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Report

The Posterior Parietal Cortex Remaps Touch into External Space

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Summary

Localizing tactile events in external space is required for essential functions such as orienting, haptic exploration, and goal-directed action in peripersonal space. In order to map somatosensory input into a spatiotopic representation, information about skin location must be integrated with proprioceptive information about body posture [1, 2]. We investigated the neural bases of this tactile remapping mechanism in humans by disrupting neural activity in the putative human homolog of the monkey ventral intraparietal area (hVIP), within the right posterior parietal cortex (rPPC), which is thought to house external spatial representations [3, 4]. Participants judged the elevation of touches on their (unseen) forearm relative to touches on their face. Arm posture was passively changed along the vertical axis, so that elevation judgments required the use of an external reference frame. Single-pulse transcranial magnetic stimulation (TMS) over the rPPC significantly impaired performance compared to a control site (vertex). Crucially, proprioceptive judgments of arm elevation or tactile localization on the skin remained unaffected by rPPC TMS. This selective disruption of tactile remapping suggests a distinct computational process dissociable from pure proprioceptive and somatosensory localization. Furthermore, this finding highlights the causal role of human PPC, putatively VIP, in remapping touch into external space.

Results and Discussion

Participants sat with their left arm suspended in a sling and oriented vertically, lateral to the face. They judged whether a brief tap at one of seven locations on the left forearm was higher or lower than a preceding tap at one of five locations on the face (see Figures 1A and 1B). Single-pulse transcranial magnetic stimulation (TMS) was applied over the putative human homolog of macaque ventral intraparietal area (hVIP) [5] in the right posterior parietal cortex (rPPC) (Montreal Neurological Institute coordinates: x = 26, y = −58, z = 43; see the Supplemental Experimental Procedures available online for localization details) or over a control site (vertex), either 60 or 250 ms after the touch on the arm. The participant's arm was passively moved between three positions along the vertical axis so that integration of skin location information (touch) and posture of the arm in space (proprioception) was required to compare tap elevations. We use the term "tactile remapping" to refer to the process whereby these two sources of information are integrated to achieve a representation of touch in terms of external space (see Figure S1 for a photograph of the setup).

Some previous studies have investigated the neural correlates of spatial remapping with tactile stimuli alone [5], but mostly focusing on the distribution of tactile spatial attention [6, 7]. However, most studies of tactile remapping in spatial perception have also involved vision. Thus, studies in animals have identified single neurons in parietal cortex that respond to both visual and tactile stimuli [8]. The visual receptive fields of such neurons track both movements of the hands through space [9] and also changes in body representation linked to tool use [10]. Human studies have also demonstrated strong visuotactile spatial interactions [11–13].

Our study focused on the remapping of spatial perception from a somatotopic to an external reference frame [2, 14, 15], but confined to the somatosensory system alone. This external reference frame is critical for rapidly attending to or directing actions in peripersonal space toward objects impinging on the body. Indeed, humans and animals can quickly orient toward their body parts across postural changes, even in the absence of vision, for example when swatting a mosquito on one's skin in darkness. This observation suggests that spatial remapping can occur within somatosensory systems, as well as with reference to vision.

We investigated whether the PPC, specifically area hVIP, is causally involved in tactile remapping. The proportion of trials in which the arm tap was judged as higher than the face tap across different vertical disparities was fitted with logistic functions to each participant's data. Two parameters were extracted: the just-noticeable difference (JND), a measure of spatial precision calculated as the semi-interquartile range, and the point of subjective equality (PSE), a measure of bias that corresponds to the point of perceived alignment between the two stimuli. We expected that disruption of tactile remapping would reduce precision, resulting in an increased JND.

The results confirmed a 20% decrease in precision (i.e., increase in JND) following TMS over rPPC compared to vertex (6.18 versus 5.19 cm; $F_{1,14} = 7.32$, $p < 0.02$; Figure 1C; Table 1). Thus, TMS over the right parietal cortex, at the putative human homolog of monkey VIP, impaired tactile judgments based on external space, suggesting a causal role of this area in the remapping of touch. The time interval between touch and TMS pulse had no effect within the range tested ($F_{1,14} = 0.80$, $p = 0.38$), nor did it interact with TMS site ($F_{1,14} = 0.37$, $p = 0.55$; Figure 1D).

