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RESEARCH ARTICLE

The role of the right temporoparietal junction in intersensory conflict: detection or resolution?

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Abstract The right temporoparietal junction (rTPJ) is a polysensory cortical area that plays a key role in perception and awareness. Neuroimaging evidence shows activation of rTPJ in intersensory and sensorimotor conflict situations, but it remains unclear whether this activity reflects detection or resolution of such conflicts. To address this question, we manipulated the relationship between touch and vision using the so-called *mirror-box illusion*. Participants' hands lay on either side of a mirror, which occluded their left hand and reflected their right hand, but created the illusion that they were looking directly at their left hand. The experimenter simultaneously touched either the middle (D3) or the ring finger (D4) of each hand. Participants judged, which finger was touched on their occluded left hand. The visual stimulus corresponding to the touch on the right hand was therefore either congruent (same finger as touch) or incongruent (different finger from touch) with the task-relevant touch on the left hand. Single-pulse transcranial magnetic stimulation (TMS) was delivered to the rTPJ immediately after touch. Accuracy in localizing the left touch was worse for D4 than for D3, particularly when visual stimulation was incongruent. However, following TMS, accuracy *improved* selectively for D4 in incongruent trials, suggesting that the effects of the conflicting visual information were reduced. These findings suggest a role of rTPJ in detecting, rather than resolving, intersensory conflict.

Keywords Visuo-spatial attention · Tactile localization · Finger-specificity · Mental body representation · Temporoparietal junction · Intersensory conflict

Introduction

The representation of one's own body depends on the integration of inputs across several sensory modalities. Signals from different modalities are normally consistent and complementary. In some situations, however, conflicting information is received, and two discrepant sources of information must be integrated (cf. Ernst and Bülthoff 2004). Several recent studies have suggested that the temporoparietal junction in the right hemisphere (rTPJ) responds to such perceptual conflict. For example, rTPJ was activated by visual information of finger movement that was incongruent with proprioception of the actual finger movement (Balslev et al. 2005). Likewise, rTPJ activity increases linearly with increasing temporal delay between active movement and visual feedback (Leube et al. 2003) and with increasing spatial distortion of visual and proprioceptive information about hand position (Farrer et al. 2004). Thus, the rTPJ seems to be associated with intersensory conflict. However, imaging studies have not identified the exact role of rTPJ in processing such conflict.

One hypothesis is that the rTPJ is involved in *resolving* intersensory conflict in order to maintain a coherent percept

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of the body (Blanke et al. 2004; Blanke and Mohr 2005; Farrer et al. 2004; Spence et al. 1997). When such conflict resolution fails, the normal coherence of the bodily self is replaced by a fragmented or dissociated experience in both clinical (Blanke et al. 2004; Brugger et al. 1997) and healthy populations (Blanke et al. 2005; Farrer et al. 2004; Zacks et al. 1999). Alternatively, rTPJ might simply *detect* the intersensory discrepancy, with other areas being responsible for attempting resolution. This hypothesis fits with a more general role of the rTPJ in spatial attention to multisensory stimuli. Indeed, neuroimaging studies suggest that rTPJ dominates a network of regions responsive to visual, auditory and tactile stimuli and, specifically, plays a key role in coding stimuli at an unexpected location or behaviorally salient changes in external space (Astafiev et al. 2006; Corbetta et al. 1998; Downar et al. 2000; Downar et al. 2002; see Corbetta and Shulman 2002 for a review). As such, the rTPJ would be responsible of bottom-up or stimulus-driven visual attention to detect any relevant event. This function of the rTPJ is consistent with evidence linking lesions in this region to unilateral spatial neglect, a common neuropsychological syndrome following injury to the right hemisphere, in which salient stimuli in the left hemispace fail to attract attention and reach awareness (Bisiach et al. 1996; Friedrich et al. 1998; Mort et al. 2003; Vallar 2001).

We created conflict between vision and touch using a tactile version of the mirror-box illusion, previously used to investigate phantom limbs (Ramachandran and Rogers-Ramachandran 1996; Ramachandran et al. 1995), perceptual conflict (e.g., Fink et al. 1999; Holmes et al. 2006) and effects of vision on somatosensory processing (e.g., Harris et al. 2007; Longo et al. 2009). Participants placed their hands on either side of a mirror aligned with their sagittal plane, in the setup shown in Fig. 1. Looking into the mirror, the reflection of their right hand appeared to be a direct view of their left hand. The experimenter synchronously touched either the middle (D3) or the ring finger (D4) of both hands. Participants judged which finger on their occluded left hand was touched. Touch could either be congruent or incongruent with vision. When touch was congruent with vision, the same finger was touched on left and right hand. What participants saw was therefore congruent with what they felt on their target left hand. When touch was incongruent, D3 was touched on the right hand and D4 on the left, or vice versa. Therefore, what participants saw was incongruent with what they felt.

