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Tactile–visual integration in the posterior parietal cortex: A functional magnetic resonance imaging study

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Abstract

To explore the neural substrates of visual–tactile crossmodal integration during motion direction discrimination, we conducted functional magnetic resonance imaging with 15 subjects. We initially performed independent unimodal visual and tactile experiments involving motion direction matching tasks. Visual motion discrimination activated the occipital cortex bilaterally, extending to the posterior portion of the superior parietal lobule, and the dorsal and ventral premotor cortex. Tactile motion direction discrimination activated the bilateral parieto-premotor cortices. The left superior parietal lobule, intraparietal sulcus, bilateral premotor cortices and right cerebellum were activated during both visual and tactile motion discrimination. Tactile discrimination deactivated the visual cortex including the middle temporal/V5 area. To identify the crossmodal interference of the neural activities in both the unimodal and the multimodal areas, tactile and visual crossmodal experiments with event-related designs were also performed by the same subjects who performed crossmodal tactile–visual tasks or intramodal tactile–tactile and visual–visual matching tasks within the same session. The activities detected during intramodal tasks in the visual regions (including the middle temporal/V5 area) and the tactile regions were suppressed during crossmodal conditions compared with intramodal conditions. Within the polymodal areas, the left superior parietal lobule and the premotor areas were activated by crossmodal tasks. The left superior parietal lobule was more prominently activated under congruent event conditions than under incongruent conditions. These findings suggest that a reciprocal and competitive association between the unimodal and polymodal areas underlies the interaction between motion direction-related signals received simultaneously from different sensory modalities.

Keywords: Crossmodal; Functional magnetic resonance imaging; Motion direction; Superior parietal lobule

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1. Introduction

Visual motion has been shown to strongly influence tactile motion judgments [5,17]. When visual motion was presented simultaneously but in the opposite direction to tactile motion, the accuracy of the tactile motion judgments was substantially reduced [17]. This decline in performance was observed when the visual display was placed either near to or at a distance from the tactile display. The extent of the effect decreased as the degree of misalignment increased [17]. A substantial effect of visual motion that was dependent of the relative direction of the motion was beyond a general visual motion effect [17]. This direction-specificity means that a general perceptual conflict is unlikely to be the cause of the interference, and instead suggests that crossmodal interaction occurs during motion direction judgment [17]. However, the neural substrates for this remain largely unknown [5].

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Crossmodal motion direction discrimination requires both the coding of motion in the two sensory modalities and a decision stage that compares the two motion direction signals. Crossmodal interference could thus occur at either stage. One candidate locus for the integration of visual and tactile motion information during the coding stage is the human middle temporal (MT)/V5 area [5]. According to visual mediation heuristics [47], tactile inputs are translated into their corresponding visual representations (visually based imagery), which are further processed by the visual system. Recent neuroimaging studies have reported that tactile motion perception tasks activate the part of the MT/V5 area [6,34], independent of imagery of visual motion [4,60]. Thus, the activity observed in the MT/V5 area during tactile stimulation might reflect bottom-up sensory input or a top-down cognitive strategy (such as imagery). It is possible that if the MT/V5 area is involved in tactile motion perception, it might be the site of the interaction between the visual and tactile modalities [5].

The integration of visual and tactile motion might also involve multisensory areas at the decision stage, because human spatial perception is highly integrated across modalities [46]. The ventral intraparietal sulcus (IPS) of non-human primates contains neurons that respond to both visual and tactile motion stimuli [20]. The caudal pole of the superior parietal lobule of non-human primates is currently considered to be a key region in the dorsal stream of signals linking somatosensory and visual input to the motor commands driving body movements [12,74]. A recent functional magnetic resonance imaging (fMRI) study revealed that, in humans, there is a parietal face area containing head-centred visual and tactile maps that are aligned with one another [71]. Hence, an alternative candidate area for crossmodal integration is the multisensory posterior parietal cortex.

To explore these alternatives, we conducted an fMRI experiment. Our hypothesis was that the spatial analysis of the direction of movement via visual and tactile modalities activates both sensory-specific and multisensory areas. The former represent the modality-specific coding stage, while the latter include the neural substrates of the decision process that requires the comparison of the two signals coming from different modalities (i.e., crossmodal integration).

Brain areas participating in crossmodal integration should show signs of convergence and interaction [59]. We initially performed independent tactile and visual unimodal experiments involving motion direction matching tasks, in order to define the common multimodal areas that are activated during each of the independent tactile and visual tasks (i.e., convergence). We then carried out tactile and visual crossmodal experiments with event-related designs, in order to identify the areas in which the crossmodal response was enhanced [67], by comparing stimuli whose directions of motion were congruent and incongruent (i.e., interaction). Previous studies of crossmodal integration suggested that the effect of crossmodal interaction is known to be subtle [3]. Thus, we tried to restrict the search volume first by defining the polymodal areas (convergence), within which the interaction effect was searched.

Semantically congruent and/or spatially coincident multisensory inputs in close temporal proximity lead to behavioural response enhancement, resulting in lower thresholds and reduced reaction times compared with unimodal stimuli [25,41,55]. By contrast, incongruent inputs slow response times and produce anomalous perceptions [52,70,77,84]. These enhancements and reductions in behavioural responses are thought to be due to crossmodal integration. Additionally, the response properties of multisensory cells in non-human primates seem to reflect this pattern of crossmodal behavioural enhancement and reduction [54,76,82,77]. Calvert et al. [13] postulated that response enhancement and depression are the hallmarks of intersensory interactions in humans. Thus, it should be possible to depict the neural substrates of crossmodal interaction by comparing congruent and incongruent sensory conditions [67]. This approach also allows us to subtract out the effects of attention, ignorance and the effect of the differences between the cues [67]. And hence the visuo-tactile crossmodal interaction we are investigating should be considered as bottom-up process.

2. Materials and methods

2.1. Subjects

In total, 15 healthy volunteers (seven men and eight women; mean age ± standard deviation [S.D.] = 27.9 ± 6.7 years) participated in this study. Among these subjects, 14 were right-handed and one was left-handed according to the Edinburgh handedness inventory [56]. None of the participants had a history of neurological or psychiatric illness. The protocol was approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan. The experiments were undertaken in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki). All subjects gave written informed consent. Each subject took part in two experiments on separate days: the unimodal block design experiment on day 1 and the crossmodal event-related design experiment on day 2. Hence any learning effect cannot be controlled for; however, we did not directly compare the block design and event-related data. Instead, the unimodal data were used to functionally define the modality-specific areas.