Furthermore, the PSE data revealed an overestimation of the perceived height of touches on the arm versus the face at short compared to long TMS intervals (main effect of interval; $F_{1,14} = 16.64$, $p = 0.001$) but irrespective of TMS site (interaction; $F_{1,14} = 0.33$, $p = 0.57$). Interestingly, stimulation site exerted a robust main effect (observed in all participants), with TMS over rPPC making participants underestimate the height of

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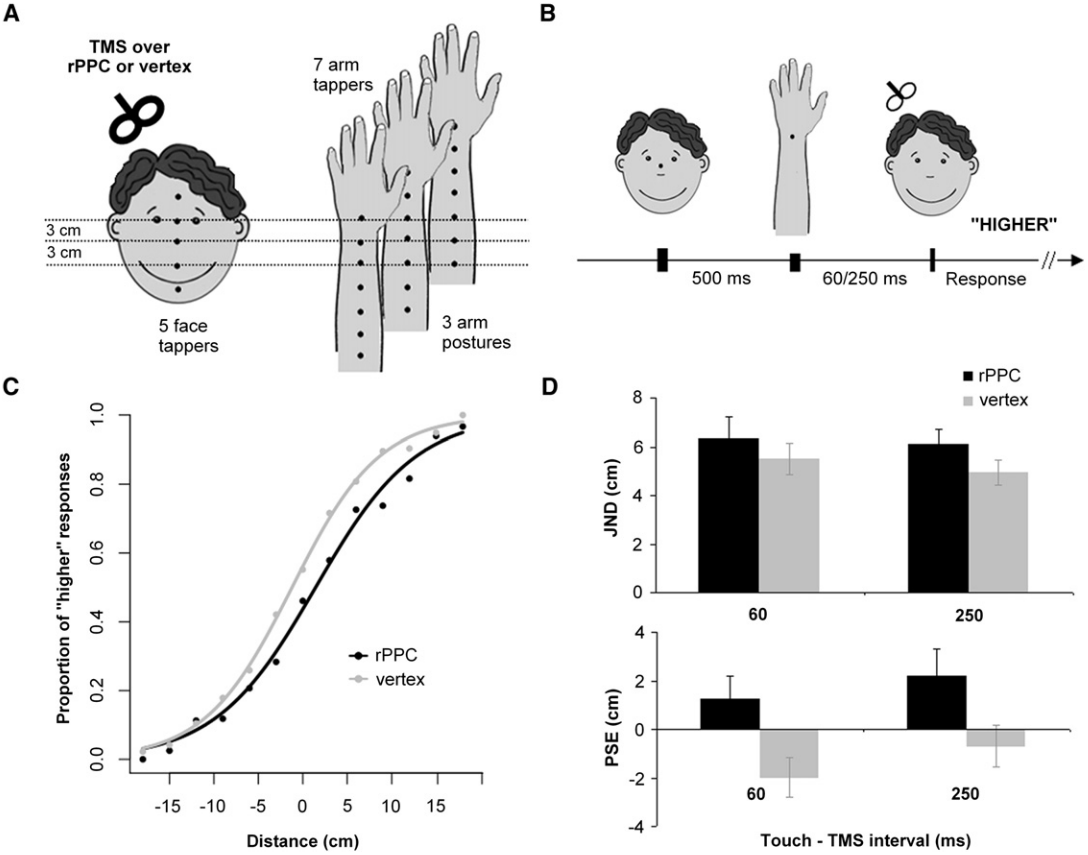

Figure 1. Experimental Setup, Trial Sequence, and Results of the Main Experiment

(A) Schematic (frontal) view of the setup used in the main experiment. The participant's left forearm was supported vertically by a sling hanging from one of three hooks in the wall (at three different heights, in 6 cm steps) and was passively moved every eight trials to one of the vertical positions. The arm was held to the left of the head and kept out of sight by a curtain. Tactile stimulation (stimulation sites shown as black dots in the figure) was delivered to one of five locations at the face (two of which were fillers, i.e., only 12.5% of trials, not analyzed) and from one of seven locations on the dorsal surface of the forearm (vertically aligned, at 3 cm intervals). The disparity between face and arm stimulation sites ranged from +18 cm (arm tap above face tap) to −18 cm (arm tap below face tap). The two extreme face tap locations (the highest, at the forehead, and the lowest, at the chin) were included as fillers to prevent biases induced by extreme locations at the ends of the stimulation range (i.e., to judge the tap following the lowest face location as "higher" and vice versa) in responses to the locations of interest.