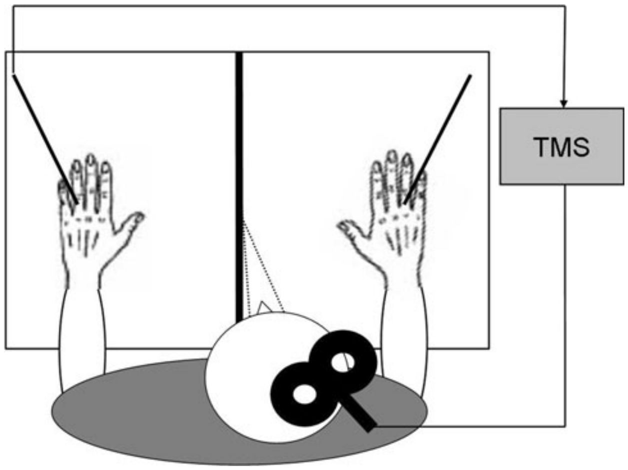

Fig. 1 Experimental setup. The participant's hands lay on either side of a mirror. The participant gazed toward her/his left hand, and therefore saw her/his right hand appearing via the mirror in the left hand's location. The participant's fingers on either hand were touched by means of two sticks, containing a microswitch which triggered TMS 350 ms after the touch onset. TMS was delivered with a coil placed tangentially over the right TPJ

Several phenomena hold that vision dominates over touch. For instance, in crossmodal congruence task, participants receive tactile stimulation on one finger, while a nonbodily visual distractor (e.g., a circle) appears proximal to the hand position. Tactile discrimination, the ability to differentiate information received through the sense of touch, is improved when visual and tactile stimulations are at congruent locations and is disrupted when the two locations are incongruent (Spence et al. 1998; Pavani et al. 2000). The influence of vision on tactile discrimination is also suggested by effects of seeing the body on somatosensation, whereby even non-informative view of body parts increases tactile acuity (e.g., Haggard 2006; Kennett et al. 2001) and suppresses acute pain (Longo et al. 2009). On this basis, the bodily visual information was expected to create a transfer of tactile sensation from one finger to another in the incongruent condition, even if participants were aware of the potential conflict. Indeed, Ro et al. (2004) reported anecdotally that the illusion of seeing one's hand touched in the mirror box could generate tactile sensations on a non-stimulated hand.

In one condition, we delivered single-pulse transcranial magnetic stimulation (TMS) to the rTPJ to alter its activity and thus investigate its role in intersensory conflict. We stimulated the right side only, because the right—but not the left—TPJ is held to process multisensory body-related information (Blanke and Mohr 2005) and portions of this region have been related to the awareness of personal space (Committeri et al. 2007). Generally, clinical (Vallar 1998), TMS (Chambers et al. 2004) and functional neuroimaging studies (Nobre et al. 2007) indicate a right hemispheric dominance for visuo-spatial attention, which was crucial for our task. In fact, given their perceptual similarity, fingers are mostly identified by their position through visuo-spatial exploration (Goldenberg 1999). Accordingly, their perceptual discrimination is particularly vulnerable to interference and narrowing of visual attention. Indeed, patients with damage to the right hemisphere may show selective impairment in processing finger postures (Goldenberg 1999) as part of generally impaired perceptual analysis. Recently, a strong association has been reported between the severity of left-sided spatial neglect and disturbed imitation of finger posture, as it poses high demand to perceptual exploration of the demonstrated gestures (Goldenberg et al. 2009). Thus, the task we used was expected to be sensitive to the TMS interference with rTPJ activity in order to test whether this region mediates the detection or the resolution of intersensory conflict.

First, we predicted that tactile localization would be modulated by concurrent visual information about which finger was touched. Specifically, the performance was expected to be impaired when vision and touch were incongruent, relative to congruent. Second, we predicted that if rTPJ contributes to conflict *resolution*, participants' performance on incongruent trials should decline when rTPJ processing was disrupted with TMS. If, in contrast, rTPJ is involved in conflict *detection*, TMS should reduce the effect of incongruent visual feedback on tactile localization, resulting in *improved* performance on incongruent trials with TMS.

Materials and methods

Participants

Fourteen healthy individuals (8 female) between 20 and 36 years participated. They were all right-handed as determined by the Edinburgh handedness inventory (Oldfield 1971). Each participant was checked for TMS exclusion criteria (Wassermann 1998) and gave written informed consent. Procedures were approved by the local ethics committee.