2.2. Experimental design and task procedure

2.2.1. Unimodal block design experiment

The unimodal block design experiment consisted of two sessions: a tactile motion direction matching task and a visual motion direction matching task. Each session of the tactile motion direction matching task consisted of eight task (T-task) periods alternating with eight rest (T-rest) periods, each of which was 20 s in duration. In the T-task periods, two Braille dot stimuli printed along parallel plastic rails were presented passively (Fig. 1A). The two Braille dot stimuli were positioned vertical to each subject's body axis. The rails were moved by ultrasonic motors (Shinsei Corp., Saitama, Japan) using power supplies (Kikusui Electronics Corp., Yokohama, Japan), and were manipulated by two personal computers (PCs) operating together from outside the MR scanner room. One PC (Physio-Tech Corp., Tokyo, Japan) transmitted information about the length and direction of the motion of the Braille stimuli using LabView software (National Instruments Japan, Tokyo, Japan), in response to signals from the other PC (NEC, Tokyo, Japan) that were generated using Presentation software (Neurobehavioral Systems, CA, USA). Each subject placed their right index finger on the proximal rail, and their right middle finger on the distal rail. Each subject placed their left hand on a button box connected to a microcomputer, which recorded their responses. During each session, the subjects were asked to fixate a cross-hair (viewing angle = 0.33° × 0.33°) on a semi-transparent viewing screen, which was projected from a liquid crystal display (LCD) projector (DLA-M200L; Victor, Yokohama, Japan) through a mirror.

During the 20-s task period, five trials (each of 4-s duration) were performed. Each trial contained an 800-ms waiting period, a 1600-ms stimulus period, and

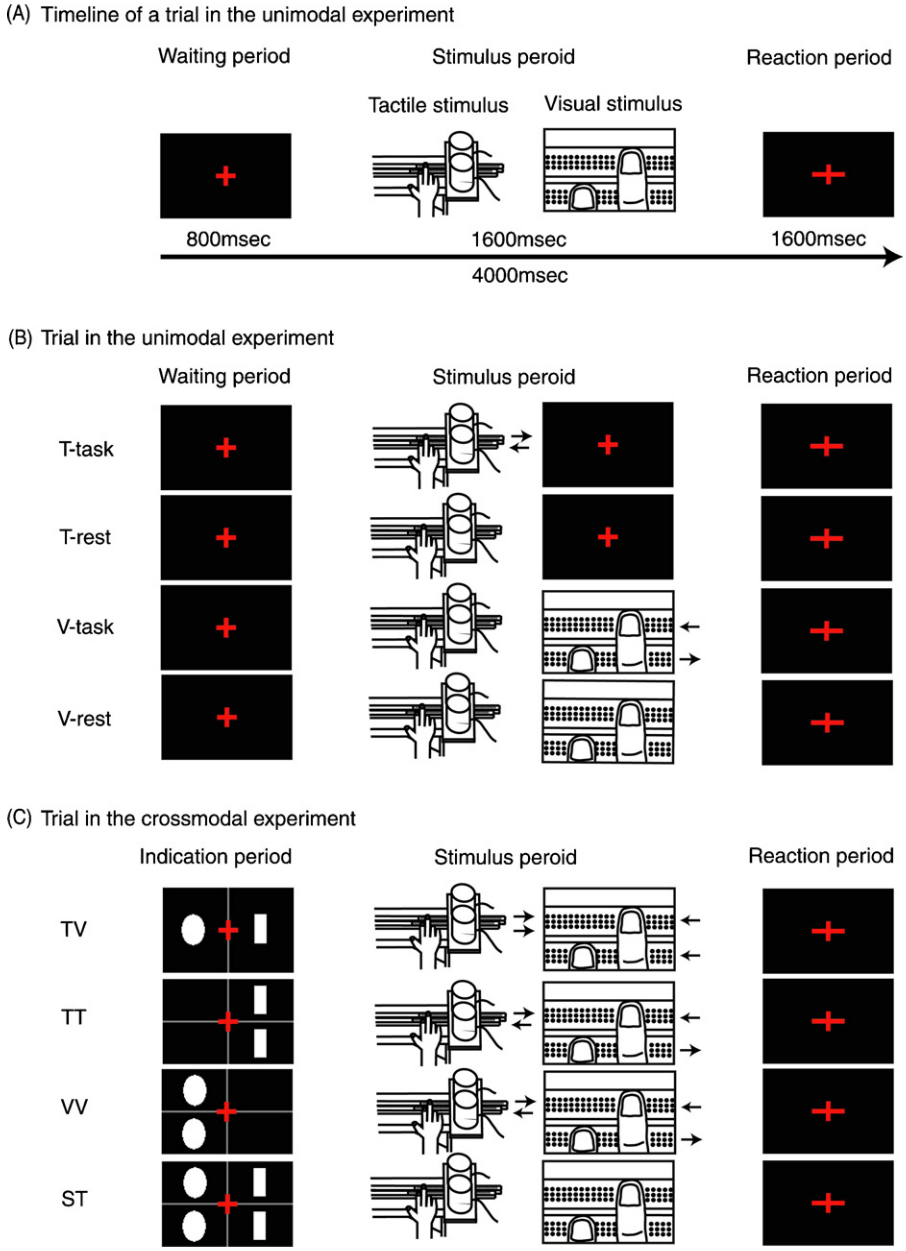

Fig. 1. (A) Timeline of a trial in the unimodal block design experiment. The tactile stimulus was presented passively. The visual stimulus was a video clip that simulated the view from the perspective of a subject who was looking down at the two rails, and the subject's right index and middle fingers were on the respective response buttons. The subjects were asked to make a button press during the reaction period, which was cued by the elongation of the horizontal bar of the cross-hair. (B). Sequence of a trial in the unimodal block design experiment. This consisted of two sessions: one for the tactile motion direction matching task and the other for the visual motion direction matching task. During the task period of the tactile session (T-task), the subjects matched the two tactile motion directions. During the task period of the visual session (V-task), the subjects matched the two visual motion directions. During the rest periods (T-rest and V-rest), no motion stimuli were presented. The subjects pressed the right index finger and right middle finger buttons alternately in response to the visual cue during the reaction period. (C). Sequence of a trial in the crossmodal event-related experiment. Both visual and tactile stimuli were presented simultaneously, and the tasks were preceded by an indication cue. In the tactile–visual condition (TV), the two tactile stimuli moved in the same direction (to the right or left), and the two visual stimuli moved in the same direction independently of the tactile motion direction. The subjects matched the motion directions of the tactile and visual stimuli. In the tactile–tactile condition (TT), the two tactile stimuli moved independently and the two visual stimuli moved independently. The subjects matched the two tactile motion directions. In the visual–visual condition (VV), the stimuli were similar to those in the TT condition, and the subjects matched the two visual motion directions. In the static condition (ST), the subjects were instructed to press the buttons according to the colour of the fixation point.

a 1600-ms reaction period. The waiting period came first, and during this time only the cross-hair was presented. This was followed by the stimulus period, during which the two Braille stimuli on the rails were moved independently to the right or left, while a static cross-hair was presented on the screen. The reaction period came next, during which the horizontal bar of the cross-hair was elongated, indicating to the subjects that they should press a response button. If the two Braille stimuli moved in the same direction, the subjects were instructed to press the left index finger button, whereas they were instructed to press the middle finger button if the two Braille stimuli moved in opposite directions. The subjects were instructed to respond as quickly as possible within the reaction period (Fig. 1A). We did not control for the auditory cues from the motors, because the sound of the motor could not be heard inside the scanner.

