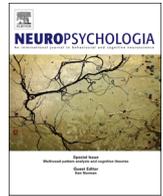




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Role of the precuneus in the detection of incongruency between tactile and visual texture information: A functional MRI study



Ryo Kitada ^{a,b,*}, Akihiro T. Sasaki ^{c,d}, Yuko Okamoto ^e, Takanori Kochiyama ^f,
Norihiro Sadato ^{a,b}

^a Division of Cerebral Integration, National Institute for Physiological Sciences, Okazaki 444-8585, Japan

^b Department of Physiological Sciences, The Graduate University for Advanced Studies (Sokendai), Japan

^c Department of Physiology, Osaka City University Graduate School of Medicine, Osaka 545-8585, Japan

^d Pathophysiological and Health Science Team, RIKEN Center for Life Science Technologies, Kobe 650-0047, Japan

^e Research Center for Child Mental Development, University of Fukui, Eiheiji 910-1193, Japan

^f ATR Brain Activity Imaging Center, Seika-cho 619-0288, Japan

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ABSTRACT

Visual clues as to the physical substance of manufactured objects can be misleading. For example, a plastic ring can appear to be made of gold. However, we can avoid misidentifying an object's substance by comparing visual and tactile information. As compared to the spatial properties of an object (e.g., orientation), however, little information regarding physical object properties (material properties) is shared between vision and touch. How can such different kinds of information be compared in the brain? One possibility is that the visuo-tactile comparison of material information is mediated by associations that are previously learned between the two modalities. Previous studies suggest that a cortical network involving the medial temporal lobe and precuneus plays a critical role in the retrieval of information from long-term memory. Here, we used functional magnetic resonance imaging (fMRI) to test whether these brain regions are involved in the visuo-tactile comparison of material properties. The stimuli consisted of surfaces in which an oriented plastic bar was placed on a background texture. Twenty-two healthy participants determined whether the orientations of visually- and tactually-presented bar stimuli were congruent in the orientation conditions, and whether visually- and tactually-presented background textures were congruent in the texture conditions. The texture conditions revealed greater activation of the fusiform gyrus, medial temporal lobe and lateral prefrontal cortex compared with the orientation conditions. In the texture conditions, the precuneus showed greater response to incongruent stimuli than to congruent stimuli. This incongruency effect was greater for the texture conditions than for the orientation conditions. These results suggest that the precuneus is involved in detecting incongruency between tactile and visual texture information in concert with the medial temporal lobe, which is tightly linked with long-term memory.

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1. Introduction

We use many manufactured objects in our daily life. Because the surface of these objects can be coated with various materials, we can easily be deceived by their visual appearance. For example, a painted plastic ring can look like it is made of gold. However, if we touch such an object, the thermal conductivity that we experience is inconsistent with the visual cues, and we can easily detect that it is made of plastic. Thus, we can identify the object's physical substance more accurately if we compare information perceived by vision with that

perceived by other sensory modalities. The present study investigated the neural mechanisms by which incongruence of physical information between vision and touch is detected.

In order to detect visuo-tactile incongruence of object properties, sensory information extracted from the two modalities must be compared in the brain. Object properties are largely classified into two categories: macro-geometric properties, such as orientation and shape; and material properties, such as roughness, softness and temperature (Jones and Lederman, 2006). Touch and vision share spatial information regarding macro-geometric properties. By employing common spatial frames of reference, spatial information between the two sensory modalities can be directly compared. Previous neuroimaging studies have identified multiple cortical regions involved in visuo-tactile interaction of macro-geometric properties such as the intraparietal sulcus (IPS)

* Corresponding author at: Division of Cerebral Integration, National Institute for Physiological Sciences, Okazaki 444-8585, Japan.
Tel.: +81 564 55 7844; fax: +81 564 55 7786.

E-mail address: kitada@nips.ac.jp (R. Kitada).

(Grefkes et al., 2002; Kitada et al., 2006; Nakashita et al., 2008; Saito et al., 2003; Tal and Amedi, 2009), claustrum/insula (Hadjikhani and Roland, 1998; Kassuba et al., 2013) and lateral occipital complex (LOC) (Amedi et al., 2001; James et al., 2002; Kassuba et al., 2013; Kim and James, 2010; Zhang et al., 2004).

In contrast to macro-geometric properties, there is little information on material properties that can be directly compared between touch and vision. More specifically, the physical properties of the object material itself (e.g., roughness, softness and temperature) are perceived by touch, whereas the properties of surface reflectance (e.g., color and gloss) are accessible only by vision. As physical object information extracted by vision and touch differs substantially, it is argued that touch and vision can contribute to the perception of material properties in an independent, rather than an integrated, manner (Whitaker et al., 2008). How then can different types of physical information (from touch and vision) be compared in the brain?

One possible heuristic is to compare physical object information extracted by touch and vision in the same “format”, after translating it from one sensory modality to the corresponding other. This comparison might be implemented by interactions between visual and tactile physical object information in the brain. For instance, we can retrieve tactile information that was previously associated with the visual appearance of an object (e.g., high thermal conductivity of gold) and compare it with incoming tactile information (e.g., low thermal conductivity of plastic). In order for this heuristic to be implemented, previously learned physical associations between vision and touch must be retrieved (Fleming, 2014); otherwise, no link for this translation is present between the two modalities. Accordingly, this heuristic indicates that comparing visuo-tactile information about material properties involves neural mechanisms that can retrieve and then utilize previously learned vision–touch associations.

Previous neuroimaging studies have identified the neural substrates involved in the unisensory perception of physical object properties. More specifically, the conventional somatosensory cortices (i.e., the postcentral gyrus and parietal operculum) are involved in the tactile processing of material properties (Burton et al., 1997; Kitada et al., 2005; Roland et al., 1998; Servos et al., 2001; Stoesz et al., 2003). The ventral visual pathway is involved in the visual processing of material properties (Cant and Goodale, 2007, 2011; Cavina-Pratesi et al., 2010a, 2010b; Hiramatsu et al., 2011). Several neuroimaging studies have investigated brain regions that receive convergent inputs from vision and touch regarding material properties (Eck et al., 2013; Sathian et al., 2011; Stilla and Sathian, 2008). These studies consistently report that parts of the occipital cortex, such as the middle occipital gyrus (Eck et al., 2013; Sathian et al., 2011), superior occipital gyrus (Stilla and Sathian, 2008) and lingual gyrus (Sathian et al., 2011), are active during tactile as well as visual perception of material properties. These findings indicate that conventional sensory cortices are involved in the comparison of visual and tactile material information.

However, if the retrieval of information shared between touch and vision is critical, additional cortical regions beyond the conventional sensory cortex should be involved. For instance, a number of previous studies have identified the neural substrates underlying the retrieval of stimulus pairs during paired-association tasks (Fuster et al., 2000; Gonzalo et al., 2000; Hasegawa et al., 1998; Krause et al., 1999; Ranganath et al., 2004; Tanabe et al., 2005; Tanabe and Sadato, 2009; Weniger et al., 2004). These neural substrates include the medial temporal lobe (Gonzalo et al., 2000; Naya et al., 2001; Ranganath et al., 2004; Tanabe et al., 2005; Weniger et al., 2004), lateral prefrontal cortex (Fuster et al., 2000; Gonzalo et al., 2000; Hasegawa et al., 1998; Ranganath et al., 2004) and precuneus (Gonzalo et al., 2000; Krause et al., 1999; Ranganath et al., 2004; Tanabe and Sadato, 2009). However, as no previous study has

investigated brain activity during a direct comparison of visual and tactile information (Eck et al., 2013; Sathian et al., 2011; Stilla and Sathian, 2008), it remains unclear whether these regions are involved in the visuo-tactile comparison of material properties.

The present study used functional magnetic resonance imaging (fMRI) to test whether brain regions related to associative memory are involved in comparing physical object properties between vision and touch. Participants used both vision and touch to perceive the surface of a plastic bar imposed on a background texture. In the texture conditions, the participant was asked to judge whether the visually- and tactually-presented background textures were congruent or incongruent. In the orientation conditions, the participant judged whether the orientations of visually- and tactually-presented bars were congruent or incongruent. We reasoned that learned associations between touch and vision are more necessary for visuo-tactile comparison of texture, relative to that of the orientation conditions. Therefore, we predicted that a cortical network involving the medial temporal lobe, the lateral prefrontal cortex and the precuneus would be more strongly activated during the texture conditions than during the orientation conditions. Furthermore, we predicted that detecting visuo-tactile incongruence of material properties would result in greater activity in the incongruent texture conditions than in the congruent texture conditions (i.e., an incongruency effect) in these regions, which can access information retrieved from associative memory.

2. Materials and methods

2.1. Participants

Twenty-two individuals participated in the experiment (13 males and 9 females, mean age \pm standard deviation [SD]=23.2 \pm 4.8 years). All participants were right-handed (Oldfield, 1971). None of the participants reported a history of major medical or neurological illness, such as epilepsy, significant head trauma or a lifetime history of alcohol dependence. All those taking part gave written informed consent for participation in the study. The protocol was approved by the local medical ethics committee at the National Institute for Physiological Sciences (Aichi, Japan).