Task and procedure

Participants sat looking into a mirror aligned with their body midline (Fig. 1). The mirror occluded their left hand and reflected their right hand. The hands lay at the same fixed distance from the mirror (17 cm from the mirror to the tip of the middle finger), so that participants saw the reflection of their right hand at the precise spatial location where their left hand was located. This creates the compelling visual illusion that one is looking directly at her own left hand, rather than at a mirror image (Ramachandran and Rogers-Ramachandran 1996; Ramachandran et al. 1995). A black baffle on the table, and a black smock over the participant's torso ensured that only the right hand was seen, without any surrounding detail of the body or environment. The experimenter synchronously touched either D3 or D4 of each hand, with two identical wooden sticks. A microswitch attached to the stick touching the left hand triggered TMS and the audio recording. The touches were punctuate and clearly suprathreshold. We instructed participants to look into the mirror and verbally report, which finger was touched on their left hand (i.e., "middle" or "ring"), as quickly and accurately as possible. A 10-trial familiarization phase preceded the experiment. A 3 s response window was allowed. Vocal responses were recorded, and RTs for each trial were computed offline in Matlab (MathWorks, Natick, MA), by identifying the first point at which absolute value of acoustic energy exceeded 50% of its peak value.

We selected the left D3 and D4 as the targets for tactile discrimination for several reasons. Confusion errors in tactile localization tasks are the most common between adjacent fingers (e.g., Schweizer et al. 2000) and particularly between D3 and D4, as they do not enjoy the distinguishing visual characteristics of shape and position of other digits (Mayer et al. 1999; Kinsbourne and Warrington 1962). Then, the spatial proximity of the two fingers critically contributes to the visual interference with touch. The effect of a visual distractor is in fact known to be strongest when it appears near the touched site than when visual and tactile stimuli are far apart (Spence et al. 1998; Pavani et al. 2000). Finally, neuropsychological evidence from neglect and extinction suggests that the disruptive effect of TMS over the right hemisphere would be the most likely in the left hemispace (Karnath et al. 2001; Mesulam 1999; Vallar 2001; but see also Corbetta et al. 2000; Perry and Zeki 2000, for evidence of bilateral representation in rTPJ). Thus, the D3–D4 finger pair of the left hand provided the best combination to elicit effects of visual interference on tactile judgments and test the involvement of rTPJ in such visuo-tactile conflict.

As the rTPJ is a key part of visuo-spatial attention network (Corbetta and Shulman 2002), we wanted to check whether rTPJ TMS could have impaired unimodal visual processing generally, as opposed to influencing visuo-tactile conflict in particular. Thus, to ensure that participants attended to the visual stimulus, at the end of each block we asked the following question: "In the block you have just finished, did you see the experimenter touching your middle finger or your ring finger more frequently?" It was clearly explained that this question concerned what they saw (the right hand via the mirror) and not what they felt (the touch on either hand).

Experimental design

The experimental design was 2 × 2 × 2 with within-subjects factors: (1) TMS condition (TMS to rTPJ vs. sham), (2) Left-hand finger (D3 vs. D4), (3) Visuo-tactile Congruence (congruent vs. incongruent). The first factor was blocked. The experiment consisted of four blocks (two TMS and two sham conditions). There were 96 trials per block. For the task-relevant left hand, half the trials (*N* = 48) in each block involved touch on D3, half on D4. The number of touches on D3 and D4 of the right hand was varied between blocks. This imbalance in right hand stimulation was used to provide a control for visual attention (see later). Briefly, in one block, 67% of touches (*N* = 64) were on one finger, and 33% (*N* = 32) on the other. In the second block with the same TMS condition (i.e., TMS or sham), this distribution was reversed. Since we pooled the two blocks for statistical analysis, the overall frequency of D3 and D4 touch was 50 and 50%, respectively, for both hands. As a result of this arrangement, half of the trials (N = 48) in each block were congruent, and the other half (*N* = 48) were incongruent. A detailed description of the distribution of touch on D3 and D4 in each block is reported in Table 1. Order of trials in each block was random. The experimenter was instructed by an on-screen text before each trial about the fingers to stimulate on that trial. Order of TMS conditions was counterbalanced across participants in an ABBA fashion. At the end of the experiment, all participants had received equal amounts of stimulation on both fingers of both hands during TMS and sham conditions.

TMS protocol

The rTPJ site was obtained by converting the coordinates of the site of interest, taken from a TMS study, into real space for individual participants using the SPM2 software (SPM, The Wellcome Department of Neurology, London, UK). In this procedure, the T1-weighted structural MRI image for each participant was normalized into a standard space. We used the mean Montreal Neurological Institute (MNI) coordinates for the rTPJ ($x = 63.4$, $y = -50.0$, $z = 22.7$) obtained by Tsakiris et al. (2008). The authors identified the rTPJ from structural MRI images as the intersection of the supramarginal, angular and superior temporal gyri and found that this region was involved in processing multisensory body-related events by experimentally manipulating visual and tactile stimulation. These coordinates were converted to the *x*, *y* and *z* coordinates of the structural space of each participant. The participant's head position was then tracked with an infra-red device (Polaris, Northern Digital, Ontario, Canada) and co-registered with the MRI image with frameless stereotaxy using the Brainsight system (Rogue Research, Montreal, Canada).