In the T-rest periods, the Braille stimuli did not move during the stimulus period. The subjects were instructed to press the left index finger and left middle finger buttons alternately in response to the visual cues during the reaction period (Fig. 1B). Prior to the fMRI session, the subjects were trained on the tactile discrimination tasks until their performance exceeded 80% accuracy. Each subject completed one fMRI session.

The visual motion direction matching task sessions were identical to the tactile sessions, except that moving streams of Braille were presented visually and the tactile apparatus did not move. During the task period (V-task), two horizontal lines of Braille stimuli were presented visually (Fig. 1B). During the stimulus period, the Braille stimuli streamed to the right or left independently, while a static cross-hair was presented. The reaction period immediately followed the stimulus period, during which the horizontal bar of the cross-hair was elongated, indicating that the subjects should press a response button.

During the rest period (V-rest), static Braille stimuli were presented visually (Fig. 1B). In the V-rest condition, the visual Braille stimuli did not move during the stimulus period. During the reaction period, the subjects were instructed to press the left index finger and left middle finger buttons alternately in response to the visual cues.

2.2.2. *Crossmodal event-related design experiment*

The settings for the crossmodal event-related design experiment were identical to those for the unimodal experiments, with the exception that both visual and tactile stimuli were presented simultaneously. In addition, the subjects were notified of the forthcoming tasks by a cue that was presented during the indication period, which corresponded to the waiting period in the unimodal experiments. These experiments involved four types of event condition: tactile–visual (TV), tactile–tactile (TT) and visual–visual (VV) matching tasks, and a static condition (ST; Fig. 1C). For the TV, TT, and VV matching tasks, both tactile and visual stimuli were presented, in order to control for the sensory input.

In the TV matching tasks, the two tactile stimuli moved in the same direction, and the two visual stimuli also moved in the same direction (independently from the tactile stimuli) during the stimulus period. The subjects were instructed to press the button with the left index finger if the tactile and visual stimuli moved in the same direction, and to press the button with the middle finger if the tactile and visual stimuli moved in opposite directions.

In the TT matching tasks, the two tactile stimuli moved to the right or left independently, and the two visual stimuli also independently moved to the right or the left. The tactile and visual stimuli moved simultaneously. The subjects were asked to compare only the two tactile stimuli.

In the VV matching tasks, the stimuli were similar to those in the TT matching task, but the subjects were asked to compare the two visual stimuli. In the ST condition, the two tactile stimuli did not move, and a static image with a blue or yellow fixation point was presented. The subjects were asked to press the left index finger button if the fixation point was blue and the middle finger button if the fixation point was yellow. The reaction times were not measured throughout the experiment. Because of long stimulus period of 1600 ms, and because of the externally cued response at fixed timing, reaction time may not reflect the discrimination process. The inter-trial interval (ITI) was fixed at 4 s. Each condition was repeated 30 times, giving a total of 120 trials during each session. We adjusted the rapid event-related fMRI design to maximize the efficiency with which we could detect differences between the TV and ST, TT and ST, VV and ST, TV and TT, TV and VV, and TT and VV conditions [30,53,65,67]. The session was repeated three times so that each condition (TV, TT, VV, and ST) was repeated 30 times. Prior to the fMRI session, the subjects were trained until their task performance exceeded 80% accuracy.

2.3. *MRI*

2.3.1. *Unimodal block design experiment*

A time-course series of 164 volumes was acquired using T2*-weighted gradient-echo echo-planar imaging (EPI) sequences with a 3 T MR scanner (Allegra, Siemens, Erlangen, Germany). Each volume consisted of 34 slices that were 4.0 mm thick without gaps, covering the entire cerebral and cerebellar cortices. The images were obtained in the interleave mode. Oblique scanning was used to exclude the eyeballs from the images. The time interval between two successive acquisitions of the same slice was 2000 ms (flip angle [FA] = 75°; echo time [TE] = 30 ms). The field of view (FOV) was 192 mm and the in-plane matrix size was 64 × 64 pixels. For anatomical reference, T1-weighted magnetization-prepared rapid gradient-echo (MPRAGE) images (repetition time [TR] = 1460 ms; TE = 4.38 ms; FA = 8°; FOV = 192 mm; matrix size = 256 × 256 pixels) were collected at the same positions as the echo-planar images, and three-dimensional (3D) MPRAGE images (TR = 2500 ms; TE = 4.38 ms; FA = 8°; FOV = 230 mm; matrix size = 256 mm × 256 mm; slice thickness = 1 mm; 192 transaxial images in total) were obtained for each subject.

2.3.2. *Crossmodal event-related design experiment*

The MRI settings for the crossmodal event-related design experiment were identical to those for the unimodal experiment, except that a time-course series of 124 volumes was acquired, each consisting of 36 slices that were 3.0 mm thick with a 0.6-mm gap, and the time interval between two successive acquisitions of the same slice was 4000 ms (FA = 85°; TE = 30 ms). We used different imaging parameters for the event-related design to adjust for the slice timing, which can be done relatively easily in the ascending mode instead of the interleave mode. In the ascending mode it is necessary to insert a gap between the slices during slice selection to represent the cross-talk. In the present study, we adopted a 3 mm slice thickness with 0.6 mm gap (20% gap), which yielded an effective slice thickness of 3.6 mm.

2.4. *Data analysis*

2.4.1. *Preprocessing*

2.4.1.1. Unimodal block design experiment. The first four volumes of each fMRI session were discarded because of unsteady magnetization, and the remaining 160 volumes per session (320 volumes per subject) were used for analysis. The data were processed using statistical parametric mapping (SPM5; Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Sherborn, MA) [26,27]. After realignment, the parameters for affine and nonlinear transformation into a template of the EPI image that was already fit to a standard stereotaxic space (the Montreal Neurological Institute template) [22] were estimated based on the first fMRI image using a least-squares means method [26]. These parameters were applied to all of the fMRI images. The normalized anatomical fMRI images were filtered using a Gaussian kernel with a full width at half-maximum of 8 mm in the x, y, and z axes.

2.4.1.2. Crossmodal event-related design experiment. The preprocessing for the crossmodal event-related design experiment was identical to that for the unimodal matching experiment, with the exception that 120 volumes per session (360 volumes per subject) were analyzed.

2.4.2. *Statistical analyses*

Statistical analyses were conducted separately for the unimodal experiment and the crossmodal experiment using SPM5. Although the first experiment had a block design, and the second experiment had an event-related design, both were handled within the general linear model framework [30], using different design matrices generated for each task. The analyses were performed at both the individual and the population level. Initially, the individual task-related activation was evaluated. Then, to make inferences at a population level, the individual data were summarized and incorporated into a random effect model [29]. Including the data of one left-handed subject into the analysis of 14 right-handed subjects may introduce some confound. However, as the individual analysis of the one left-handed subject showed a similar activation pattern as the right-handed subjects, the data were incorporated into the group analysis.