2.2. Data acquisition

fMRI was performed using a 3T Siemens Allegra whole-head MRI system (Siemens, Erlangen, Germany). Standard sequence parameters were used to obtain the functional images as follows: gradient-echo echo-planar imaging (EPI) with a repetition time (TR) of 2500 ms; echo time (TE)=30 ms; flip angle=80°; 39 axial slices of 3-mm thickness with a 17% slice gap; field of view=192 \times 192 mm²; and in-plane resolution=3.0 \times 3.0 mm². Each participant completed 16 functional runs. A T1-weighted high-resolution anatomical image was obtained for each participant (voxel size=0.9 \times 0.9 \times 1 mm³) after first half of the functional runs.

2.3. Stimuli

We produced surface stimuli that could be used for both texture matching and orientation matching. These surfaces were made of one of four textures (textile, soapstone, wood and leather) and a rectangular plastic sheet placed in a specific orientation was glued to each surface (Fig. 1A). As detailed below, we matched the sensory components between the texture and orientation tasks by presenting the same number of rectangles in each orientation and the same number of each of the textures to each participant. Similarly, in the congruent and incongruent conditions, the same total sensory components were included by utilizing the same number of rectangles in each orientation and the same number of background textures.

2.3.1. Tactile stimulus

We produced the surfaces using the following procedure. Initially, we selected four different types of texture (textile, soapstone, wood and leather) for which visuo-tactile associations are commonly established during daily life. For each texture, we created two exemplars (30 mm long \times 60 mm wide \times 5 mm thick). We then attached a plastic sheet (2 mm wide \times 20 mm long \times 0.2 mm thick) to the center of each surface in one of four different orientations (horizontal, slanted rightward, vertical and slanted leftward). As with the textures, we produced two orientation

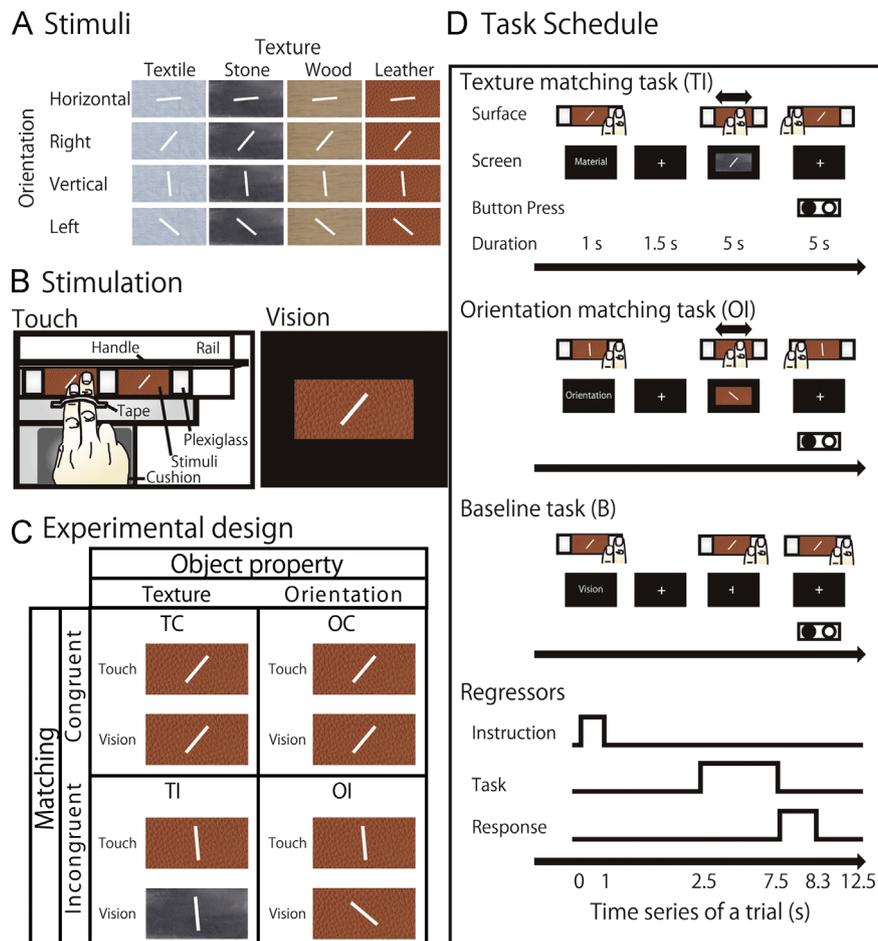


Fig. 1. Experimental design. (A) Stimuli. We produced surface stimuli that could be used for both texture and orientation matching. The background of each surface was made of one of four textures (textile, soapstone, wood and leather) and a rectangular sheet of plastic in one of four orientations was glued onto the surface of the background texture. (b) Stimulation. While visually observing images presented on screen, the participants placed their right index and middle fingertips lightly on the surface of the slider. The experimenter moved the slider manually. (C) Experimental design. Our task design included the four task conditions with two levels of the two factors: attended object property (texture and orientation conditions) and matching (congruent and incongruent conditions). The orientation task served as a control. In addition, we added the baseline task (B) as a low-level control for the button responses (not shown). (D) Task schedule. A single trial consisted of the instruction, test and response periods. The instruction cue was presented for 1 s. During the test period (5 s), the participant viewed an image of one surface on the screen, whereas a real surface moved five times on their fingers. Visually- and tactually-presented textures were identical in the TC condition and different in the TI condition. Similarly, visually- and tactually-presented rectangular sheets were in the same orientation in the OC condition and in different orientations in the OI condition. During the response period, the participant pressed one of the two buttons to indicate whether the visually- and tactually-presented textures were the same in the TC and TI conditions, and whether the rectangular sheets were in the same orientation in the OC and OI conditions. In the baseline task (B), no tactile stimulation was provided. Either the left or right bar of a white cross disappeared during the test period. The participant was instructed to press the button which corresponded to the side of the white cross that remained on the screen.

subtypes: the rectangle was placed at an orientation of 5°, 50°, 95° and 140° for one of the exemplars for each texture type, and at -5°, 40°, 85° and 130° for the other exemplar. In total, we prepared 32 different surfaces (4 textures × 4 rectangles in different orientations × 2 exemplars). We produced these surfaces for each of the orientation and texture tasks (32 surfaces × 2 tasks = 64 surfaces in total).

2.3.2. Visual stimulus

To produce visual stimuli, we scanned and digitalized the surfaces. As the rectangular plastic sheet was transparent and could be difficult to see, we replaced it with a white rectangle of the same size using photo-editing software (Photoshop, Adobe Systems, San Jose, CA). The stimuli subtended visual angles of approximately 12.8° × 6.4°.

2.3.3. Pairs of tactile and visual stimuli

We produced congruent and incongruent pairs of tactile and visual stimuli. First, we divided the 32 surfaces for the texture task into two subsets (with 16 surfaces in each). The total number of surfaces made of each texture and the total number of rectangles placed in each orientation were the same for the two subsets. In one subset, we paired each surface with a matching image (congruent pairs). In the other subset, we paired each surface with an image showing a different texture but a rectangle in the same orientation (incongruent pairs). Similarly, we produced congruent and incongruent pairs for the orientation task. The procedure was identical to that for the texture task, except that each surface was paired with an image with the same texture but a rectangle in a different orientation in incongruent pairs.

2.4. Stimulus presentation

We utilized the system described in our previous studies for visual and tactile stimulation (Harada et al., 2004; Kitada et al., 2006) (Fig. 1B). Presentation software (Neurobehavioral Systems Inc., Albany, CA) was used to present visual stimuli to the participant and auditory cues to the experimenter via headphones. The participants lay supine on a bed with their eyes open and their ears plugged. The right and left arms of each participant were extended along the side of their body and comfortably supported by a cushion. The index and middle fingers of the left hand were placed on each of two buttons of the response box.

2.4.1. Tactile stimulation

The participants placed their right index and middle fingertips lightly on the surface of a slider, with the other fingers resting on a cushion outside of the rail (Fig. 1B). The finger was immobilized against the horizontal movement of the slider. We explained to the participants that they should avoid applying excessive pressure to the stimulator.

We placed eight surfaces onto each slider: two surfaces from each subset in the orientation task and two surfaces from each subset in the texture task (2 surfaces for each subset × 2 subsets × 2 tasks = 8 surfaces). In other words, each slider included two congruent and two incongruent surfaces for the orientation task, and two congruent and two incongruent surfaces for the texture task. The order of these surfaces was pseudo-randomized using a genetic algorithm that maximized the estimation efficiency for the tested contrasts (Wager and Nichols, 2003). We

inserted a sheet of smooth plexiglass between the surfaces, which was where the fingers were placed during the baseline condition. Consequently, we produced eight sliders (4 surfaces for the orientation task + 4 surfaces for the texture task) \times 8 sliders = 64 surfaces altogether).

The experimenter moved the slider back and forth in the horizontal direction, guided by auditory cues. These cues were presented only to the experimenter through a pair of ceramic-condenser headphones (Hitachi Medical Corporation, Tokyo, Japan). A single slider was utilized during each run.

2.4.2. Visual stimulation

The participants observed visual stimuli on the screen through a mirror attached to the head coil.

Stimuli were back-projected via a liquid crystal display (LCD) projector (LT 265; NEC Viewtechnology, Tokyo, Japan) onto a translucent screen located at the rear of the scanner.