A Magstim 200 stimulator (Whitland, UK) was used to deliver TMS via a 70-mm figure-of-eight coil, placed tangentially to the participant's scalp. In this stimulator model, the pulse has duration of 1 ms (Jalinous 1995). Before starting the experiment, the intensity of TMS over the rTPJ was established for each participant by initially setting it at 60% of maximum stimulator output with the purpose to gradually reduce it to 55 or 50% if the pulses elicited facial muscle twitches or participants reported discomfort. However, we did not need to go through this procedure since all participants could tolerate well the 60% intensity. TMS pulses were delivered 350 ms after visuo-tactile stimulation, in line with reports of rTPJ activity in electrophysiological studies of somatosensory processing (Blanke et al. 2005; Yamaguchi and Knight 1991).

The same TMS intensity and timing were used in the sham condition, except that the coil was held perpendicularly to the scalp surface over rTPJ. This reproduced the acoustic and tactile sensations of the TMS condition, including their spatial aspects, thus controlling for the unspecific effects of TMS, but did not effectively stimulate the rTPJ (Robertson et al. 2003).

Control experiment

The current study aimed at investigating the tactile discrimination during visuo-tactile conflict and the role of the rTPJ in such conflict. However, our experiment actually

Table 1 Arrangement of the two block of each TMS condition (sham and TMS)

	Block 1			Block 2		
	Number of trials	Tactile target location		Number of trials	Tactile target location	
		Right hand	Left hand		Right hand	Left Hand
Congruent trials	32	D3	D3	32	D4	D4
	16	D4	D4	16	D3	D3
Incongruent trials	32	D3	D4	32	D4	D3
	16	D4	D3	16	D3	D4

There were two types of congruent trials (D3 to right hand/D3 to the left hand; D4/D4) and two types of incongruent trials (D3/D4 and D4/D3). There were 96 trials per block. In the column "*N* trials", it is reported the number of each trial type in each block. In one block, the distribution of touches on the right hand was 64 trials (67%) on one finger and 32 (33%) on the other finger. The opposite was true for the second block. Touches on the left hand were equally distributed among the two fingers (48 trials on D3 and 48 trials in D4). However, this arrangement resulted in the same amount of congruent (*N* = 48) and incongruent trials (*N* = 48) in each block contained two potential sources of information, which could conflict with the perceived touch on the occluded left hand: the *vision* of touch, and the actual *touch* on the right hand. That is, in addition to the visuo-tactile conflict, there was also potentially tactile–tactile conflict, which could have influenced our results.

To investigate this issue, we performed a control experiment with twelve new participants (8 female) between 25 and 36 years. The experimental setup and the task instructions were as before except that participants wore a blindfold, and no TMS was applied. After an eight-trial familiarization phase, each participant performed 16 test trials, of which 8 were congruent (touch on the same finger of either hand), and 8 were incongruent (touch on different fingers). Touches on the left and right hands were independently randomized and equiprobably divided between D3 and D4.

Results

No adverse effects of TMS were noted, and no participant reported discomfort due to TMS.

We first checked whether each participant showed a visual-tactile congruence effect. This screening procedure follows directly from the design of our study. Only if a congruence effect is present one can investigate how disrupting rTPJ would modulate this effect. We checked for presence of a congruence effect by investigating whether each participant had greater accuracy and/or faster responses on congruent than incongruent trials (see Maravita et al. 2003) in the sham TMS condition. Two out of our fourteen original participants failed to show a numerical congruence effect both in RTs and in accuracy. We could not therefore disrupt congruence effects in these participants. Therefore, their data were excluded, and subsequent analyses used only the 12 participants in whom visual-tactile congruence effects were found.

Visual frequency judgments

The number of touches to D3 and D4 on the visible right hand was varied across blocks (see methods). By asking participants, which finger on the right hand was touched more frequently in each block, we could assess participants' visual processing. The remaining twelve participants provided at least three correct responses over the four blocks (mean accuracy = 87.5% correct), which was well above the chance level of 50%: $t(11) = 23.22$, $P < .0001$. For these 12, frequency judgments were identical in the TMS and sham conditions (78.5 vs. 78.5% correct), $t(11) = 0$, suggesting that rTPJ TMS did not impair the perception of visual stimuli as such. Thus, these participants did process the congruent and incongruent visual information from the right hand and did so equally in both TMS conditions. Any effect of rTPJ TMS cannot therefore be attributed to impaired unimodal visual perception or attention.

Tactile judgements

Mean accuracy and RT data for judgments of touch on the left hand from the twelve participants were then subjected to a 2 × 2 × 2 repeated-measures analysis of variance (ANOVA) with factors TMS condition (TMS and sham), Left Finger (D3 and D4) and Visuo-tactile Congruence (Congruent vs. Incongruent).