The signal time course for each subject was modelled using a box-car function convolved with a haemodynamic response function and its temporal derivative [40], a session effect, and high-pass filtering (128 s). Global mean scaling was not applied, in order to avoid inducing type II errors in the assessment of negative blood-oxygen-level-dependent (BOLD) fMRI responses [1]. To test hypotheses about regionally-specific condition effects, the estimates for each model parameter were compared with the linear contrasts (Table 1). Then, the weighted sums of the parameter estimates in the individual analyses were used as ‘contrast’ images for the group analysis. These represented the normalized task-related increment of the MR signal of each subject. For each contrast,

Table 1
Predefined contrasts unimodal block design experiment

Name of contrasts	Tactile		Visual	
	Task	Rest	Task	Rest
T	1	−1	0	0
−T	−1	1	0	0
V	0	0	1	−1
−V	0	0	−1	1
T–V	1	−1	−1	1
V–T	−1	1	1	−1

Name of contrasts	Tactile–visual		Tactile–tactile		visual-visual		ST
	c	i	c	i	c	i	
Crossmodal event-related design experiment							
TV	1	1	0	0	0	0	−2
TT	0	0	1	1	0	0	−2
VV	0	0	0	0	1	1	−2
TT–TV	−1	−1	1	1	0	0	0
VV–TV	−1	−1	0	0	1	1	0
TT–VV	0	0	1	1	−1	−1	0
VV–TT	0	0	−1	−1	1	1	0
TVc–TVi	1	−1	0	0	0	0	0
TTc–TTi	0	0	1	−1	0	0	0
VVc–VVi	0	0	0	0	1	−1	0

c, Congruent; i, incongruent.

a one sample *t*-test was performed for every voxel within the brain to make population inferences.

We concentrated on the second-level random effect analysis, as our main focus was on the population inferences. Using the unimodal block design experiment data, we initially delineated the areas that were active during the T-task and V-task conditions compared with those that were active during the rest periods of the same sessions, T-rest and V-rest, respectively. During the T-rest condition, subjects were required to press the left index finger and left middle finger buttons alternately in response to the visual cues during the reaction period. This was to control for the activation related to the button presses. The perceptual decision was not well-controlled for, because during the T-task condition subjects decided which buttons to press based on the direction of tactile motion (the perceptual decision). However, during the V-rest condition, the button presses were controlled for in the same manner in order to depict the neural substrates of the perceptual decision that subjects made based on the direction of visual motion. Hence, comparison between the visual and tactile sessions was possible. Modality-specific areas were defined by the contrast of T–V (masked with T) and V–T (masked with V). T represents the task-related activation highlighted by the contrast of T-task – T-rest (Table 1), which corresponds to motion discrimination in the tactile modality. In the same vein, V represents motion discrimination in the visual modality. Hence, T–V and V–T are reasonable comparisons to use to define the modality-specific areas for motion discrimination. Polymodal areas were defined by T and V as depicted by the intersection of the areas defined by each contrast. Using the data from the crossmodal event-related design experiment, we depicted the task-related activation within the modality-specific and polymodal areas that were revealed by the block design experiment. The set of voxel values resulting from each comparison yielded a statistical parametric map (SPM) of the *t*-statistic (SPM$\{t\}$). The SPM$\{t\}$ was transformed to normal distribution units SPM$\{Z\}$. The threshold for the SPM$\{Z\}$ was set at $Z > 3.09$ corresponding to $P < 0.001$ (uncorrected). We utilized the consistent statistical threshold to define the polymodal areas, instead of the corrected *P* values that depend on the size of the search volume. The corrected *P* values at the cluster level [28] and voxel level with a false discovery rate (FDR) [31] are also reported in Tables 2–4 to ensure the statistical significance of the activated areas. The cluster-level correction was based on the theory of Gaussian random fields, which considers clusters as ‘rare events’ that occur in a given searched volume according to a Poisson distribution [28]. The FDR is the proportion of false positives (incorrect rejections of the null hypothesis) among multiple voxel-wise tests for which the null hypothesis is rejected, and hence this procedure controls the family-wise error rate [31].

Our initial hypothesis was that crossmodal interaction occurs in the multimodal areas. We therefore searched for the neural substrates of crossmodal interaction in the areas that were activated by both the T and V conditions, and TV, as depicted by the intersection of the areas defined by each contrast. Within these areas, we compared the TV sessions with congruent stimuli (TVc) to those with incongruent stimuli (TVi). The percentage signal change was calculated from the beta value. As the time series of the global signals (i.e., the average values across all voxels) in a session was normalized to 100, the percentage signal change was calculated in units of the percentage of the global signal. As the MR sequences and task designs of the unimodal and crossmodal experiments were different, the percentage signal change could not be directly compared across the experiments.

The MNI coordinates of the local maxima were transformed to Talairach’s coordinates [79] using an established formula (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml) [11], in order to label the activated foci according to the anatomical nomenclature of the Talairach and Tournoux atlas [79]. Additional anatomical labels were adopted, such as the secondary somatosensory area (SII) [24,62], dorsal premotor cortex (PMd), ventral premotor cortex (PMv), supplemental motor cortex (SMA), pre-SMA [35], and MT/V5 [21,80,83]. These areas were identified using the previously-reported Talairach’s coordinates and anatomical criteria.

Table 2
Bimodal (tactile and visual) activation patterns ($N = 15$)

Side	Location	Tactile motion direction matching							Visual motion direction matching				
		Cluster		*Z*-value	FDR corrected *P*	MNI coordinates			*Z*-value	FDR corrected *P*	MNI coordinates		
		Size	Corrected *P*			*x*	*y*	*z*			*x*	*y*	*z*
L	LPs	60	0.056	3.68	0.007	−20	−62	60	3.9	0.011	−18	−68	56
				3.54	0.009	−34	−62	62	3.61	0.014	−26	−64	60
				3.39	0.012	−16	−68	56	3.3	0.023	−30	−56	58
L	PMd	159	0.003	4.66	0.002	−26	−4	56	4.41	0.01	−22	−4	50
R	PMd	49	0.084	3.9	0.004	30	−4	54	4.07	0.01	28	−6	48
R	Cerebellum	58	0.06	4.58	0.002	30	−56	−24	4.01	0.01	26	−70	−22
				3.8	0.005	22	−70	−22	3.88	0.011	32	−54	−24
				3.72	0.006	28	−64	−22					

FDR, false discovery rate; MNI, Montreal Neurological Institute; LPs, superior parietal lobule; PMd, dorsal premotor cortex; R, right; L, left. The clusters were delineated by the intersection of the areas activated by the visual motion matching and tactile motion matching tasks (both thresholds defined as $Z > 3.09$ corresponding to $P < 0.001$ uncorrected). *P* values of clusters are corrected in the search volume defined by the V contrast with $Z > 3.09$. *P* values of local maximum were FDR corrected in the same search volume. Clusters >40 voxels are reported.