2.5. Task

Our design included four task conditions with two levels of two factors: attended object properties (texture and orientation), and matching of visual and tactile information (congruent and incongruent) (Fig. 1C). In the texture task, the participant was instructed to judge whether the background textures were the same between the tactually- and visually-presented surfaces. Congruent pairs of surfaces were presented during texture-congruent (TC) conditions. Incongruent pairs were presented during texture-incongruent (TI) conditions. Similarly, in the orientation task, the participant was instructed to judge whether the orientation of the rectangles was the same between the tactually- and visually-presented surfaces. We defined conditions when congruent pairs were presented as orientation-congruent (OC) conditions, and conditions in which incongruent pairs were presented as orientation-incongruent (OI) conditions. In addition to these four conditions, there was a low-level control (baseline, B) condition.

We used a single slider for each run. We presented all eight sliders in the first half of the experiment, and then presented the same sliders again in the second half of the experiment (16 runs in total). The participants were not aware that the same set of sliders was used during the two halves of the experiment. The sliders were presented in a pseudo-randomized order. A single run consisted of a 22.5-s rest (fixation) period, followed by a 125-s task period, and then a second 12.5-s fixation (rest) period (64 volumes per run, 160 s). The task period contained 10 trials, two for each of the five conditions. The duration of each trial was 12.5 s (10 trials \times 12.5 s = 125 s). In the MRI room before scanning, the participants were familiarized with the tasks using a set of stimuli that were not used in the experiment.

2.5.1. Texture matching task (TC and TI)

A single trial consisted of the instruction (2.5 s), test (5 s) and response (5 s) periods (Fig. 1D). The instruction cue (viewing angle, $6.2^\circ \times 2.9^\circ$) was presented for the first second of the instruction period. Then, the finger pads were stimulated by a surface during the test period. The slider was moved five times in 5 s: 60 mm from left-to-right for the first second, 50 mm from right-to-left for the next second, 50 mm from left-to-right for the third second, 50 mm from right-to-left for the fourth second, and 60 mm from left-to-right for the fifth second. The surface always moved from the smooth regions alongside the surfaces. During the test period, the participant viewed the congruent surface in the texture-congruent (TC) condition (i.e., a surface made of the same texture with a rectangle in the same orientation), as opposed to a surface from the incongruent pair (i.e., a surface made of a different texture with a rectangle in the same orientation) in the texture-incongruent (TI) condition. During the response period, the participant was asked to press one of two buttons to indicate whether the textures in the tactually- and visually-presented surfaces were the same or different. The order of the buttons was counterbalanced across the participants.

2.5.2. Orientation matching task (OC and OI)

The experimental design for the orientation matching task was the same as in the texture task, except for the task instructions. The participant was asked to press one of two buttons to indicate whether the orientation of the rectangles in the tactually- and visually-presented surfaces was the same or different.

2.5.3. Baseline task (B)

This task was designed as a low-level control for the button responses and involved no tactile stimulation. During the test period, either the left or right bars of a white cross disappeared. The participant was instructed to press the button that corresponded to the side of the white cross that remained on the screen.

2.6. Data processing

Image processing and statistical analyses were performed using the Statistical Parametric Mapping package (SPM8; Friston et al., 2007). The first five volumes of

each fMRI run were discarded to allow the signal to reach a state of equilibrium. The remaining 59 volumes were used for the subsequent analyses. To correct for head motion, functional images from each run were realigned to the first image and then realigned to the mean image after the first realignment. The T1-weighted anatomical image was co-registered to the mean of the realigned images. Each co-registered T1-weighted anatomical image was normalized to Montreal Neurological Institute (MNI) space using the DARTEL procedure (Ashburner, 2007). More specifically, each anatomical image was first segmented into the tissue class images using the unified segmentation approach (Ashburner and Friston, 2005). The gray and white matter images were transformed to a common coordinate space to create a study-specific template using the DARTEL registration algorithm. The study-specific template was then affine normalized to MNI space with the ICBM Tissue Probabilistic Atlases. The parameters from the process of DARTEL registration and normalization to MNI space were then applied to each functional image and T1-weighted anatomical image. The normalized functional images were filtered using a Gaussian kernel of 6 mm full width at half maximum (FWHM) in the x, y and z axes.

2.7. Statistical analysis

Linear contrasts between conditions were calculated for individual participants, and incorporated into a random-effects model to make inferences at a population level (Holmes and Friston, 1998).

2.7.1. Initial individual analysis

We fitted a general linear model to the fMRI data for each participant (Friston et al., 1994; Worsley and Friston, 1995). Neural activation during both tasks was modeled with box-car functions convolved with the canonical hemodynamic-response function. The design matrix for each participant comprised 16 runs each of which included the following seven task-related regressors: one regressor for 1 s of the instruction period for all conditions; one regressor for the response period for all conditions; and five regressors for the test periods for each of the five conditions (OC, OI, TC, TI and B). The duration of the response period was 0.8 s, based on the mean response time from the behavioral data. The time series for each voxel was high-pass filtered at 1/128 Hz. Assuming a first-order autoregressive model, the serial autocorrelation was estimated from the pooled active voxels with the restricted maximum likelihood (ReML) procedure, and was used to whiten the data (Friston et al., 2002). Motion-related artifacts were minimized by incorporating six parameters (three displacements and three rotations) from the rigid-body realignment stage into each model.

We evaluated the contrast estimates for OC, OI, TC and TI by comparing each of them with the B condition. We used these obtained contrast images for the random-effects group analysis.

2.7.2. Random-effects group analysis

Contrast images from the individual analyses were used for the group analysis, with between-subjects variance modeled as a random factor. We employed a full factorial design to construct a single design matrix that included the four regressors (2 levels of object property \times 2 levels of matching). These conditions were modeled as within-subject (dependent) levels. We included behavioral data (e.g., response time) as a covariate if the behavioral data showed a significant difference between conditions. The estimates for these conditions were compared using linear contrasts. The resulting set of voxel values for each contrast constituted the SPM $\{t\}$, which was transformed into normal distribution units (SPM $\{z\}$). The threshold for the SPM $\{z\}$ was set at $Z > 3.09$ (equivalent to $P < 0.001$ uncorrected). The statistical threshold for the spatial extent test on the clusters was set at $P < 0.05$ and corrected for multiple comparisons over the whole brain (Friston et al., 1996).

Brain regions were anatomically defined and labeled according to a probabilistic atlas (Shattuck et al., 2008), with supplementary data from the published literature (Squire and Zola-Morgan, 2001) and probabilistic maps (the Anatomical Toolbox, Eickhoff et al., 2005; the probabilistic map of the perirhinal cortex, Holdstock et al., 2009) relating to regions around the hippocampus. We utilized the NeuroElf toolbox (<http://neuroelf.net/>) and Brain Voyager QX (Brain Innovation, Maastricht, The Netherlands) to display activation patterns on surface-rendered T1-weighted MR images averaged across the participants.

We evaluated the predefined contrasts described below (Table 1). The search volume was the whole brain in all the analyses, avoiding possible double-dipping problems (Kriegeskorte et al., 2009).

2.7.3. Main effect of object property

In order to reveal the brain regions that were more active during the texture conditions than the orientation conditions (a texture task effect), we evaluated the conjunction of (TC + TI) vs. (OC + OI), TC vs. B, and TI vs. B (with the conjunction null hypothesis; Friston et al., 2005; Nichols et al., 2005). This analysis was intended to identify brain regions for which activation was greater during texture conditions relative to both baseline and orientation conditions, as a negative response during texture conditions relative to baseline would be difficult to interpret. The contrast of (TC + TI) vs. (OC + OI) was used to reveal greater activation in the texture

Table 1
Predefined contrasts.

Regressors	Texture		Orientation		Baseline task B
	Congruent TC	Incongruent TI	Congruent OC	Incongruent OI	
Contrasts					
c01. TI vs. B	0	1	0	0	–1
c02. TC vs. B	1	0	0	0	–1
c03. OI vs. B	0	0	0	1	–1
c04. OC vs. B	0	0	1	0	–1
c05. (TC+TI) vs. (OC+OI)	1	1	–1	–1	0
c06. (OC+OI) vs. (TC+TI)	–1	–1	1	1	0
c07. (TI+OI) vs. (TC+OC)	–1	1	–1	1	0
c08. (TC+OC) vs. (TI+OI)	1	–1	1	–1	0
c09. TI vs. TC	–1	1	0	0	0
c10. TC vs. TI	1	–1	0	0	0
c11. (TI vs. TC) vs. (OI vs. OC)	–1	1	1	–1	0
c12. (TC vs. TI) vs. (OC vs. OI)	1	–1	–1	1	0
Conjunction analysis					
Main effects of object property					
Texture task effect	c01, c02, c05		(Fig. 3 and Table 2)		
Orientation task effect	c03, c04, c06		(Fig. 3 and Table 2)		
Main effects of matching					
Incongruency effects	c01, c03, c07				
Congruency effects	c02, c04, c08				
Interaction effects					
Texture-specific incongruency effect	c01, c09, c11		(Fig. 4 and Table 3)		
Texture-specific congruency effect	c02, c10, c12				

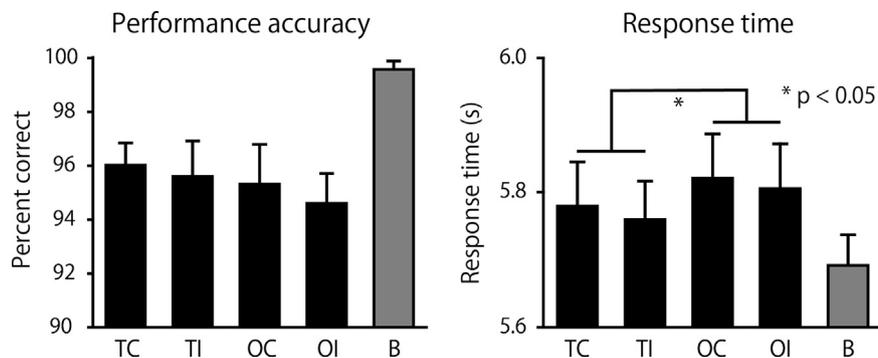


Fig. 2. Behavioral results. Data are presented as the mean \pm standard error of the mean (SEM) of 22 participants. The asterisk indicates a significant main effect of object property in the 2-way ANOVA (2 levels of object property \times 2 levels of matching). We included response times (relative to the baseline task) as covariates of no interest in the fMRI analyses.

conditions than in the orientation conditions, whereas the contrasts of TC vs. B and TI vs. B were used to identify positive responses during the texture conditions relative to baseline.