Accuracy

There was a significant main effect of Congruence, $F(1,11) = 8.250$, $P < .02$, $\eta_{\mathrm{p}}^{2} = .43$, with the mean percentage of correct responses being higher on congruent (93%) than incongruent (70%) trials. This result is unsurprising, given the exclusion criteria earlier. There was a significant three-way interaction between TMS condition, Finger and Congruence, $F(1,11) = 5.142$, $P < .05$, $\eta_{\mathrm{p}}^{2} = .32$ (Fig. 2). Post hoc comparisons (LSD Fisher's test, $\alpha \leq .05$) revealed no difference between fingers D3 and D4 on congruent trials, in either TMS or sham conditions (all Ps > .38). When vision and touch were incongruent, tactile judgments were better for D3 than for D4 during sham stimulation ($P = .02$). Compared with this condition, rTPJ TMS significantly improved the tactile judgments on D4 ($P = .01$), whereas it did not influence the performance on D3

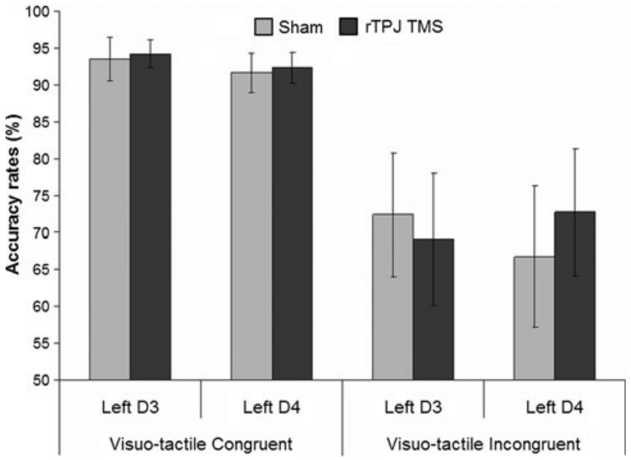

Fig. 2 Accuracy (% of correct responses) of tactile judgements as a function of TMS condition, target stimulus location (middle finger, "D3", and ring finger, "D4") and visuo-tactile congruence. Note that TMS improved the performance for D4 in incongruent trials and eliminated the performance difference between fingers. *Vertical bars* show the standard error of the mean

($P = .14$). Thus, the three-way interaction occurred because TMS improved performance only for D4 and only on incongruent trials. This differential effect of TMS on D3 and D4 resulted in the abolition of any performance difference between fingers ($P > .1$). To directly test the hypothesis of finger-specificity, we also compared the D3–D4 difference in the incongruent condition in sham TMS with that in rTPJ TMS. This test showed a trend for rTPJ TMS to reduce finger-specificity, $t(11) = 1.88$, $P = .08$. This suggests that rTPJ TMS may have abolished the gradient of performance between fingers and, therefore, the finger-specificity of performance (see the "Discussion"). To further test the hypothesis of finger-specificity, we also compared the D3–D4 difference in the incongruent condition in sham TMS with that in rTPJ TMS. This test showed a trend for rTPJ TMS to reduce finger-specificity, $t(11) = 1.88$, $P = .08$. This suggests that rTPJ TMS may have abolished the gradient of performance between fingers and, therefore, the finger-specificity of performance (see the "Discussion"). No other ANOVA effect or interaction approached significance (all Ps > .1).

Reaction times

Reaction times (RTs) were computed using a threshold corresponding to the 50% of the maximum acoustic energy peak of each response. This criterion gives RTs that are less affected by environmental noise variation than onset detection. The correlation between the RTs obtained algorithmically and the onset of 20 random vocal response traces obtained by manual inspection was highly significant ($r(19) = .95$, $P < .0001$).

Error trials (19.8%) and trials with RTs more than two SDs from the individual mean of each condition (4.78% of correct responses) were excluded from the analysis. ANOVA revealed a main effect of Congruence, $F(1,11) = 4.61$, $P = .05$, $\eta_p^2 = .30$. Responses were faster when vision was congruent with touch than when it was incongruent, which is unsurprising given our selection criteria. There was a significant interaction between TMS condition and Congruence, $F(1,11) = 5.720$, $P < .03$, $\eta_p^2 = .34$ (Fig. 3). Post hoc comparisons (LSD Fisher's test, $\alpha \leq .05$) revealed that participants responded faster when vision and touch were congruent than when they were not. This effect was significant both in sham and in TMS conditions (Ps < .0001). However, post hoc comparisons also showed that RTs were significantly slower after TMS than sham stimulation on congruent trails ($P = .01$), but not on incongruent trials ($P = .6$). That is, TMS had a stronger impact on congruent than incongruent trials. To further investigate this, we performed a two-tailed t test to compare the size of the congruence effect in TMS and sham, computed as the difference between incongruent and congruent trials. The size of congruence effect resulted significantly reduced following rTPJ TMS, $t(11) = 2.39$ $P < .03$, confirming that TMS delivery to rTPJ reduced the advantage of congruent over incongruent trials. There were no other significant effects.