Table 3
Activation by the crossmodal motion direction matching task within the bimodal areas

Cluster		Z-value	FDR corrected P	MNI coordinates			Side	Location
Size	Corrected P			x	y	z		
6	0.058	3.62	0.013	−32	−62	60	L	LPs
6	0.047	3.34	0.013	−20	−66	60	L	LPs
9	0.058	3.44	0.013	−26	0	46	L	PMd

LPs, superior parietal lobule; PMv, ventral premotor cortex; L, left; R, right. Thresholds defined as $Z > 3.09$. Clusters larger than 5 voxels are reported.

3. Results

3.1. Unimodal block design experiment

In the unimodal experiments, the mean ± S.D. percentages of correct responses were 92.0 ± 5.5% for the T-task and 94.3 ± 7.8% for the V-task, which did not significantly differ ($P = 0.09$, paired t-test).

Tactile motion direction discrimination activated the bilateral inferior parietal lobule (LPi), LPs, secondary somatosensory area (SII), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), inferior frontal gyrus (GFi), insula, putamen, left primary sensorimotor area (SM1), postcentral gyrus (GPoC), supplementary motor area (SMA), and pre-SMA (Fig. 2). Deactivation was observed in the occipital cortices including MT/V5, and the medial prefrontal, orbitofrontal, parietal, and temporal cortices (Fig. 2).

Visual motion orientation discrimination activated the bilateral cuneus (Cu), fusiform gyrus (GF), lingual gyrus (GL), MT/V5, inferior occipital gyrus (GOi), middle occipital gyrus (GOm), precuneus (PCu), LPs, IPS, PMv, and right GPoC, (Fig. 3). Activation was observed in the right prefrontal cortex, left middle temporal gyrus (GTm), right superior temporal gyrus, and right PMd (Fig. 3).

Areas that were activated by both tactile and visual tasks were found within the bilateral posterior parietal cortex, including the left LPs, and the PMd and PMv bilaterally, and right cerebellum (Fig. 2).

Task-related activities specific to tactile motion direction matching (T–V, masked with T) were seen in the bilateral parieto-premotor cortices, SIIs, insula, left putamen, and right cerebellum. Visual-specific activities (V–T, masked with V) were observed in the occipital cortices.

In the areas involved in matching the direction of visual motion, the bilateral GOm, MT gyrus (GTm) and superior occipital gyrus (GOs) showed significantly less activity during tactile motion discrimination than during the rest conditions (Fig. 2). No significant deactivation was found during visual motion direction matching in the areas implicated in tactile motion direction matching (Fig. 2).

3.2. Crossmodal event-related design experiment

In the crossmodal experiment, the mean ± S.D. percentages of correct responses were 92.3 ± 8.4% for the TVc condition and 91.9 ± 9.7% for the TVi condition. In the TT conditions, accuracy scores were 83.1 ± 13.1% for the TTc condition and 87.6 ± 7.3% for the TTi condition. In the VV conditions, scores were 96.7 ± 5.1% for the VVc condition and 94.4 ± 9.7% for the VVi condition. Scores were 97.5 ± 2.5% for the ST condition. Repeated measures analysis of variance (ANOVA) with a 3 × 2 design revealed a significant

Table 4
Deactivation by the tactile–visual motion direction matching task compared with tactile–tactile or visual–visual motion direction matching, within the areas detected during unimodal specific motion direction matching

Cluster		Z-value	FDR corrected P	MNI coordinates			Side	Location
Size	P corrected			x	y	z		
TT > TV								
642	<0.001	5.04	<0.001	60	−22	32	R	GPoC
		3.79	0.002	60	−14	14	R	SII
729	<0.001	4.83	<0.001	−54	−24	46	L	GPoC
43	0.039	3.49	0.003	−52	−28	16	L	SII
VV>TV								
286	<0.001	4.18	0.005	−46	−84	2	L	MT/V5
395	<0.001	3.51	0.005	48	−74	0	R	MT/V5
		3.88	0.005	40	−86	14	R	GOm
		3.56	0.006	22	−96	20	R	Cu
40	0.086	3.52	0.006	−34	−92	18	L	GOm
281	0.001	4.38	0.005	−20	−72	−10	L	GL

Cu, cuneus; GOm, middle occipital gyrus; GPoC, postcentral gyrus; MT, middle temporal; SII, secondary somatosensory area; L, left; R, right. Threshold was $Z > 3.09$. Clusters equal or larger than 40 voxels were reported.

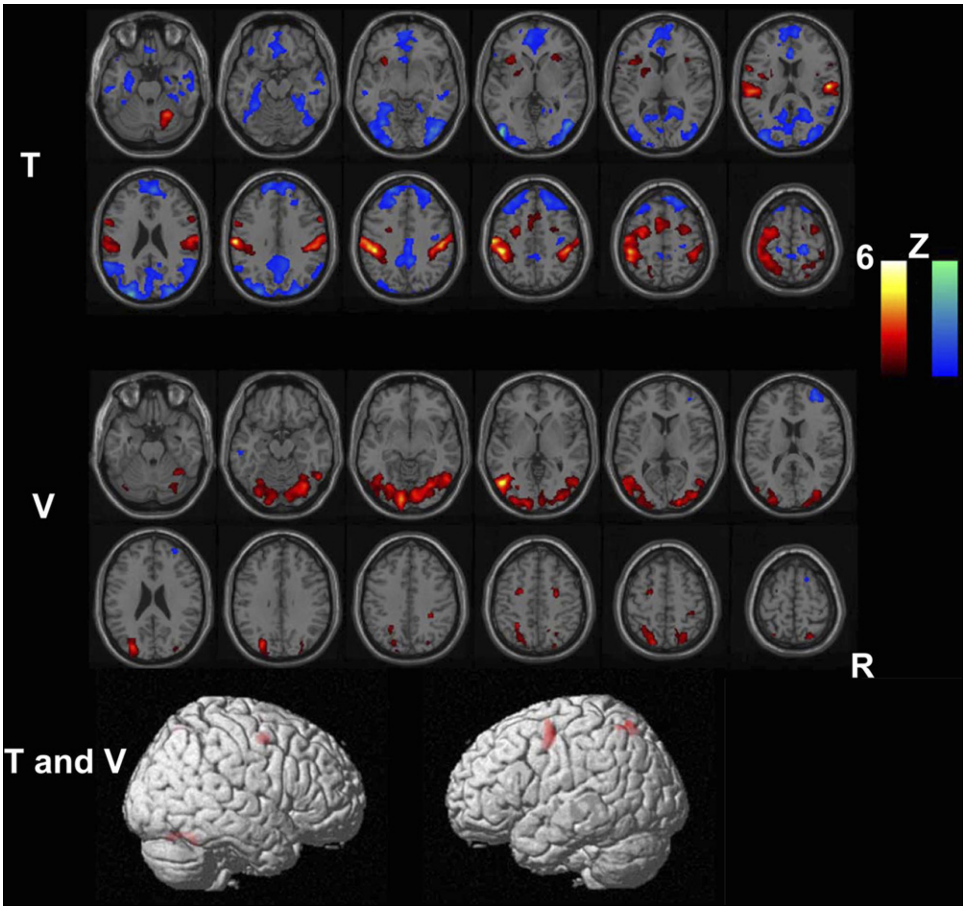

Fig. 2. SPMs of the unimodal block design experiment. (Upper two rows) Neural activities during the tactile motion direction matching task. Activated (red) and deactivated (blue) foci are shown as a pseudocolour fMRI superimposed on a high-resolution anatomical MRI in 12 contiguous transaxial planes with an 8-mm interval, extending from 24 mm below the anterior commissure (AC)–posterior commissure (PC) plane (top left) to 64 mm above the AC–PC plane (bottom left). The statistical threshold was uncorrected $P < 0.001$. The colour bars indicate the Z scores of each comparison. (Middle two rows) Neural activities during the visual motion direction matching task with the same format as the tactile session. (Bottom row) Areas that were commonly activated by the tactile and visual matching tasks were superimposed on the surface-rendered high-resolution MR images. The statistical threshold was $P < 0.001$ (uncorrected) for each comparison. The clusters >40 voxels are shown.