Similarly, we evaluated the conjunction of (OC+OI) vs. (TC+TI), OC vs. B, and OI vs. B to identify brain regions that were more active during the orientation conditions than the texture conditions (an orientation task effect). More specifically, we used the contrast of (OC+OI) vs. (TC+TI) to investigate the main effect of orientation task, whereas we employed the contrasts of OC vs. B, and OI vs. B to identify brain regions showing positive activation during the orientation tasks relative to the baseline task.

2.7.4. Main effect of matching

We then evaluated the brain regions that exhibited incongruency effects for both the texture and orientation tasks by performing the conjunction of (TI+OI) vs. (TC+OC), TI vs. B, and OI vs. B. The contrast of (TI+OI) vs. (TC+OC) was used to reveal activation during the incongruency conditions relative to the congruency conditions. The contrasts with the baseline (TI vs. B and OI vs. B) were used to identify a positive response during the incongruency conditions relative to the baseline task. Similarly, we evaluated congruency effects by performing the conjunction of (TC+OC) vs. (TI+OI), TC vs. B, and OC vs. B.

2.7.5. Interaction effects between matching and object properties

In order to identify brain regions that showed a stronger incongruency effect in the texture conditions than in the orientation conditions (a texture-specific

incongruency effect), we evaluated the conjunction of (TI vs. TC) vs. (OI vs. OC), TI vs. TC, and TI vs. B. In this conjunction analysis, the contrast of (TI vs. TC) vs. (OI vs. OC) was used to investigate the incongruency effect specific to the texture task. We also included the contrast of TI vs. TC, because the texture-specific incongruency effect is evaluated based on the assumption that the incongruency effect *per se* is present in the texture conditions. Finally, we used the contrast of TI vs. B to ensure that the texture incongruency effect was observed only when a positive response was present during the texture incongruency condition relative to the baseline task. Similarly, we also examined the texture-specific congruency effect by performing the conjunction of (TC vs. TI) vs. (OC vs. OI), TC vs. TI, and TC vs. B.

3. Results

3.1. Task performance

3.1.1. Performance accuracy

Performance accuracy was similar for the four conditions (TC, TI, OC and OI; Fig. 2 left). A two-way analysis of variance (ANOVA; [2 object properties: texture and orientation] \times [2 levels of matching: congruency and incongruency]) on accuracy scores produced neither a significant main effect nor an interaction between the

two factors (P values > 0.4). We confirmed that the visuo-tactile tasks (TC, TI, OC and OI) showed significantly lower performance accuracy than the baseline task (P values < 0.05 , paired t -tests comparing the baseline task with each of the other tasks).

3.1.2. Response times

The same ANOVA performed on the response times revealed a significant main effect of object property: response times were significantly longer during the orientation conditions than the texture conditions ($F_{1,21}=5.9$, $P < 0.05$; Fig. 2, right). Neither a main effect of matching nor a significant interaction was observed (P values > 0.2). We confirmed that response times on the visuo-tactile tasks were significantly slower than during the baseline task (P values < 0.05 , paired t -tests comparing the baseline task with each of the other tasks).

Collectively, although performance accuracy was comparable across the four task conditions, response times were longer for the orientation than the texture tasks. As this factor might reflect differences in attentional demand, we excluded it by including the response times as covariates of no interest.

3.2. fMRI analysis

3.2.1. Main effects of attended object properties

3.2.1.1. Texture task effect. We examined the brain regions that were activated more strongly during texture conditions than during the orientation and baseline conditions (a texture task effect). The conjunction of (TC+TI) vs. (OC+OI), TC vs. B, and TI vs. B revealed regions of significant activation bilaterally in the fusiform gyrus, lingual gyrus, parahippocampal gyrus, inferior occipital gyrus, middle occipital gyrus and superior occipital gyrus. In addition, we observed regions of significant activation in the left hemisphere, including the inferior temporal gyrus, hippocampus, entorhinal/perirhinal cortex, inferior frontal gyrus, middle frontal gyrus, angular gyrus and superior parietal lobule (Table 2 and Fig. 3). Activation in the entorhinal/perirhinal cortex ($x = -32$, $y = -6$, $z = -36$) was located in and around the collateral sulcus beneath the hippocampus and amygdala (Squire and Wixted, 2011). The parietal operculum showed only sub-threshold activation ($x = -58$, $y = -14$, $z = 12$, Z value = 2.73).

3.2.1.2. Orientation task effect. We conducted supplemental analyses on the orientation task effect (Table 2 and Fig. 3). We confirmed our previous finding that the orientation task effect revealed regions of significant activation including the IPS (Kitada et al., 2006).

3.2.2. Main effects of matching

3.2.2.1. Incongruency effect for both the texture and orientation conditions. We evaluated the conjunction of (TI+OI) vs. (TC+OC), TI vs. B, and OI vs. B. However, this contrast produced no significant activation.

3.2.2.2. Congruency effect for both the texture and orientation conditions. The conjunction of (TC+OC) vs. (TI+OI), TC vs. B, and OC vs. B revealed no significant activation.

3.2.3. Interaction effects between object properties and matching

3.2.3.1. Texture-specific incongruency effect. We determined the brain regions showing a greater incongruency effect in the texture conditions than the orientation conditions (the conjunction of [TI vs. TC] vs. [OI vs. OC], TI vs. TC and TI vs. B). This contrast yielded significant activation in the left precuneus and the medial part of the superior parietal lobule (Table 3 and Fig. 4). None of these regions overlapped with the texture task effect brain regions (Fig. 4).

Table 2
Task effects.

Spatial extent test Cluster size (mm ³)	P values	MNI coordinates			Z value	Hem	Anatomical region
		x	y	z			
Texture task effect							
Conjunction of (TC+TI) vs. (OC+OI), TC vs. B and TI vs. B							
78,784	$P < 0.001$	-26	-60	-8	6.74	L	Lingual gyrus
		18	-84	-6	7.23	R	Lingual gyrus
		-30	-48	-20	6.72	L	Fusiform gyrus
		32	-50	-16	7.18	R	Fusiform gyrus
		28	-28	-26	4.45	R	Parahippocampal gyrus
		-18	-32	-4	6.33	L	Parahippocampal gyrus
		-32	-6	-36	3.91	L	Entorhinal/perirhinal cortex ^a
		-26	-74	-10	Inf	L	Inferior occipital gyrus
		26	-70	-8	Inf	R	Inferior occipital gyrus
		-28	-86	20	6.51	L	Middle occipital gyrus
		16	-92	0	6.55	R	Middle occipital gyrus
		-26	-84	20	6.52	L	Superior occipital gyrus
		28	-82	18	6.66	R	Superior occipital gyrus
		-48	-48	-16	4.41	L	Inferior temporal gyrus
1760	$P < 0.01$	-22	-28	-10	4.90	L	Hippocampus ^b
7256	$P < 0.001$	-50	34	12	6.71	L	Inferior frontal gyrus
		-42	12	32	4.53	L	Middle frontal gyrus
1400	$P < 0.05$	-32	-68	44	4.26	L	Angular gyrus
		-26	-62	36	3.87	L	Superior parietal lobule
Orientation task effect							
Conjunction of (OC+OI) vs. (TC+TI) and OC vs. B and OI vs. B							
23,856	$P < 0.001$	48	-30	48	6.98	R	Supramarginal gyrus
		48	-36	62	6.88	R	Superior parietal lobule
		42	-32	50	6.62	R	Postcentral gyrus
		40	-44	44	5.35	R	Angular gyrus
11,720	$P < 0.001$	-42	-40	50	6.91	L	Superior parietal lobule
		-46	-40	52	6.81	L	Supramarginal gyrus
		-34	-40	42	5.93	L	Superior parietal lobule
		-30	-50	52	5.70	L	Superior parietal lobule
		-56	-30	36	5.40	L	Supramarginal gyrus
		-62	-32	34	4.88	L	Supramarginal gyrus
5192	$P < 0.001$	54	10	22	6.39	R	Precentral gyrus
		58	12	14	6.30	R	Inferior frontal gyrus
2456	$P < 0.001$	-52	2	20	6.33	L	Precentral gyrus
6632	$P < 0.001$	28	4	52	6.20	R	Middle frontal gyrus
		20	0	64	3.89	R	Superior frontal gyrus
3592	$P < 0.001$	-30	-6	52	5.67	L	Precentral gyrus
		-26	6	54	3.93	L	Middle frontal gyrus
		-20	4	50	3.39	L	Superior frontal gyrus
1504	$P < 0.01$	-22	-64	-30	5.08	L	Cerebellum
1368	$P < 0.05$	-32	-46	-36	4.59	L	Cerebellum
1264	$P < 0.05$	-20	-74	-50	4.30	L	Cerebellum

The threshold for the size of activation was $P < 0.05$, corrected for multiple comparisons over the whole brain, with the height threshold set at $Z > 3.09$. x , y and z are stereotaxic coordinates (mm). Inf, Z value > 8.0 ; Hem, hemisphere; R, right; L, left.