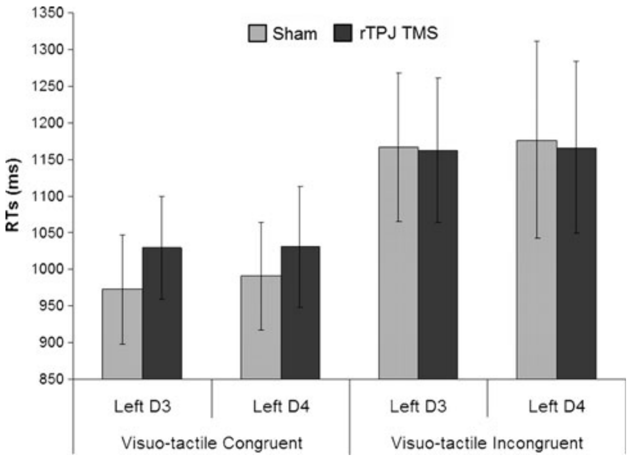

Fig. 3 RTs (ms) as a function of TMS condition, target stimulus location (middle finger, "D3", and ring finger, "D4") and visuo-tactile congruence. TMS over rTPJ reduced congruence effect relative to sham. *Vertical bars* show the standard error of the mean

Finally, we investigated whether the three-way interaction between TMS condition, Finger and Congruence found for accuracy data could reflect a speed-accuracy trade-off. In fact, the three-way interaction for RTs was far from significance $F(1,11) < 1$ and was opposite to what would be predicted by a speed-accuracy trade-off. In particular, we checked that the TMS-related improvement in accuracy for D4 stimulation on incongruent trials was not associated with slower RTs. In fact, tactile judgments for D4 were 10 ms faster in TPJ TMS than sham. This difference did not approach significance $t(11) = .007$, $P > .1$.

Tactile–tactile conflict: control experiment

In contrast to the main experiment, all participants were 100% accurate demonstrating that tactile–tactile conflict did not play a major role in the congruence effect we reported earlier. RTs were subjected to a 2 × 2 repeated-measures ANOVA with Left-hand Finger and Tactile–tactile Congruence as factors. No effect or interaction approached significance (all Ps > .14). The difference between congruent and incongruent conditions was far from significance (701 vs. 739 ms; $t(11) = .39$, $P > .1$) and numerically smaller than the differences found in the main experiment. This control experiment suggests that the tactile–tactile component of conflict is minimal and that the conflict effects found in our main experiment largely reflect visuo-tactile conflict.

Discussion

We designed an experiment involving a visuo-tactile conflict in which a touch was observed on one finger of what appeared to be the participant's left hand (actually the right hand viewed via a mirror), but was felt on a different finger of the left hand. This produced a mislocalization of tactile sensation from one finger to another in twelve of fourteen participants. We found clear effects of conflicting visual information on touch, in terms of both accuracy and RT: participants' tactile discrimination was dramatically reduced in incongruent relative to congruent condition. Application of single-pulse TMS to the rTPJ reduced the effects of conflicting visual information on touch. When conflicting visual and tactile stimulations were provided during sham TMS, tactile judgments were more accurate for D3 than for D4. In the same incongruent condition, rTPJ TMS improved the accuracy of judgments on D4, but not on D3, resulting in comparable performance for both fingers. Moreover, rTPJ TMS reduced the congruence effect for RT. These results suggest that the rTPJ is involved in the detection, rather than in the resolution, of intersensory conflict. Performance on an additional visual judgment on each block ruled out the possibility that rTPJ TMS simply attenuated visual processing, and a control experiment ruled out the possibility that rTPJ TMS simply affected tactile–tactile integration between the two hands.

These findings reveal three aspects of visuo-tactile conflict. First, visual and tactile stimuli appearing simultaneously and spatially close on a participant's body, can give rise to congruence effect, even when participants are aware of the potential conflict between them (see Rock and Victor 1964). Previous multisensory studies showed that integration between two sensory modalities is strongly temporally (Shore et al. 2005; Spence et al. 2003; Yamamoto and Kitazawa 2001) and spatially dependent (Spence et al. 1998; Pavani et al. 2000). In our study, visual-tactile integration is defined over very specific body parts that lie very close together in external space, their spatial disparity being no more than the few centimeters separating D3 and D4. Second, under these circumstances, vision has greater weight than touch. Both observations confirmed the reported effects of visual dominance in perception (see Spence 2009 for a recent review and discussion). Indeed, attention may be strongly biased by vision that information occurring from other modalities may be prevented from reaching awareness (Posner et al. 1976). However, rather than a visual bias in attention, the visual dominance may reflect a preferential weighting on the sensory modality that provides the most accurate (Ernst and Banks 2002) and stable information (Harris 1965) in spatial discrimination tasks. The results of the present study also extend previous research by showing that, though vision may dominate over touch, this relationship varies with the location of touch: the visual effect was stronger for tactile judgments on D4 than on D3.