(B) In each trial, a 30 ms touch was delivered at the face followed by another 30 ms touch at the forearm (stimulus site varied randomly on a trial-by-trial basis), with a 500 ms interstimulus interval (chosen to avoid confusions of temporal order between the touches [2]). After the onset of the arm tap (either 60 or 250 ms, equiprobable and random), a single transcranial magnetic stimulation (TMS) pulse was applied over the right posterior parietal cortex (rPPC) or vertex (in different blocks, order counterbalanced between participants). Participants made speeded judgments (i.e., were asked to respond as quickly as possible, though accurately) of whether the tap on the arm was higher or lower than the one on the face, responding by index and middle finger keypresses with the right (dominant) hand. An intertrial interval of 3 s led to the next trial. The experimental session included two blocks (rPPC and vertex TMS) of 288 trials (including 36 arm position changes) separated by a 5 min break.

(C) Interparticipant mean proportion of "higher" responses as a function of tap disparity (dots). The logistic fits (lines) to the group average data are shown for reference. The black line and symbols represent data from the rPPC TMS condition; the gray line and symbols represent data from the vertex control TMS condition. Eighteen female volunteers were tested (mean age 25 years, standard deviation 4.20 years). Data from three participants were excluded on the basis of poor model fit ($R^2 < 0.7$) or an outlier rejection procedure (extreme studentized deviate method [38]).

(D) Mean just-noticeable difference (JND, top panel) and point of subjective equality (PSE, bottom panel). Black bars represent data from the rPPC TMS condition; gray bars represent data from the vertex control TMS condition. Error bars represent standard error of the mean. See also Figures S1 and S2.

touches on the arm compared to vertex (PSE = +1.73 cm versus −1.32 cm, respectively; $F_{1,14} = 26.66$, $p < 0.001$; Figure 1D; Table 1). This PSE shift was not due to proprioceptive interference, because a control experiment (reported below) revealed no loss of proprioceptive acuity about arm position following rPPC TMS. This underestimation of the height of arm taps could suggest that rPPC disruption caused the online postural schema [16, 17], based on current proprioceptive information, to revert toward a "default posture," in which the arms are represented in their canonical position below the face (i.e., with arms at their anatomical side and the shoulder and elbow joints midway though their range of flexion [18]). We speculate that this default posture operates in the absence of other information, for example when remapping has not yet had time to complete [19] or is disrupted (this study). Postural schema and canonical posture would therefore play roles similar to "current evidence" and "prior probability" terms, respectively, in Bayesian models of skilled motor control [20].

Analysis of reaction times (RTs) did not reveal any significant main effects (vertex: 603 ms; rPPC: 589 ms; all $p > 0.7$; Table 1) or interactions, suggesting that differences in accuracy between conditions did not reflect speed/accuracy tradeoffs.

Table 1. Interparticipant Mean JND, PSE, and RT in the Main Experiment and Controls

	rPPC-hVIP			Vertex		
	JND	PSE	RTs	JND	PSE	RTs
Main experiment	6.18 (0.7)*	1.73 (1.0)**	589 (27)	5.19 (0.6)	−1.32 (0.8)	603 (33)
Proprioceptive control	1.69 (0.2)	−2.85 (0.3)	–	1.56 (0.1)	−2.91 (0.4)	–
Localization control (arm)	2.23 (0.5)	0.16 (0.6)	575 (58)	2.64 (0.5)	0.78 (0.6)	594 (65)
Localization control (face)	1.23 (0.3)	−0.52 (0.3)	551 (41)	0.92 (0.3)	0.05 (0.3)	560 (56)

Just-noticeable difference (JND) and point of subjective equality (PSE) values are given in cm; reaction time (RT) values are given in ms. The interparticipant standard error of the mean is shown in parentheses. *$p < 0.05$, **$p < 0.001$ between right posterior parietal cortex (rPPC) and vertex conditions for JND, PSE, and RTs by two-tailed t test.