condition effect ($F(2,28) = 19.1$, $P < 0.001$), but no significant congruency effect ($F(1,14) = 0.049$, $P = 0.828$) or condition × congruency interaction ($F(2,28) = 1.229$, $P = 0.126$). The accuracy of performance during the TT condition was significantly worse than the performance during the VV and TV conditions ($F(1,14) = 37.973$, $P < 0.001$, with a pre-defined contrast).

Within the polymodal areas defined by the unimodal block design experiment (Table 2), the left LPs and the PMd showed significant activation during the TV condition in the event-related design experiment (Table 3). The left LPs showed a congruency effect specific to the TV condition. No congruency effect was found during the VV or TT conditions (Fig. 3).

To identify brain areas with significantly lower activity during crossmodal matching than during intramodal matching, the following contrasts were used (Table 1): TT–TV masked with T and (T–V), and VV–TV masked with V and (V–T). Compared with the TT condition, the TV condition showed a decrease in signal in the bilateral secondary somatosensory area and postcentral gyrus (Fig. 4, Table 4). Compared with the VV condition, the activities in the bilateral MT/V5, GOm and right Cu were significantly reduced during the TV condition (Fig. 4).

4. Discussion

4.1. Task performance

The crossmodal experiment did not reveal a congruency effect during either the crossmodal or intramodal conditions. This might have been due to a ceiling effect, as the performance levels were relatively high. Performance in the TT condition was significantly worse than that during the VV or TV conditions. During this task, tactile stimuli were presented simultaneously, but independently, to the index and middle fingers. This might have made performance in the TT condition more difficult than in the TV condition, during which tactile stimuli that were moving in the same direction were presented to both fingers. The intrinsic difficulty of motion direction discrimination in the tactile modality compared with the visual modality is also reflected

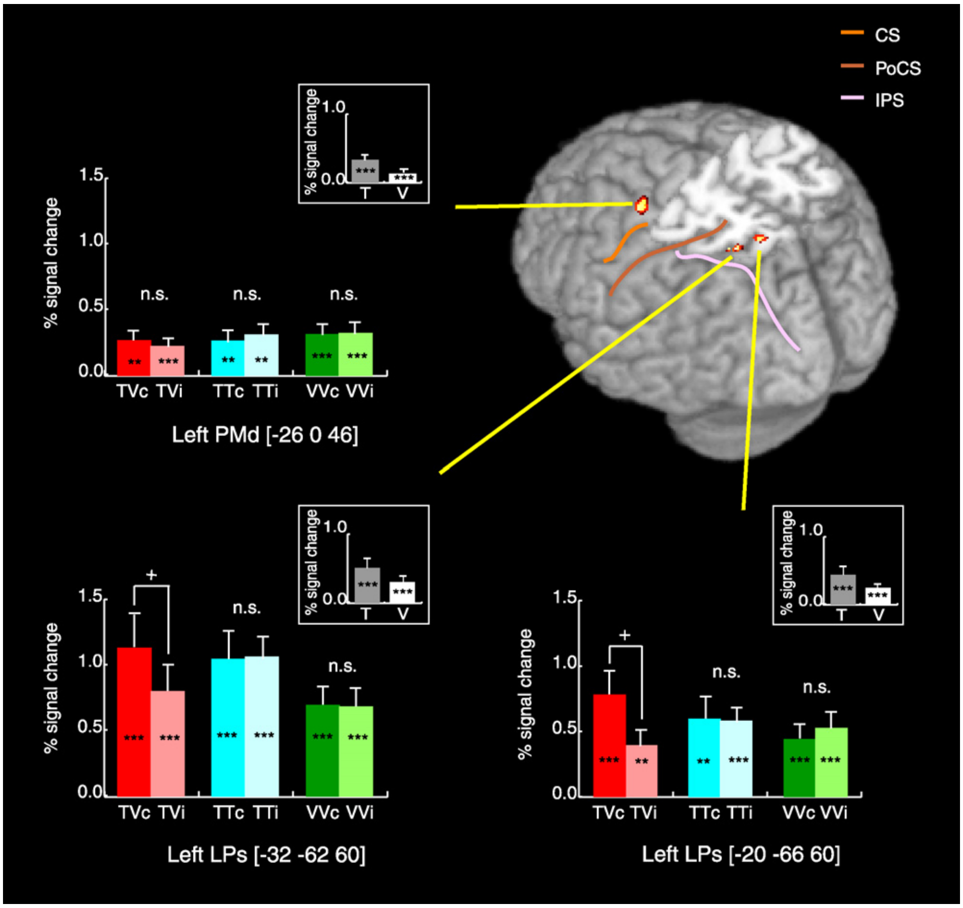

Fig. 3. Tactile–visual convergence and interaction during motion direction matching according to the SPMs of the group data. Within the areas activated by both the visual and tactile motion direction matching tasks, those that showed significant activation in the TV condition were superimposed on a surface-rendered high-resolution MR image to depict the relationship with the IPS, postcentral sulcus (PoCS), and central sulcus (CS). The statistical threshold was $P < 0.001$. The coloured bar graphs indicate the task-related activation induced by the congruent and incongruent stimuli during the TV, TT and VV conditions. The monochrome insets show task-related activation induced by the T and V conditions. The percentage signal change relative to the global mean of the MR signal was calculated using the beta value multiplied by the amplitude of the regressor of interest. The error bars indicate the standard error of the mean. $^{**}P < 0.01$, $^{***}P < 0.001$ (one sample *t*-test), $^{+}P < 0.05$ (paired *t*-test).

in the unimodal tasks, in which T-task performance was slightly worse than performance on the V-task.

4.2. Modality-specific activation/deactivation

The unimodal tactile motion direction matching task revealed an activation pattern similar to that observed during passive tactile shape discrimination tasks using Braille characters [37]. As the task materials did not contain shape information, the task itself is not similar to shape discrimination tasks. Instead, this finding was consistent with the idea that the analysis of the direction of motion is the basis for the recognition of the size and shape of objects [66]. The unimodal visual motion direction matching tasks mainly activated the occipital cortex, including the MT/V5 area. The parieto-premotor areas, but not MT/V5, were activated by both the visual and tactile tasks. This finding suggests that the parieto-premotor network may be related to the comparison and/or decision processes involved in the tasks, rather than motion perception *per se*.