Several lines of evidence suggest that D3 has a more clearly defined neural representation than D4. Finger gnosis studies suggested that D4 has the weakest individual representation of all the fingers (Benton 1959). Similarly, there is a decreasing gradient from the index to little fingers both in cortical magnification (Duncan and Boynton 2007) and in tactile acuity (Vega-Bermudez and Johnson 2001). The relatively weak representation of D4 may therefore explain why it was more affected by intersensory conflict than D3. Weak signals are generally more subject to interference than stronger signals. More specifically, multisensory effects may be stronger for stimuli close to perceptual threshold than for those well above threshold (Stein and Meredith 1993). Equally, the principle of optimal multisensory integration (Ernst and Banks 2002) would suggest signals from D4 are given a low weighting in visuo-tactile integration, because of their low reliability.

As might be expected, therefore, the two fingers were indeed differently affected by TMS: the effect of rTPJ TMS on accuracy appeared to be limited to D4, without apparent effect on D3. Specifically, during rTPJ TMS, performance on tactile discrimination *improved* on incongruent trials, i.e., when the target touch was on D4 but participants saw touch on D3. This result suggests that rTPJ TMS may have prevented incongruent visual information from affecting or dominating tactile judgments. Intriguingly, the TMS-induced improvement of performance may also relate to Collins et al. (1997) findings that human perception of weak (subthreshold) tactile stimuli can be enhanced by introducing a particular level of noise. The lack of a similar result for D3 may be the consequence of the better tactile discrimination on this finger. Task-irrelevant vision might then have less effect, in both sham and rTPJ TMS conditions. Our finger-specific effect could therefore arise from differences in the tactile signal strength and/or reliability from different skin regions.

We focused on D3 and D4 because they are spatially adjacent, because they form the most visually similar digit pair and the most easily confused in tactile localization (Mayer et al. 1999; Kinsbourne and Warrington 1962). Thus, we anticipated stronger visuo-tactile conflict for this pair than for other finger pairs. Testing just one finger pair clearly limits our ability to generalize to other fingers and body parts. However, if our interpretation based on strength and reliability of tactile signals in visuo-tactile conflict is correct, then the TMS-induced improvement of performance in conflict conditions should be found for other body parts as well as D4, under appropriate circumstances. For example, using a more difficult localization task, adaptive matching of stimulus detectability across skin regions, providing stronger visual interference, or more disruptive TMS should all boost the effect we have observed for D4, and could demonstrate the effect on other body parts. Future research could systematically investigate the relationship between tactile sensitivity, somatosensory representation and susceptibility to intersensory conflict, and the role of TPJ in visual-tactile interactions.

Before considering further implications of these data, one possible confound needs to be discussed. TMS might simply have impaired the detection of *visual* stimuli (i.e. the view of the right hand in the mirror), rather than affecting visuo-tactile conflict as such. However, there are several reasons to reject this explanation. First, TMS differentially affected D3 and D4. This difference cannot be explained by any plausible selective impairment of visual processing, but it can be explained by their known somatosensory properties. Second, post-block frequency judgments provide a direct test of detection of and attention to the visual stimuli. Frequency judgments were equally accurate in both conditions, suggesting no visual impairment due to rTPJ TMS. One might wonder whether these frequency judgments were truly visual, or whether they could have been influenced by touches on the right hand. Our main experiment showed that touch was strongly biased by vision, suggesting that visual frequency judgments were unlikely to be influenced by touch.

The performance improvement on incongruent trials suggests that rTPJ TMS prevented incongruent visual information from affecting tactile judgments. This diminished effect of vision on touch is unlikely to reflect a mere weakening of visual sensation. Studies of rTPJ's role in the visual pathways suggest that, while it does respond to visual stimulus, it is not concerned with simple transmission of information along the early stages of the primary visual pathway (Lewis et al. 2000). Therefore, rTPJ disruption is unlikely to produce a simple global attenuation of visual sensation. These results are rather consistent with the proposal of Corbetta and colleagues that rTPJ serves a "circuit-breaking" function, interrupting ongoing cognitive activity in response to salient sensory stimuli (Corbetta and Shulman 2002). Consistently with this model, the rTPJ is recruited during the detection of salient and unexpected events in the space, independently of their location (Corbetta et al. 2002), sensory modality (Downar et al. 2000) and response demands (Astafiev et al. 2006). Moreover, lesions in the rTPJ are associated with spatial neglect of the left side of body (Mort et al. 2003) and external space (Vallar 2001; Friedrich et al. 1998). Accordingly, rTPJ TMS was found to provoke an extinction-like behavior in the contralateral hemifield confirming a functional involvement in visual attention (Meister et al. 2006). In the case of our study, visual information about the apparent location of touch would activate the circuit-breaker, and, when it is incongruent, would interfere with tactile localization. rTPJ TMS reduced this visual intrusion, and thus prevented visual conflict from interfering with tactile localization.