Although these results are consistent with selective disruption of tactile remapping after rPPC TMS, they could also result from disruption either of tactile localization on the skin or of proprioception. It may seem unlikely that single-pulse TMS could disrupt a perceptual process such as proprioception in which many afferent signals are tonic and continuously present. Indeed, repetitive TMS over PPC in a previous study proved ineffective in disrupting proprioception [21]. Nevertheless, we conducted a control experiment to test for any potential effects of rPPC single-pulse TMS on proprioceptive localization of the arm in space. Participants judged whether their right hand was higher or lower than their left. The participant's left arm was passively moved as in the main experiment while the right arm was moved, above or below the left arm, before each trial (see Figure 2A for details). TMS was applied immediately after each right arm movement. rPPC TMS had no effect on either JND ($F_{1,13} = 0.63$, $p = 0.44$) or PSE ($F_{1,13} = 0.03$, $p = 0.86$), confirming that the perceived position of the arm in space was unaffected by TMS (Figure 2D; Table 1).

We conducted two further control experiments to isolate potential disruption of tactile localization on the skin. In the first, we adapted the paradigm used in the main experiment to measure participants' judgments of relative elevation of two touches applied within a single body part, either the left forearm or the face (see Figures 2B and 2C for details), rather than between body parts. Thus, the position of each body part in space was irrelevant and the task could be performed based entirely on tactile localization on the skin surface (thus, regardless of whether or not remapping occurred). Given the lack of any effect of TMS timing in the main experiment, TMS was applied always 60 ms after the onset of the first tap. No differential effect of stimulation site was observed on either JND (arm: $F_{1,8} = 1.01$, $p = 0.35$; face: $F_{1,8} = 1.61$, $p = 0.24$) or PSE (arm: $F_{1,8} = 1.55$, $p = 0.25$; face: $F_{1,8} = 1.62$, $p = 0.24$) in the arm or face sessions (Figures 2E and 2F; Table 1). Analyses on RTs revealed no effect of TMS (all $p = 0.8$; Table 1). This finding suggests that the effect of rPPC TMS observed in the main experiment did not result from disruption of tactile localization as such, or from any ancillary requirement of the elevation comparison task. Whereas overall performance level in the control tasks was somewhat higher than in the main task, additional analyses (see Supplemental Experimental Procedures) showed no relation between TMS effects and overall performance levels (Figure S2).

To investigate further whether rPPC TMS might cause subtle deficits in tactile localization missed by our forced-choice elevation comparison task, we ran a second control using a more sensitive assessment of tactile localization [22]. Participants marked the perceived location of single taps (at the forearm locations used in the main experiment) on a schematic drawing of a forearm. TMS was applied 60 ms after touch onset. For analysis, physical and judged stimulus locations were put into a common coordinate system, with units scaled to the length of each participant's forearm (Supplemental Experimental Procedures). To estimate the precision of tactile localization, we calculated variable error, analogous in this task to the JND parameter of the main experiment, as the average distance between the location of each individual judgment and the average location of all judgments of that stimulus location. Thus, if rPPC TMS disrupts tactile localization on the skin, variable error should increase. In fact, TMS site had no effect (both TMS conditions: 0.057, defined in arm-scaled units; $F_{1,8} = 0.005$, $p = 0.95$; Figure S3A), corroborating that precision of tactile localization was unaffected by TMS. We also measured localization bias, as constant error, calculated as the distance between the actual location of each stimulus on the arm and the average judgment of that stimulus location. There was no significant effect of TMS site (vertex: 0.136; rPPC: 0.138, defined in arm-scaled units; $F_{1,8} = 0.02$, $p = 0.89$; Figure S3C), further supporting the idea that tactile localization on the skin was unaffected by rPPC TMS (see Supplemental Experimental Procedures for additional analyses; Figure S3B). These data suggest that the decrease in precision and the shift in PSE observed in the main experiment following rPPC TMS did not result from alteration of the perceived location of touch on the skin.

PPC and the Remapping of Touch: Remapping as a Distinct Computational Step

The present results highlight the causal role of the PPC, putatively the VIP, in the spatial remapping of tactile events into an external frame of reference. Tactile remapping is a computational process involving integration of tactile localization on the skin with proprioceptive localization of body parts in space. Yet, rPPC TMS had no effect on either of these unimodal processes individually but had significant effects on the multimodal process of tactile localization in external space. In this sense, selective disruption with single-pulse TMS identifies the remapping process as a distinct, integrative computational step dissociable from the proprioceptive and somatosensory inputs on which it depends and further links this process to a specific cortical area.