The tactile task deactivated the visual cortical areas, including MT/V5. A negative BOLD signal is known to be tightly coupled with cerebral blood flow (CBF) and CMRO$_2$ in the human visual cortex [73] and M1 [75], and with cerebral blood volume in the primary visual cortex (V1) of anesthetized cats [38]. Recent simultaneous fMRI and electrophysiological measurements in the monkey V1 revealed that both positive and negative BOLD responses were strongly correlated with neuronal activity [73]. Hence, a negative BOLD response represents a decrease in neural activity.

Deactivation of the visual cortex during the tactile task was consistent with the results of previous functional neuroimaging studies investigating tactile shape discrimination [44,63,64] and speed discrimination of stimuli moving across the skin [8]. The deactivation of cortical regions that are not directly related to task modalities might be functionally significant, in that it reduces the probability that there will be interference due to information from other sensory modalities [44]. Crossmodal deactivation is therefore an essential component of the selective attention mechanism, playing a complementary role to the activation of cortical areas that are required for the performance of a given task [39,44]. This might explain the apparently conflicting results of two previ-

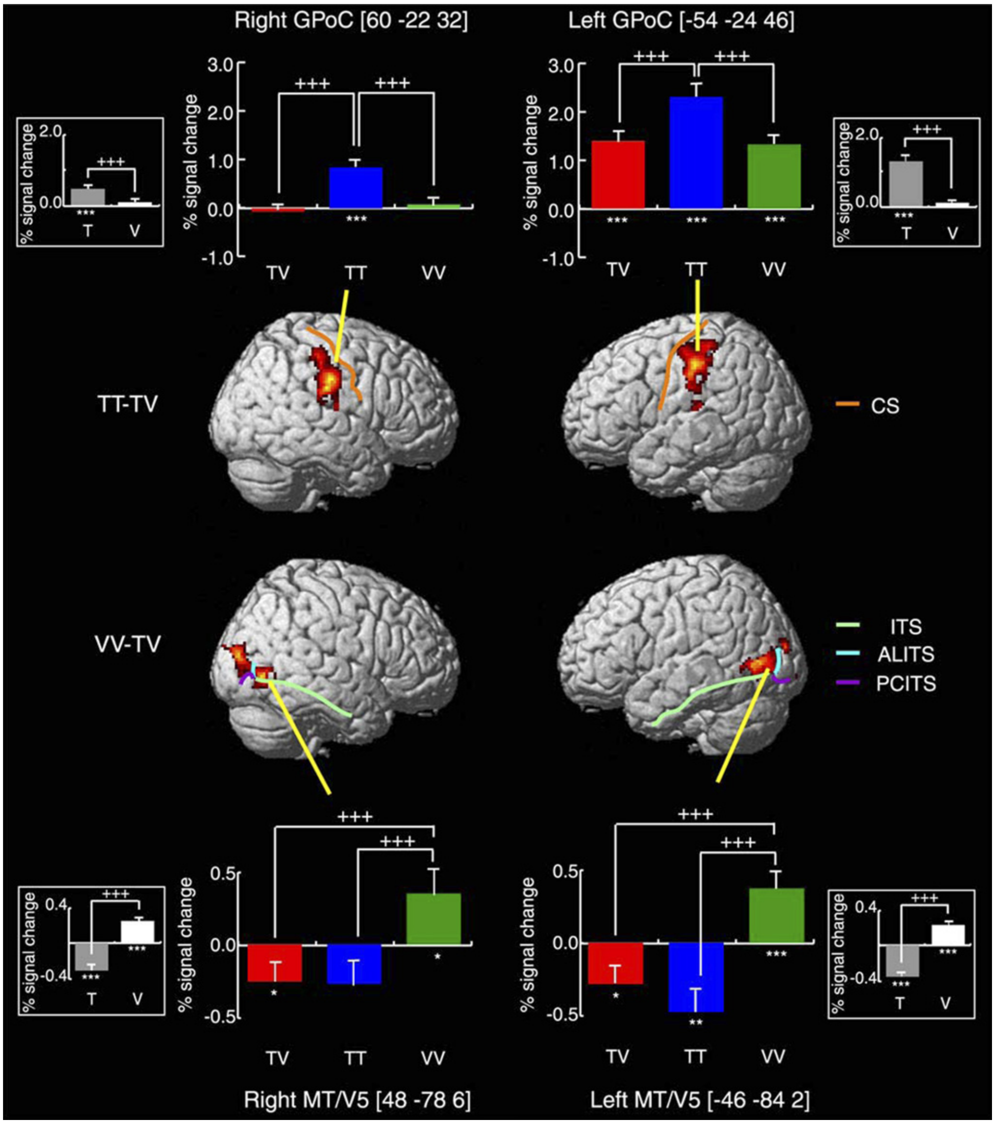

Fig. 4. Areas with lower activity during the crossmodal matching conditions (TV) compared with the intramodal matching conditions (TT, top row and VV, bottom row) within each unimodal area. Areas with lower activation during the TV condition compared with the TT condition were explored within the tactile-specific areas that were defined using the contrast T–V masked with T. Areas with lower activation during the TV condition compared with the VV condition were explored within the visual-specific areas defined by V–T masked with V. The areas were superimposed on surface-rendered high-resolution MR images to depict the relationship with the CS, the ascending limb of the inferior temporal sulcus (ALITS), the ITS and the posterior continuation of the ITS (PCITS), as viewed from the right (left column) and the left (right column). The statistical thresholds were uncorrected $P < 0.001$ for each contrast. The coloured bar graphs indicate the task-related activation (percentage signal change) induced by the TV, TT, and VV conditions. The monochrome insets show the task-related activation induced by the T and V conditions. The percentage signal change relative to the global mean of the MR signal was calculated using the beta value multiplied by the amplitude of the regressor of interest. The error bars indicate the standard error of the mean. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one sample *t*-test), $^{+++}P < 0.001$ (paired *t*-test).

ous functional neuroimaging studies in which tactile motion appeared to activate MT/V5 [6,34], as the tasks in these studies did not require motion direction discrimination, and hence the deactivation caused by this selective attention mechanism was minimal.

Recently, Ricciardi et al. [60] showed that tactile flow perception activated the anterior part of MT/V5 whereas the posterior portion was deactivated. They also found that congenital or early-onset blind subjects showed activation in MT/V5 during tactile flow tasks, and the authors concluded that the activation of MT/V5 is not caused by visual imagery, but that it instead represents supramodal motion perception [60]. In their study, no response was required. Beauchamp et al. [4] also showed that the anterior region of MT/V5 responded to the stationary vibrotactile stimuli with a strong preference for the contralateral hand. In this study no behavioral response was required. In contrast, in the present study the subjects kept their eyes open, which might have kept the visual input to MT/V5 at a constant level. Thus, the deactivation of the visual cortices during the tactile motion discrimination task in the present study may be interpreted as masking the supramodal motion perception in MT/V5, by the selective attentional mechanism which is used to conduct the cognitively highly-demanding task of direction discrimination.