That TMS reduced the magnitude of congruence effects on RTs further supports this view. rTPJ TMS slowed RTs relative to sham when vision and touch were congruent, as though the beneficial effect of congruent vision on touch (e.g., Press et al. 2004) was attenuated. Although this effect is selective for congruent—but not incongruent—trials, the pattern of RTs does not simply reflect a speed-accuracy trade-off given with the increased accuracy for D4 in incongruent trials. According to the role of rTPJ in stimulus-driven attention discussed earlier, our RT result suggests that TPJ might mediate the detection of *any* novel sensory stimulus requiring a shift of attention, whether or not it matches the currently attended stimulus. The pattern of RT results would then reflect a general attentional salience function of rTPJ, while the accuracy results would reflect a more specific multisensory integration function, which is the focus of our interest here. However, RTs and accuracy results are partial, in that the RT effects concern only congruent trials and the accuracy effects concern only incongruent trials. Congruent trials make less demand on the attentional/monitoring system because no conflict is perceived. In this sense, the visual enhancement of touch appears as more automatic than the visuo-tactile conflict processing. Evidence suggests that when the task requires more attentional control, people benefit from accuracy instructions, whereas they benefit from speeded instructions in more automatic task conditions (e.g., Beilock et al. 2002, 2004). This might establish a specific relationship between accuracy and attention-demanding conditions and between RTs and automatic task conditions. Accuracy would be more sensitive to the behavior in attention-demanding conditions and RTs would be more susceptible to performance in more automatic task conditions. Taking this as a tentative explanation, we will return later to the theoretical issue of whether these diverse effects mean that rTPJ co-houses several independent cognitive modules, or whether a single general processing mechanism might underlie several apparently different cognitive functions.

To recap, we observed that TMS to rTPJ reduced the congruence effect both for accuracy and for RTs, though in different ways. TMS eliminated the interfering effect of an incongruent visual feedback on tactile judgments in accuracy, but reduced the facilitating effect of congruent stimuli on RTs. These effects are both consistent with a role of rTPJ in the *detection* of intersensory conflict. The role of rTPJ in conflict detection could result from a general involvement of this area in processing unexpected or novel stimuli. An alternative hypothesis suggests that rTPJ *resolves* intersensory conflicts. Importantly, resolving conflict implies reducing the interference of incongruent visual and tactile information, and thus reducing the congruence effects. Therefore, disrupting a brain area that performs congruence resolution should *increase* congruence effects. In fact, we found that rTPJ TMS produced the opposite result, since it reduced congruence effects. Put in another way, if TPJ subserved conflict resolution, then rTPJ TMS would have led to a failure of integration of incongruent visual information, and tactile localization should have been impaired. In fact, tactile localization was improved under these conditions. We investigated the involvement of TPJ in the right hemisphere only, because the literature strongly suggests a right hemisphere specialization for spatial processing and a specific role of rTPJ in multisensory processing. Left temporoparietal regions may also be involved in multisensory processing of right-sided bodily information (e.g., Li et al. 2007). This leaves open the possibility that the intersensory conflict detection is not confined to the TPJ in the right hemisphere.

rTPJ TMS also had the interesting result of abolishing the normal gradient of performance between fingers (see accuracy results), as if disrupting rTPJ activity eliminated the specificity of different body parts. This might be a mere epiphenomenon of difference between D3 and D4 innervation, with weaker tactile representation of D4 resulting in greater susceptibility to incongruent visual information for this digit. However, it could also reflect a role for rTPJ in maintaining a mental representation that distinguishes between body parts. This is suggested by our finding that rTPJ TMS tended to reduce finger-specificity. Tsakiris et al. (2008) showed that TMS to rTPJ impaired the distinction between corporeal and non-corporeal objects, as if TMS altered the internal model of one's body that distinguishes between one's own body and the external world. By extension, rTPJ may distinguish between one's own and another's body (Decety and Sommerville 2003). The abolition of performance difference between fingers in our experiment suggests that such body representations not only distinguish *between* self and non-self but also distinguish individual parts *within* one's own body. There is evidence for direct connections from sensory areas to the rTPJ (e.g., see for evidence on monkeys, Lewis and van Essen 2000; for evidence on humans, Mesulam 1998). These could maintain body-part specificity within TPJ and explain our finger-specific effects.

Theories of self-representation in the TPJ have proposed *test-for-fit* mechanisms, in which external stimuli are compared to internal predictions (Decety and Lamm 2007). This theory has been applied to body representation (Tsakiris et al. 2008), attention (Shulman et al. 2007) and, as suggested by Decety and Lamm (2007), can also explain the involvement of rTPJ in high-level social cognition. The circuit-breaker situation would be a special case in which a novel sensory input does not fit with current predictions, and the test-for-fit therefore fails. Thus, the specific effect of body-related conflict studied here is consistent with a general involvement of the rTPJ in integrating multisensory inputs, to form coherent predictions and representations both about the body and about the world.

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