Our results also show that remapping can be selectively disrupted up to 250 ms after tactile contact, suggesting that this process lasts for a relatively long period of time. Electrophysiological results show attentional modulations influenced by an external reference frame as early as 100 ms after touch [6], whereas behavioral findings prove that remapping is already completed by 200 to 360 ms [2, 13, 19, 23], although its exact duration is uncertain. That TMS applied 250 ms after touch could still disrupt remapping in our task suggests an upper temporal bound. Alternatively, tactile remapping could

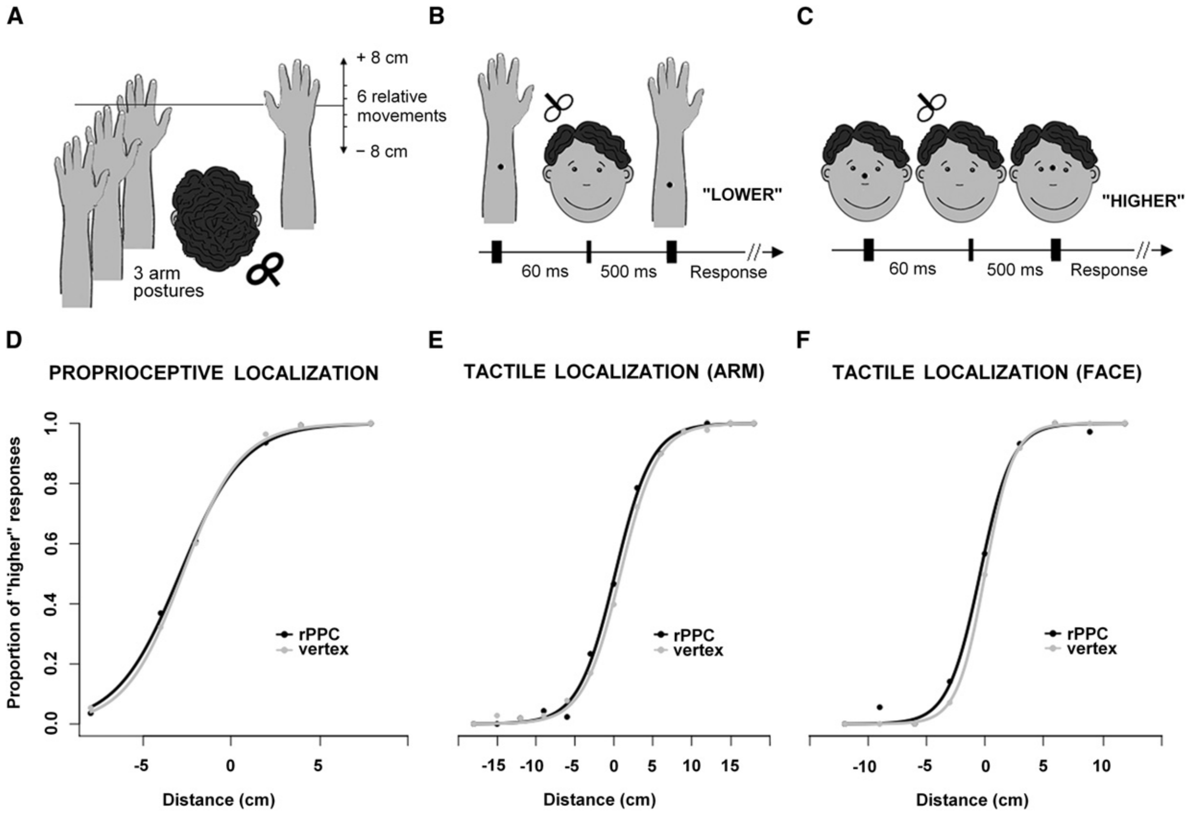

Figure 2. Setup and Results of the Control Experiments

(A) Proprioceptive control experiment. The left arm was passively moved between the three positions used in the main experiment while the right arm was moved in each trial to one of six locations above or below the left arm (±8 cm). Single-pulse TMS over the rPPC or vertex was applied immediately after the end of the right arm movement. Participants made verbal speeded judgments about the relative elevation of the tip of their right middle finger ("higher" or "lower") with respect to their left.

(B) Somatosensory localization control on the arm. Tactile stimulation was delivered at the dorsal surface of the forearm through two of seven solenoid tappers (arranged as in the main experiment). In each trial, two tactile stimuli (30 ms tap) were delivered at the forearm with an interstimulus interval duration of 500 ms (i.e., much longer than the intervals associated with apparent motion or cutaneous rabbit effects [39, 40]). A single TMS pulse was applied over the rPPC or vertex 60 ms after the onset of the first arm tap. The arm did not move relative to the face in either TMS condition. Participants made speeded judgments of whether the second tap was higher or lower than the first and responded by index and middle finger keypresses with the right (dominant) hand. Each participant performed one block of 49 trials per TMS condition (order counterbalanced).