^a Probability values on cytoarchitectonic maps: 82% for the perirhinal cortex (Holdstock et al., 2009).

^b Probability values on cytoarchitectonic maps: 60% for the hippocampus (subiculum) (Amunts et al., 2005).

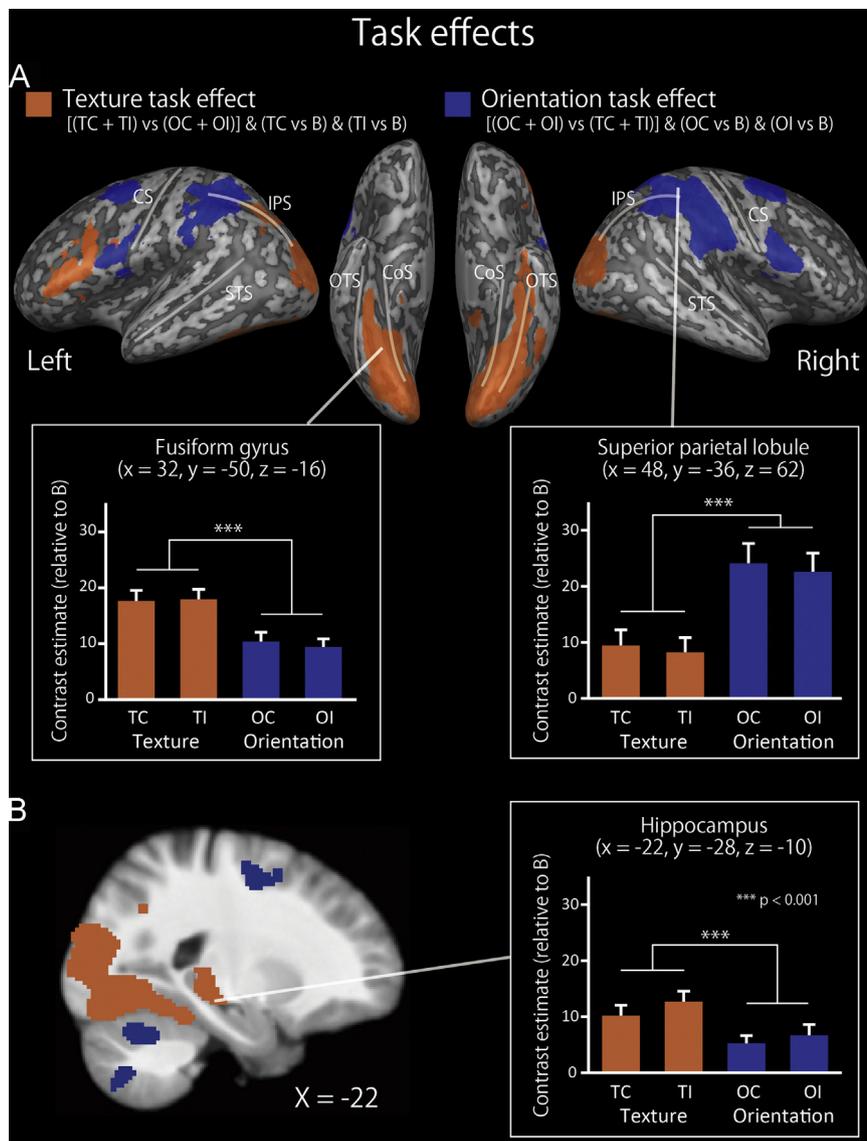


Fig. 3. Texture task effects. Task-related activations were superimposed on a surface-rendered T1-weighted MR image averaged across the participants (A) and a sagittal section of the same MR image (B). The orange-colored area indicates the brain regions showing greater activation during the texture matching than the orientation matching (evaluated by the conjunction of TC+TI vs. OC+OI, TC vs. B and TI vs. B). The blue-colored area indicates the brain regions showing greater activation during the orientation matching than the texture matching (evaluated by the conjunction of OC+OI vs. TC+TI, OC vs. B and OI vs. B). The size of the activation was thresholded at $P < 0.05$, corrected for multiple comparisons over the whole brain, with the height threshold set at $Z > 3.09$. Gray lines on the rendered MR image indicates the following sulci: CS, central sulcus; IPS, intraparietal sulcus; STS, superior temporal sulcus; OTS, occipito-temporal sulcus; CoS, collateral sulcus. The bar graphs indicate activity (i.e., contrast estimates) relative to the baseline task for each peak coordinate. Asterisks indicate the main effect of matching revealed by the two-way ANOVA (object property \times matching). Data are presented as the mean \pm SEM of 22 participants.

3.2.3.2. *Texture-specific congruency effect.* Similarly, we evaluated the conjunction of (TC vs. TI) vs. (OC vs. OI) TC vs. TI, and TC vs. B; this contrast produced no significant areas of activation.

4. Discussion

4.1. Texture-specific incongruency effect in the precuneus

Our main finding here was that the precuneus showed a stronger incongruency effect in the texture task than in the orientation task. This indicates that the precuneus is involved in the detection of visuo-tactile incongruencies for texture information. Previous neuroimaging studies have highlighted the fact that the occipital cortex is involved in both visual and tactile texture perception (Eck et al., 2013; Sathian et al., 2011; Stilla and Sathian,

2008). However, none of these studies used tasks in which a direct comparison of visual and tactile texture information was needed. By using a cross-modal matching task, we have revealed that the precuneus is involved in detecting incongruency between visual and tactile material information.

The precuneus is considered to be a hub that links to cortical areas involved in diverse functions (Bullmore and Sporns, 2009). It has been reported to play a role in processing visuo-spatial attention (Culham et al., 1998; Simon et al., 2002). For instance, Simon et al. (2002) showed that the precuneus was active during saccades to a target location relative to fixation and during covert attention to specific locations. However, in the present study, the tactile and visual stimuli were identical among all of the task conditions. Moreover, the participant attended to the same background textures in the congruent and incongruent conditions in the texture task. The frontal eye field, another critical node for visuo-spatial attention

(Corbetta et al., 1998), is located in the vicinity of the precentral sulcus and/or deep in the caudal-most part of the superior frontal sulcus (Paus, 1996). We observed neither an incongruency effect nor a texture task effect in this region (i.e., greater activation in the texture conditions than in the orientation conditions). Therefore, it is unlikely that the incongruency effect can be explained by a shift in visuo-spatial attention.

The posterior portion of the precuneus is also associated with long-term memory (Cavanna and Trimble, 2006; Wagner et al., 2005). Two lines of research suggest the involvement of the precuneus in long-term memory. Alzheimer's disease (AD) is characterized not only

by medial temporal lobe atrophy, but also by a reduction of glucose metabolism in the cingulo-parietal cortex, including the precuneus (Matsuda, 2007). Activity in the precuneus is reduced in patients with very early-stage AD who exhibit only memory impairment without general cognitive decline (Minoshima et al., 1997). Moreover, previous neuroimaging studies with healthy participants have shown that the precuneus is active during long-term memory recall for visuo-visual associations (Krause et al., 1999; Ranganath et al., 2004), audio-visual associations (Gonzalo et al., 2000) and audio-auditory associations (Krause et al., 1999; Tanabe and Sadato, 2009). These findings suggest that the precuneus is involved in processing sensory representations in long-term memory during visuo-tactile texture matching.

So, does the precuneus play a direct role in retrieving sensory representations from long-term memory? The present study matched sensorimotor components and task instructions between incongruent and congruent conditions in the texture task. Congruent and incongruent conditions should place similar demands on memory retrieval processes, so this component should be subtracted out by comparing incongruency with congruency conditions (i.e., an incongruency effect). Thus, it is unlikely that the precuneus directly retrieves sensory information in the long-term memory. Rather, as we found an incongruency effect, this region might be involved in utilizing the retrieved information to detect incongruence between visual and tactile texture information. This account is consistent with Gonzalo et al. (2000) who compared brain activity during the recognition of associated audio-visual pairs (consistent pairs) with that during the recognition of unassociated pairs (inconsistent pairs). The authors found that the difference in activity between consistent and inconsistent

Table 3
Interaction of visuo-tactile matching and object property.

Spatial extent test	P values	MNI coordinates			Z value	Hem	Anatomical region
		x	y	z			
Cluster size (mm ³)							
Texture-specific incongruency effect							
Conjunction of (TI vs. TC) vs. (OI vs. OC), TI vs. TC and TI vs. B							
1080	$P < 0.05$	-8	-74	38	3.93	L	Precuneus/superior parietal lobule
		-8	-64	38	3.82	L	Precuneus
Texture-specific congruency effect							
Conjunction of (TC vs. TI) vs. (OC vs. OI), TC vs. TI and TC vs. B							
	n.s.						

