc tests (see Table S1 and the Supplemental Results). The *session* by *side* by *stimulus* interaction was significant for the touch task (F = 16.43, p < 0.00002), but not for the no-touch task (F = 1.15, p = 0.2). In the touch task, congruent and incongruent vision-touch stimuli (with the visual stimulus contralateral to ppTMS) differed during SI ppTMS ($p_{Bonf} = 0.0001$), but not in the baseline (p = 0.9); when the visual touch was ipsilateral, congruent and incongruent stimuli did not differ

in any session (p > 0.6). In the no-touch task, the main effect of session and its interaction with other factors were not significant (p > 0.2; see the Supplemental Results); no difference was found between congruent and incongruent vision-touch trials (p > 0.1). In the touch task, subjective reports of synesthesia-like sensations were assessed with the same questionnaire as in experiment 1 (see Figure 2). A different questionnaire was used for the no-touch task, comprising three judgments: (1) "I felt a touch on my hand when I saw the hand moving," (2) "when I saw the moving hand, it was more difficult to localize the actual touch," and (3) "it was difficult to localize the touch on my hands"; no change in subjective reports were induced by SI ppTMS (p > 0.6; see Table S2 and the Supplemental Results).

connectivity with the PPC provides the SI of crossmodal and mirroring processes for expressing its social functioning. In this perspective, mirror-touch synesthesia reflects the anomalous counterpart of the otherwise normal social activity of the SI, ranging from the understanding of others' touch to the synesthetic touch [1, 2].

Nevertheless, besides the changes of SI activity, additional structural differences in the SII and in temporoparietal and prefrontal regions involved in self-other monitoring mechanisms, may be necessary for inducing reliable and everlasting conscious somatic experience through vision; such structural alterations, detected in the synesthetic brain [6], cannot be reproduced with TMS, which can modulate only functional, but not structural, cerebral organization in a reversible way [35].

Supplemental Information

Supplemental Information includes Supplemental Results, Supplemental Discussion, Supplemental Experimental Procedures, one figure, and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.05.025.

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