4.3. Bimodal activation

We found that the left LPs, the PMd, and the PMv were activated by both visual and tactile motion direction discrimination. These areas should represent the processes that are common to both visual and tactile intra-modal motion direction discrimination. Hence, the commonly activated parieto-premotor areas might be partly related to the decision stage that compares the two motion direction signals. The posterior parietal cortex consists of multiple subdivisions, each of which is involved in a particular aspect of visual or somatosensory information processing. In macaque monkeys, the ventral intraparietal area (VIP), located in the fundus of the intraparietal sulcus (IPS), is known to contain many neurons that show polymodal, directionally-selective discharges (i.e., these neurons respond to moving visual, tactile, vestibular, and auditory stimuli) [15,20]. Thus, the VIP is thought to be involved in multisensory integration, based on multidirectional sensory predictions [2]. The VIP is connected with somatosensory areas 2, 1, and 3a, which are primarily related to digit or digit/face representation [48]. The fundus of the IPS has reciprocal connections with visual-related areas, such as visual area 3, the ventral posterior area [23], and the parieto-occipital area [16]. The lateral portion of the VIP tends to have stronger connections with visual-related areas, whereas the medial portion is more strongly connected to sensorimotor-related areas [48]. The lateral bank of the IPS is extensively interconnected with known visual areas [9,16]. The LIP, in the lateral wall of the IPS, is interconnected with the frontal eye fields and the superior colliculus [49,7]. Area CIP is situated in the lateral bank of the caudal IPS, posterior to area LIP [14,81]. Recent comparative studies revealed that the anterior parts of the IPS, comprising areas AIP and VIP as defined in macaque monkeys, are relatively well-preserved in humans, whereas the LIP and CIP were found more medially in humans [33]. In human imaging studies, the IPS and LPi are known to be activated by tactile and visual motion stimuli [10,34].

The posterior parietal cortex and BA 6 are connected in a specific pattern to form several fronto-parietal circuits [32,61]. These two cortical areas function in concert during cognitive operations, motor control [19] and voluntary attentional control [42]. Recent functional neuroimaging studies indicate that the PMd might also have non-motor cognitive functions [43,18,36,35,37]. The role of the parieto-premotor networks in tactile shape discrimination was discussed previously by Harada et al. [37], who used fMRI to evaluate the laterality of the neural substrates involved. Passive tactile discrimination tasks, along with appropriate control tasks, were performed with both hands to evaluate the effects of the hand used as well as the hemispheric effects (i.e., the laterality of the activation pattern). Irrespective of the hand used, the right dorsolateral prefrontal cortex, posterior parietal cortex, pre-SMA and PMdr were activated asymmetrically during tactile discrimination. Harada et al. [37] linked the right parieto-premotor-prefrontal networks with spatial attention. Hand effects were detected in the left caudal PMd (PMdc) adjacent to the central sulcus, which showed prominent activation during discrimination tasks with the right, but not the left, hand. Harada et al. [37] attributed this asymmetric activation in the left PMdc to the output of the sensory categorization process in the parieto-premotor network, which is driven by tactile information from the right hand. Both the T-task and V-task share common motor selection processes based on a perceptual decision. This process was not controlled for in the T-rest or V-rest conditions, in which subjects alternately pressed the response buttons. Motor selection is known to activate the parieto-premotor network [57]. Thus, the present results suggest that the posterior parieto-premotor networks might include the neural substrates for the evaluation of the direction of tactile motion, which is the basis for tactile shape discrimination [66]. As the present study showed that visual intramodal motion direction discrimination tasks recruited these areas, the evaluation process might be supra-modal.

The right lateral prefrontal area may be crucial for comparing successively-presented tactile stimuli [8,78], or for scaling the magnitude of roughness [45]. These authors attributed this role to working memory processes. In the present study, the tactile stimuli were presented simultaneously and hence the contribution of the working memory was likely to be small.

4.4. Crossmodal interaction in the bimodal areas

Within the areas of bimodal activation, the posterior portion of the left LPs showed a congruency effect. Using quantitative receptor autoradiography, the human LPs has been subdivided into anterior (area 5 and anterior area 7) and posterior (posterior area 7) regions [68,69]. The posterior part has receptor distributions similar to those of the visual cortices, suggesting that visual inputs dominate this area [68].

In macaque monkeys, area PEc in the posterior portion of the superior parietal lobule [68] responds to visual stimuli [74] as well as somatosensory stimuli [12]. The caudal pole of the LPs, including the PEc [58], is thought to be a higher-order somatosensory area [51]. The PEc is connected to the PE parietal area, the inferior PEc (PEci), the PG, the medial intraparietal area (MIP) [50,58] and the PMd [50,51], all of which are regions where somatosensory cells exist [12]. A recent non-human primate study [12] showed that the PEc contained somatosensory cells, most of which were activated by contralateral stimulation. One-half of the PEc somatosensory cells were also sensitive to visual stimuli [12]. The PEc area is the target of direct projections from visual area V6A [72], and contains neuronal populations that specifically signal local visual motion and possibly encode the direction of moving objects [74]. Reciprocal connections link the PEc with the dorso-caudal premotor cortex [85], which might be related to tactile shape discrimination [37]. Hence, the PEc area is a key region in the dorsal stream of signals linking somatosensory and visual inputs. These non-human primate studies suggest that the LPs probably is the site where the crossmodal interaction of visual and tactile motion discrimination signals occurs.

Previous neuroimaging studies demonstrated that visuotactile interactions may also occur in the anterior intraparietal cortex and the adjacent cortex of the inferior parietal lobe. The functional differences between the anterior and posterior IPS and the adjacent cortices have been discussed by Saito et al. [67]. Saito et al. [67] suggested that different aspects of crossmodal shape processing occur in discrete areas of the polymodal IPS; the anterior portion is related to the amodal 3D shape processes requiring short-term memory, and the posterior portion is involved in the amodal transformation of shape information [67].

Thus, it is conceivable that the crossmodal congruency effect observed in this study reflects the interaction at the decision stage that requires the comparison of the two motion signals that have been coded in the modality-specific areas.

4.5. Crossmodal suppression in modality-specific areas

In the TV condition, the motion-related MT/V5 activity was suppressed compared with the VV condition. The activity in the tactile unimodal areas was also reduced compared with the TT condition. This pattern was not observed in the parieto-premotor areas that showed activation during the tactile and visual tasks. These findings support the notion of different roles for the modality-specific areas and the polymodal areas in crossmodal motion discrimination: the coding of motion is modality-specific, whereas the decision stage might be represented by the polymodal parieto-premotor networks with 'competitive' interactions between modality-specific areas [67]. In this regard, the left posterior LPs might represent a node through which the senses can access each other directly from their sensory-specific systems [67].

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