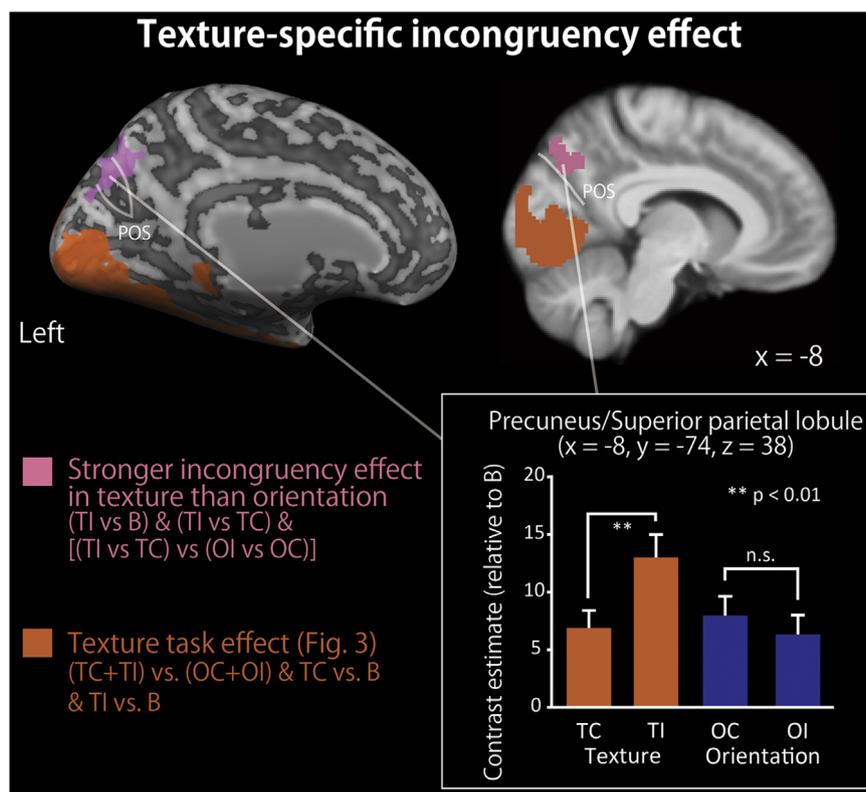


Fig. 4. Texture-specific incongruency effect. The texture incongruency effect was superimposed on a surface-rendered T1-weighted MR image averaged across the participants (upper left) and a sagittal section of the same MRI (upper right). Pink indicates the regions of greater incongruency effect in the texture matching than the orientation matching (evaluated by the conjunction of (TI vs. TC) vs. (OI vs. OC), TI vs. TC and TI vs. B). The orange-colored area indicates the brain regions showing greater activation during the texture matching than the orientation matching (evaluated by the conjunction of TC+TI vs. OC+OI, TC vs. B and TI vs. B; Fig. 3). The size of the activation was thresholded at $P < 0.05$, corrected for multiple comparisons over the whole brain, with the height threshold set at $Z > 3.09$. The bar graphs indicate the activity of the peak coordinate (i.e., contrast estimates) relative to the baseline task. Asterisks indicate the results of paired *t*-tests. Data are presented as the mean \pm SEM of 22 participants. Gray lines on the rendered MRI indicate the parieto-occipital sulcus (POS).

pairs in the precuneus increased as associative learning proceeded. We found texture task effects in the medial temporal lobe and the occipito-temporal cortex. Because the precuneus is functionally connected to these regions during the resting state (Libby et al., 2012; Margulies et al., 2009; Vincent et al., 2006), this region might constitute a hub of the brain network underlying the visuo-tactile texture matching, by functionally connecting with the medial temporal lobe and occipito-temporal cortex.

4.2. Texture task effect in the medial temporal lobe

We observed greater activation during texture than orientation matching conditions (i.e., a texture task effect) in the occipito-temporal cortex, medial temporal lobe and lateral prefrontal cortex. To the best of our knowledge, we demonstrate for the first time that the medial temporal lobe is involved in visuo-tactile texture matching.

In the present study, the participant could perceive both texture and object orientation in the texture task. Previous studies suggested that material properties of an object can be automatically encoded with its macro-geometric properties in the long-term memory (Lacey et al., 2010, 2011; Nicholson and Humphrey, 2004). However, the participant in the present study should not use object orientation to perform the texture task, because we avoided any possible association between texture and object orientation (see Section 2.3). More critically, even if the participant perceived object orientation in the texture task, such component was subtracted out in the texture task effect. Accordingly, the texture-task effect should reflect processing of textures, but not processing of object orientation.

Previous studies have shown that regions of the medial temporal lobe play essential roles in memory retrieval (Miyashita, 2004; Ranganath et al., 2004; Simons and Spiers, 2003). For instance, Ranganath et al. (2004) employed two visual delayed-matching tasks to examine brain activity during associative memory recall vs. encoding. During an associative memory task, the participant was prompted to recall a paired associate upon presentation of the first stimulus, whereas during a control task, the participant was prompted to encode the first stimulus into working memory. When the first stimulus was presented, the hippocampus showed greater activity in the visual associative memory task than in the control task. Therefore, it is possible that the medial temporal lobe is also involved in recall from memory of sensory associations during visuo-tactile texture matching.

In the present study, the participant may have relied upon sensory imagery during the visuo-tactile texture matching task. Thus, activity within the medial temporal lobe could reflect visual imagery of textures during the visuo-tactile matching task. Indeed, the medial temporal lobe can be critical for visual imagery of familiar objects, since it is implicated in associative memory retrieval of visual representations (Albright, 2012; Sakai and Miyashita, 1994). Sathian and his colleagues have investigated the role of visual imagery in haptic object processing (Deshpande et al., 2008, 2010; Peltier et al., 2007; Zhang et al., 2004). They found that visual imagery in haptic shape processing is implemented via top-down influences from fronto-parietal cortices to the LOC (LOC, Deshpande et al., 2008, 2010; Peltier et al., 2007). In contrast to shape processing, however, they found little evidence of visual imagery in haptic texture processing. Actually, unisensory texture discrimination in these studies does not require visual imagery; haptically perceived textures can be compared in terms of intensive coding (i.e., perceived magnitudes of roughness, softness and temperature; Lederman and Klatzky, 1997). Therefore, it is possible that the medial temporal lobe was activated due to the nature of visuo-tactile matching, in which tactually-perceived textures need to be compared with visually-perceived textures. Here we propose a model of

sensory information processing in these brain regions during the comparison of bi-sensory texture information.

4.3. Possible mechanisms underlying visuo-tactile texture matching

We propose that the following three major steps are involved in visuo-tactile texture matching: first, tactile texture information is extracted in the somatosensory cortex and then sent to the medial temporal lobe; second, the visual information associated with the tactile input is retrieved by interactions among the medial temporal lobe, lateral prefrontal cortex and fusiform gyrus; and third, the precuneus compares retrieved visual information with incoming perceptual information from the visual stimulus in order to detect incongruence between them. To the best of our knowledge, there is no model of neural systems underlying the visuo-tactile interaction of material properties. Thus, the proposed mechanisms may guide future research on how visual and tactile material information is interacted with each other in the brain. We elaborate these steps below (and in Supplemental Fig. S1).

First, the tactile input needs to access the long-term memory to retrieve the associated visual information. There are indirect anatomical connections between the medial temporal lobe and somatosensory cortices. More specifically, the medial temporal lobe contains the entorhinal/perirhinal cortex and parahippocampal gyrus, which are connected to a wide range of brain regions (Suzuki and Amaral, 1994). For instance, functional connectivity between the entorhinal/perirhinal cortex and the postcentral gyrus (presumably the primary somatosensory cortex) has been shown in humans using resting-state functional connectivity data (Libby et al., 2012). The entorhinal/perirhinal cortex in non-human primates is anatomically connected to the insula, which has anatomical connections with the somatosensory cortices (Friedman et al., 1986; Suzuki and Amaral, 1994). Thus, it is possible that tactile texture information in the somatosensory cortex is sent to the medial temporal lobe via the insula.

Second, previous studies have shown that the retrieval of long-term memories involves several nodes of a cortical network including the medial temporal lobe and the lateral prefrontal cortex (Fuster et al., 2000; Gonzalo et al., 2000; Hasegawa et al., 1998; Ranganath et al., 2004). These two regions are thought to work together to retrieve information about the associated memory (Miyashita, 2004; Simons and Spiers, 2003). According to the model proposed by Miyashita (2004), the medial temporal lobe might communicate automatically with anterior portions of the ventral visual pathway (e.g., the IT cortex in monkeys and the fusiform gyrus in humans) to retrieve visual information associated with tactually-perceived textures. The lateral prefrontal cortex might contribute to this retrieval process by sending a top-down signal to anterior portions of the ventral visual pathway for active memory retrieval (Miyashita, 2004).

Third and finally, the precuneus is functionally connected to regions in and around the hippocampus (Libby et al., 2012; Vincent et al., 2006) and the fusiform gyrus (Margulies et al., 2009). The ventral visual pathway including the fusiform gyrus and collateral sulcus are involved in texture perception in vision (Cant and Goodale, 2007, 2011; Cavina-Pratesi et al., 2010a, 2010b; Hiramatsu et al., 2011). Therefore, the precuneus receives two types of information: retrieved information associated with touch from the medial temporal lobe, and visual stimulus texture information from the ventral visual pathway. The precuneus might detect incongruence between these two types of information.