(C) Somatosensory localization control on the face. The setup and procedure were identical to the arm localization experiment, except that tactile stimulation was delivered at the face through two of five solenoid tappers vertically aligned as in the main experiment.

(D–F) Interparticipant average proportion of "higher" responses as a function of stimulus disparity in each control experiment. Fourteen female volunteers participated in the proprioceptive control experiment (13 from the original sample; mean age 25 years, standard deviation 4.45 years), and nine participated in the tactile localization controls (7 from the original sample; mean age 26 years, standard deviation 4.65 years). Data labeling and statistical analysis conventions are as in Figure 1C. See also Figure S3.

be a fast but not self-terminating process. Namely, the results of remapping could be available quickly after touch but may need to be actively maintained. In that sense, TMS may have disrupted such sensory memory traces being held until response. Indeed, primary and secondary somatosensory cortices as well as premotor cortex are known to hold such traces [24, 25], so it is possible that circuits involving the hVIP engage in a similar process.

Our results are consistent with those of a previous study linking the PPC to spatial transformations between vision and touch [11]. In that study, the probability of reporting TMS-induced phosphenes was higher in the presence of concurrent tactile stimuli spatially aligned with the (putative) phosphene location, even with crossed hands. Critically, prior disruption of PPC by repetitive TMS reversed this spatially specific visual enhancement, so that tactile facilitation of visual detection was instead observed at the anatomically congruent hand location. However, because that study focused on visuotactile interactions and the large spatial realignment generated by crossing the hands, it remained unclear whether the area stimulated housed a general, supramodal module for tactile remapping, used also for proprioceptive-tactile interactions. Our results substantially extend findings based on crossmodal interactions [11, 12] by showing that processing in hVIP not only is involved in multisensory visuotactile integration [8, 26, 27] but plays a role in the transformation and realignment of tactile representations based on somatic spatial information more generally.

Neural Bases of Tactile Remapping

We targeted the coordinates identified by Lloyd et al. [5] as the human homolog of macaque area VIP (Supplemental Experimental Procedures), a region associated with multisensory representations of limb position. VIP houses multisensory coding of stimulus motion direction [27, 28] and location in space [3, 4] that define peripersonal space [27]. However, evidence for direct proprioceptive encoding in monkey VIP is modest, although some VIP neurons respond to joint rotation [27]. This suggests that the integration of touch and proprioception required for tactile remapping might involve a network of several structures. For example, area 5 encodes arm location in a body-centered coordinate system [29, 30], and its projections to the fundus of the intraparietal sulcus are known [27, 31, 32]. Thus, tactile location information (either directly from primary somatosensory cortex or via somatosensory association areas [33]) and proprioceptive information from area 5 may converge in hVIP, providing the two necessary inputs for tactile remapping [34]. Note, however, that it is unlikely that the TMS applied in our study affected area 5 directly, because we observed no disruption of purely proprioceptive judgments.

Categorical Remapping into Left/Right Hemispace

Most previous studies of tactile remapping, and indeed of multisensory attention in general, have focused (explicit or implicitly) on categorical left/right divisions of space involving touches to both hands placed in different hemifields [14, 15, 35]. Indeed, remapping has often been operationalized as an effect of crossing the hands on tactile processing. However, crossing the hands may involve a process of remapping quite different from much smaller spatial displacements within one hemispace [36], as reflected in the reduced effects observed in the latter [7, 37]. Our results confirm that PPC can process spatial transformations involving a single hemispace and provide further evidence that remapping is a general perceptual process, not limited to the specific case of crossing the body midline.

Conclusions

This study provides direct evidence for a causal role of human PPC, in particular the putative human homolog of macaque area VIP, in remapping touch from a somatotopic to an external spatial frame of reference. In our study, remapping could be dissociated from both pure tactile localization on the skin and proprioceptive information about limb position. Remapping therefore involves not only integration between these sensory inputs but also a core spatial transformation that establishes a common external representation for perception and action. In our task, neither the tactile-proprioceptive integration nor the resulting external spatial representation required any explicit (online) visual component. To that extent, our findings suggest a representation of external space that is multisensory in origin but also amodal in character.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.05.063.

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