4.4. Weak tactile texture effect in the parietal operculum

In the present study, the parietal operculum showed no significant difference between the texture and orientation tasks. This result appears to contradict previous neuroimaging findings, which showed

greater activation during haptic perception of material properties than that of macro-geometric properties (Roland et al., 1998; Sathian et al., 2011; Stilla and Sathian, 2008). However, the present study is critically different from these studies in that our stimuli were identical between the tasks; the previous studies used different stimuli between the material and macro-geometric tasks. For instance, the stimuli used for texture tasks can produce greater vibration than those used for macro-geometric tasks (e.g., a box covered by a textile for the texture condition vs. a wooden form for shape perception in Stilla and Sathian (2008)). The parietal operculum is sensitive to vibration stimuli (Francis et al., 2000; Harrington and Hunter Downs, 2001). Therefore, greater vibration induced by stimuli in the texture task might have contributed to activation in the parietal operculum. This speculation is consistent with Kitada et al. (2006), who reported only a weak, non-significant activation during the roughness classification of linear gratings compared to the orientation classification of the same stimuli. Indeed, in electrophysiological studies in non-human primates, the parietal operculum contained neurons that are sensitive to macro-geometric properties such as object orientation (Fitzgerald et al., 2006). Accordingly, future studies are necessary to determine the relative contributions of the parietal operculum to processing of material properties and macro-geometric properties.

4.5. Interpretational issues

Two interpretational issues should be considered. First, it is not clear to what extent our findings can be generalized to the dissociation of the neural substrates involved in the visuo-tactile interaction of macro-geometric and material properties. For instance, the visuo-tactile comparison of other macro-geometric properties (e.g., shape) might involve not only common spatial frames of reference, but also cross-modal association (Holdstock et al., 2009). Thus, it remains critical to examine the dissociation by employing different types of material and macro-geometric stimuli. Second, Sathian et al. (2011) showed that the occipital cortex is involved in both visual and tactile processing. However, the task design in the present study cannot determine whether the texture task effect (i.e., TC+TI vs. OC+OI) in the occipital cortex reflects both the visual and tactile processing (e.g., the processing of visual input and retrieval of visual memory associated with the tactile input). It remains important to confirm that the activation observed in the occipital cortex is stronger in the bisensory conditions than unisensory conditions by including unisensory control conditions (e.g., comparison of tactile stimuli presented at two skin areas).

In addition, we stimulated the right hand of the participants in the present study. Stimulation of both right and left hands is critical to examine the laterality of brain activation during tactile object processing (e.g., Harada et al., 2004; Kitada et al., 2006). However, the primary purpose of the present study was not to test the laterality of brain activation, but rather to test whether brain regions such as the medial temporal lobe and precuneus are involved in visuo-tactile matching of textures. Future studies should investigate whether laterality effects are present in the cortical network underlying visuo-tactile interaction of texture by stimulating both hands.

4.6. Conclusion

The present study investigated the neural substrates involved in the visuo-tactile comparison of surface textures. The visuo-tactile comparison of textures revealed greater activation of the ventral visual pathway, medial temporal lobe and lateral prefrontal cortex compared with that of object orientation. The precuneus showed a stronger incongruency effect to cross-modally perceived textures than to perceived orientations. These results suggest that the precuneus is involved in detecting incongruency between tactile and visual texture

information, working in concert with the medial temporal lobe which is implicated in long-term memory.

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Appendix A. Supplementary information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2014.09.028>.

References

- Albright, T.D., 2012. On the perception of probable things: neural substrates of associative memory, imagery, and perception. *Neuron* 74 (2), 227–245.
- Amedi, A., Malach, R., Hendler, T., Peled, S., Zohary, E., 2001. Visuo-haptic object-related activation in the ventral visual pathway. *Nat. Neurosci.* 4 (3), 324–330.
- Amunts, K., Kedo, O., Kindler, M., Pieperhoff, P., Mohlberg, H., Shah, N.J., et al., 2005. Cytoarchitectonic mapping of the human amygdala, hippocampal region and entorhinal cortex: intersubject variability and probability maps. *Anat. Embryol.* 210 (5–6), 343–352.
- Ashburner, J., 2007. A fast diffeomorphic image registration algorithm. *NeuroImage* 38 (1), 5–113.
- Ashburner, J., Friston, K.J., 2005. Unified segmentation. *NeuroImage* 26, 839–851.
- Bullmore, E., Sporns, O., 2009. Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* 10 (3), 186–198.
- Burton, H., MacLeod, A.M., Videen, T.O., Raichle, M.E., 1997. Multiple foci in parietal and frontal cortex activated by rubbing embossed grating patterns across fingerpads: a positron emission tomography study in humans. *Cereb. Cortex* 7 (1), 3–17.
- Cant, J.S., Goodale, M.A., 2007. Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cereb. Cortex* 17 (3), 713–731.
- Cant, J.S., Goodale, M.A., 2011. Scratching beneath the surface: new insights into the functional properties of the lateral occipital area and parahippocampal place area. *J. Neurosci.* 31 (22), 8248–8258.
- Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain* 129 (Pt 3), 564–583.
- Cavina-Pratesi, C., Kentridge, R.W., Heywood, C.A., Milner, A.D., 2010a. Separate processing of texture and form in the ventral stream: evidence from fMRI and visual agnosia. *Cereb. Cortex* 20 (2), 433–446.
- Cavina-Pratesi, C., Kentridge, R.W., Heywood, C.A., Milner, A.D., 2010b. Separate channels for processing form, texture, and color: evidence from fMRI adaptation and visual object agnosia. *Cereb. Cortex* 20 (10), 2319–2332.
- Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., et al., 1998. A common network of functional areas for attention and eye movements. *Neuron* 21 (4), 761–773.
- Culham, J.C., Brandt, S.A., Cavanagh, P., Kanwisher, N.G., Dale, A.M., Tootell, R.B., 1998. Cortical fMRI activation produced by attentive tracking of moving targets. *J. Neurophysiol.* 80 (5), 2657–2670.
- Deshpande, G., Hu, X., Lacey, S., Stilla, R., Sathian, K., 2010. Object familiarity modulates effective connectivity during haptic shape perception. *NeuroImage* 49 (3), 1991–2000.
- Deshpande, G., Hu, X., Stilla, R., Sathian, K., 2008. Effective connectivity during haptic perception: a study using Granger causality analysis of functional magnetic resonance imaging data. *NeuroImage* 40 (4), 1807–1814.
- Eck, J., Kaas, A.L., Goebel, R., 2013. Crossmodal interactions of haptic and visual texture information in early sensory cortex. *NeuroImage* 75, 123–135.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage* 25 (4), 1325–1335.

- Fitzgerald, P.J., Lane, J.W., Thakur, P.H., Hsiao, S.S., 2006. Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. *J. Neurosci.* 26 (24), 6473–6484.
- Fleming, R.W., 2014. Visual perception of materials and their properties. *Vis. Res.* 94, 62–75.
- Francis, S.T., Kelly, E.F., Bowtell, R., Dunseath, W.J., Folger, S.E., McGlone, F., 2000. fMRI of the responses to vibratory stimulation of digit tips. *NeuroImage* 11 (3), 188–202.
- Friedman, D.P., Murray, E.A., O'Neill, J.B., Mishkin, M., 1986. Cortical connections of the somatosensory fields of the lateral sulcus of macaques: evidence for a corticollimbic pathway for touch. *J. Comp. Neurol.* 252 (3), 323–347.
- Friston, K.J., Ashburner, J., Kiebel, S.J., Nichols, T.E., Penny, W.D., 2007. *Statistical Parametric Mapping: The Analysis of Functional Brain Images*. Academic Press, London.
- Friston, K.J., Glaser, D.E., Henson, R.N., Kiebel, S., Phillips, C., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: applications. *NeuroImage* 16 (2), 484–512.
- Friston, K.J., Holmes, A., Poline, J.B., Price, C.J., Frith, C.D., 1996. Detecting activations in PET and fMRI: levels of inference and power. *NeuroImage* 4 (3), 223–235.
- Friston, K.J., Jezzard, P., Turner, R., 1994. Analysis of functional MRI time-series. *Hum. Brain Mapp.* 1, 153–171.
- Friston, K.J., Penny, W.D., Glaser, D.E., 2005. Conjunction revisited. *NeuroImage* 25 (3), 661–667.
- Fuster, J.M., Bodner, M., Kroger, J.K., 2000. Cross-modal and cross-temporal association in neurons of frontal cortex. *Nature* 405 (6784), 347–351.
- Gonzalo, D., Shallice, T., Dolan, R., 2000. Time-dependent changes in learning audiovisual associations: a single-trial fMRI study. *NeuroImage* 11 (3), 243–255.
- Grefkes, C., Weiss, P.H., Zilles, K., Fink, G.R., 2002. Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. *Neuron* 35 (1), 173–184.
- Hadjikhani, N., Roland, P.E., 1998. Cross-modal transfer of information between the tactile and the visual representations in the human brain: a positron emission tomographic study. *J. Neurosci.* 18 (3), 1072–1084.
- Harada, T., Saito, D.N., Kashikura, K., Sato, T., Yonekura, Y., Honda, M., Sadato, N., 2004. Asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study. *J. Neurosci.* 24 (34), 7524–7530.
- Harrington, G.S., Hunter Downs 3rd, J., 2001. fMRI mapping of the somatosensory cortex with vibratory stimuli. Is there a dependency on stimulus frequency? *Brain Res.* 897 (1–2), 188–192.
- Hasegawa, I., Fukushima, T., Ihara, T., Miyashita, Y., 1998. Callosal window between prefrontal cortices: cognitive interaction to retrieve long-term memory. *Science* 281 (5378), 814–818.
- Hiramatsu, C., Goda, N., Komatsu, H., 2011. Transformation from image-based to perceptual representation of materials along the human ventral visual pathway. *NeuroImage* 57 (2), 482–494.
- Holdstock, J.S., Hocking, J., Notley, P., Devlin, J.T., Price, C.J., 2009. Integrating visual and tactile information in the perirhinal cortex. *Cereb. Cortex* 19 (12), 2993–3000.
- Holmes, A.P., Friston, K.J., 1998. Generalisability, random effects and population inference. *NeuroImage* 7, S754.
- James, T.W., Humphrey, G.K., Gati, J.S., Servos, P., Menon, R.S., Goodale, M.A., 2002. Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia* 40 (10), 1706–1714.
- Jones, L.A., Lederman, S.J., 2006. *Human Hand Function*. Oxford University Press, New York.
- Kassuba, T., Klinge, C., Holig, C., Roder, B., Siebner, H.R., 2013. Vision holds a greater share in visuo-haptic object recognition than touch. *NeuroImage* 65, 59–68.
- Kim, S., James, T.W., 2010. Enhanced effectiveness in visuo-haptic object-selective brain regions with increasing stimulus salience. *Hum. Brain Mapp.* 31 (5), 678–693.
- Kitada, R., Hashimoto, T., Kochiyama, T., Kito, T., Okada, T., Matsumura, M., et al., 2005. Tactile estimation of the roughness of gratings yields a graded response in the human brain: an fMRI study. *NeuroImage* 25 (1), 90–100.
- Kitada, R., Kito, T., Saito, D.N., Kochiyama, T., Matsumura, M., Sadato, N., Lederman, S.J., 2006. Multisensory activation of the intraparietal area when classifying grating orientation: a functional magnetic resonance imaging study. *J. Neurosci.* 26 (28), 7491–7501.
- Krause, B.J., Schmidt, D., Mottaghy, F.M., Taylor, J., Halsband, U., Herzog, H., et al., 1999. Episodic retrieval activates the precuneus irrespective of the imagery content of word pair associates. *A PET study. Brain* 122 (2), 255–263.
- Kriegeskorte, N., Simons, W.K., Bellgowan, P.S., Baker, C.L., 2009. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.* 12 (5), 535–540.
- Lacey, S., Hall, J., Sathian, K., 2010. Are surface properties integrated into visuohaptic object representations? *Eur. J. Neurosci.* 31 (10), 1882–1888.
- Lacey, S., Lin, J.B., Sathian, K., 2011. Object and spatial imagery dimensions in visuohaptic representations. *Exp. Brain Res.* 213 (2–3), 267–273.
- Lederman, S.J., Klatzky, R.L., 1997. Relative availability of surface and object properties during early haptic processing. *J. Exp. Psychol.: Hum. Percept. Perform.* 23 (6), 1680–1707.
- Libby, L.A., Ekstrom, A.D., Ragland, J.D., Ranganath, C., 2012. Differential connectivity of perirhinal and parahippocampal cortices within human hippocampal subregions revealed by high-resolution functional imaging. *J. Neurosci.* 32 (19), 6550–6560.
- Margulies, D.S., Vincent, J.L., Kelly, C., Lohmann, G., Uddin, L.Q., Biswal, B.B., et al., 2009. Precuneus shares intrinsic functional architecture in humans and monkeys. *Proc. Natl. Acad. Sci. USA* 106 (47), 20069–20074.
- Matsuda, H., 2007. Role of neuroimaging in Alzheimer's disease, with emphasis on brain perfusion SPECT. *J. Nucl. Med.* 48 (8), 1289–1300.
- Minoshima, S., Giordani, B., Berent, S., Frey, K.A., Foster, N.L., Kuhl, D.E., 1997. Metabolic reduction in the posterior cingulate cortex in very early Alzheimer's disease. *Ann. Neurol.* 42 (1), 85–94.
- Miyashita, Y., 2004. Cognitive memory: cellular and network machineries and their top-down control. *Science* 306 (5695), 435–440.
- Nakashita, S., Saito, D.N., Kochiyama, T., Honda, M., Tanabe, H.C., Sadato, N., 2008. Tactile-visual integration in the posterior parietal cortex: a functional magnetic resonance imaging study. *Brain Res. Bull.* 75 (5), 513–525.
- Naya, Y., Yoshida, M., Miyashita, Y., 2001. Backward spreading of memory-retrieval signal in the primate temporal cortex. *Science* 291 (5504), 661–664.
- Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. *NeuroImage* 25 (3), 653–660.
- Nicholson, K.G., Humphrey, G.K., 2004. The effect of colour congruency on shape discriminations of novel objects. *Perception* 33 (3), 339–353.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113.
- Paus, T., 1996. Location and function of the human frontal eye-field: a selective review. *Neuropsychologia* 34 (6), 475–483.
- Peltier, S., Stilla, R., Mariola, E., LaConte, S., Hu, X., Sathian, K., 2007. Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. *Neuropsychologia* 45 (3), 476–483.
- Ranganath, C., Cohen, M.X., Dam, C., D'Esposito, M., 2004. Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *J. Neurosci.* 24 (16), 3917–3925.
- Roland, P.E., O'Sullivan, B., Kawashima, R., 1998. Shape and roughness activate different somatosensory areas in the human brain. *Proc. Natl. Acad. Sci. USA* 95 (6), 3295–3300.
- Saito, D.N., Okada, T., Morita, Y., Yonekura, Y., Sadato, N., 2003. Tactile-visual cross-modal shape matching: a functional MRI study. *Brain Res. Cognit. Brain Res.* 17 (1), 14–25.
- Sakai, K., Miyashita, Y., 1994. Visual imagery: an interaction between memory retrieval and focal attention. *Trends Neurosci.* 17 (7), 287–289.
- Sathian, K., Lacey, S., Stilla, R., Gibson, G.O., Deshpande, G., Hu, X., et al., 2011. Dual pathways for haptic and visual perception of spatial and texture information. *NeuroImage* 57 (2), 462–475.
- Servos, P., Lederman, S., Wilson, D., Gati, J., 2001. fMRI-derived cortical maps for haptic shape, texture, and hardness. *Brain Res. Cognit. Brain Res.* 12 (2), 307–313.
- Shattuck, D.W., Mirza, M., Adisetiyo, V., Hojatkashani, C., Salamon, G., Narr, K.L., et al., 2008. Construction of a 3D probabilistic atlas of human cortical structures. *NeuroImage* 39 (3), 1064–1080.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33 (3), 475–487.
- Simons, J.S., Spiers, H.J., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. *Nat. Rev. Neurosci.* 4 (8), 637–648.
- Squire, L.R., Zola-Morgan, J.T., 1991. The cognitive neuroscience of human memory since H.M. *Annu. Rev. Neurosci.* 14, 259–288.
- Stilla, R., Sathian, K., 2008. Selective visuo-haptic processing of shape and texture. *Hum. Brain Mapp.* 29 (10), 1123–1138.
- Stoesz, M.R., Zhang, M., Weisser, V.D., Prather, S.C., Mao, H., Sathian, K., 2003. Neural networks active during tactile form perception: common and differential activity during macrospatial and microspatial tasks. *Int. J. Psychophysiol.* 50 (1–2), 41–49.
- Suzuki, W.A., Amaral, D.G., 1994. Perirhinal and parahippocampal cortices of the macaque monkey: cortical afferents. *J. Comp. Neurol.* 350 (4), 497–533.
- Tal, N., Amedi, A., 2009. Multisensory visual-tactile object related network in humans: insights gained using a novel crossmodal adaptation approach. *Exp. Brain Res.* 198 (2–3), 165–182.
- Tanabe, H.C., Honda, M., Sadato, N., 2005. Functionally segregated neural substrates for arbitrary audiovisual paired-association learning. *J. Neurosci.* 25 (27), 6409–6418.
- Tanabe, H.C., Sadato, N., 2009. Ventrolateral prefrontal cortex activity associated with individual differences in arbitrary delayed paired-association learning performance: a functional magnetic resonance imaging study. *Neuroscience* 160 (3), 688–697.
- Vincent, J.L., Snyder, A.Z., Fox, M.D., Shannon, B.J., Andrews, J.R., Raichle, M.E., et al., 2006. Coherent spontaneous activity identifies a hippocampal-parietal memory network. *J. Neurophysiol.* 96 (6), 3517–3531.
- Wager, T.D., Nichols, T.E., 2003. Optimization of experimental design in fMRI: a general framework using a genetic algorithm. *NeuroImage* 18 (2), 293–309.
- Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. *Trends Cognit. Sci.* 9 (9), 445–453.
- Weniger, G., Boucsein, K., Irle, E., 2004. Impaired associative memory in temporal lobe epilepsy subjects after lesions of hippocampus, parahippocampal gyrus, and amygdala. *Hippocampus* 14 (6), 785–796.
- Whitaker, T.A., Simoes-Franklin, C., Newell, F.N., 2008. Vision and touch: independent or integrated systems for the perception of texture? *Brain Res.* 1242, 59–72.
- Worsley, K.J., Friston, K.J., 1995. Analysis of fMRI time-series revisited-again. *NeuroImage* 2 (3), 173–181.
- Zhang, M., Weisser, V.D., Stilla, R., Prather, S.C., Sathian, K., 2004. Multisensory cortical processing of object shape and its relation to mental imagery. *Cognit. Affect. Behav. Neurosci.* 4, 251–259.