

Haptic face identification activates ventral occipital and temporal areas: An fMRI study

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Abstract

Many studies in visual face recognition have supported a special role for the right fusiform gyrus. Despite the fact that faces can also be recognized haptically, little is known about the neural correlates of haptic face recognition. In the current fMRI study, neurologically intact participants were intensively trained to identify specific facemasks (molded from live faces) and specific control objects. When these stimuli were presented in the scanner, facemasks activated left fusiform and right hippocampal/parahippocampal areas (and other regions) more than control objects, whereas the latter produced no activity greater than the facemasks. We conclude that these ventral occipital and temporal areas may play an important role in the haptic identification of faces at the subordinate level. We further speculate that left fusiform gyrus may be recruited more for facemasks than for control objects because of the increased need for sequential processing by the haptic system.

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1. Introduction

Visual face processing is of strong evolutionary significance across many biological species because the face carries different categories of information that are all critical to survival: stranger or friend? predator or prey? potential mate? However, recent research has shown that face processing is not the sole purview of human vision. People are also capable of haptically recognizing both live faces (Kilgour & Lederman, 2002) and rigid 3-D

facemasks (Casey & Newell, 2005; Kilgour & Lederman, submitted; Kilgour, de Gelder, & Lederman, 2004; Pietrini et al., 2004).

For example, Kilgour and Lederman (2002) demonstrated that with no practice, blindfolded neurologically intact college students haptically identified unfamiliar live faces with ~80% accuracy in a 3-AFC match-to-sample task. Participants initially explored a standard face, followed by a set of three comparison faces presented in sequence. From among the three comparison faces, they were required to choose the one that they had first examined. Chance-level performance was therefore 33%. Removing the usual material properties by presenting rigid 3-D facemasks of the live exemplars impaired performance (58%), thus highlighting the critical importance

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of both material and 3-D cues for haptic object processing, including faces (Klatzky, Lederman, & Metzger, 1985; Lederman & Klatzky, 1997). Pietrini et al. (2004) subsequently confirmed that with only 5 h of training, both blindfolded neurologically intact and blind (2 congenitally blind, 2 early blind) subjects learned to recognize faces haptically with over 90% accuracy.

An important focus of neuroscience face research is to determine which brain areas are involved in face recognition independent of the input modality. Visual neuroscience research has established that a specific area in the right fusiform gyrus is dedicated to visual face identification (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Kanwisher, McDermott, & Chun, 1997; Rhodes, Byatt, Michie, & Puce, 2004). However, very little is known about the neural substrates that subserve haptic face recognition, the issue addressed by the current study.

Pietrini et al. (2004) included faces as one of several object categories in a study derived from earlier visual research by this group, which asked if response activation patterns produced during visual object recognition are category-dependent (Haxby et al., 2001). Pietrini et al. subsequently questioned whether category-related neural response patterns in the ventral visual pathway, measured with functional MRI, serve to represent either sensory images or more abstract category-related representations of object form. To address this issue, they compared neural response patterns during haptic and visual object recognition. In one experiment, five sighted, blindfolded subjects performed tasks involving human-made objects (i.e., bottles, shoes) and facemasks molded from live faces. Visual and haptic processing were contrasted using a 2-AFC match-to-sample task, in which observers were required to say whether two objects presented in sequence were the same or different. A second task involved simple haptic exploration. Three important results were obtained using the blindfolded, sighted group. First, when all object categories were collapsed, a region of the lateral occipital cortex (LOC) produced a multisensory visual and tactile response that was similar to other studies (Amedi, Malach, Kendler, Peled, & Zohary, 2001; Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; James et al., 2002; Reed, Shoham, & Halgren, 2004). Second, non-face objects produced different spatially localized patterns of brain activation than faces when haptic exploration was used, thus providing evidence for haptically derived category specificity. Third, despite the fact that both visual and haptic exploration of faces produced activation in the ventral temporal cortex, the pattern of activation produced by exploring faces haptically was different from that produced by exploring faces visually. Together, these findings suggest that between-category object recognition recruits the same multisensory process within the LOC whether the input is haptic or visual; however, category-

specific object recognition recruits different ventral occipitotemporal regions depending on whether the input is haptic or visual. Previous studies of visual face recognition have compared face stimuli with control stimuli and have described face-specific activation in a region of the right fusiform gyrus (Kanwisher, etc.). Pietrini et al. (2004) designed their study to analyze distributed patterns of activation rather than to describe the foci of face-specific activation. Nevertheless, their study does predict that a haptic face-specific activation focus, if it were shown to exist, would not overlap with the focus for visual face-specific activation.

The focus of the present study is complementary to that of Pietrini et al. (2004), inasmuch as ours concerns haptic face processing per se. Like Tadoma, the tactile method used successfully by a small number of deaf-blind individuals to track continuous speech in real time (Reed et al., 1985), our previous work (Kilgour & Lederman, 2002; Kilgour et al., 2004) clearly confirms that manual contact with the face constitutes a highly informative input channel. Moreover, unlike Tadoma proficiency which is rare, haptic face recognition is not limited to only a few trained users. As mentioned above, therefore, face processing is not unique to vision. For both scientific and applied reasons, we believe it is important to study haptic face processing in its own right.

To begin our neural investigation, we choose to address the neural network that mediates haptic face recognition in the posterior brain. Note that as memory is always a component of recognition, it is not possible here to clearly separate its unique contribution from those related to other aspects of the current task. In our fMRI study of haptic face processing, we explicitly ask: which regions of the posterior brain are activated when people are *haptically* trained to differentiate objects as faces with a high degree of proficiency?

To provide reasonable assurance that observers are processing the facemasks specifically as faces, we use an identification task, instead of the same/different and match-to-sample tasks used by Kilgour and Lederman (2002) and Pietrini et al. (2004). Observers are also highly trained (i.e., 10–12 h) so that they are able to identify specific faces by name with 100% accuracy and within a relatively short time (i.e., ~7 s on average).

Our predictions are guided by three sets of neural studies. The first set involves a recent study by Kilgour et al. (2004) which reports that an individual with prosopagnosia (LH), a neurological deficit in visual face recognition, differentiated 3-D clay facemasks very poorly by hand, in contrast to 3-D clay teapot controls. To our knowledge, that study reports the first documented case of haptic prosopagnosia. LH's brain had several cortical and subcortical lesions including the right temporal lobe such as the hippocampus, left subcortical occipitotemporal white matter, and bilateral parietooccipital regions (Etcoff, Freeman, & Cave, 1991).

A second complementary set, which includes several studies that used common or nonsense non-face objects and one that presented lifelike facemasks, has also shown involvement of temporal and occipital regions. An individual with a lesion involving areas of the occipital and temporal lobes was reported as experiencing haptic, as well as visual, agnosia (Feinberg, Roth, & Heilman, 1986). Covert haptic identification of non-face common objects with identifiable shapes (e.g., button) activated the occipital lobe (including calcarine cortex and extrastriate areas) relative to baseline (i.e., haptic discrimination of “non-real” textured items) (Deibert, Kraut, Kremen, & Hart, 1999). Similarly, Amedi et al. (2001; see also Amedi et al., 2002) showed that covert naming of haptically explored common objects with solid 3-D forms (e.g., fork) activated occipitotemporal areas more than covert naming of familiar texture controls (e.g., sandpaper); moreover, both tasks produced greater activation in these same areas relative to a simpler baseline condition (rest). Haptic object recognition of real common objects (e.g., tennis ball) activated the inferior temporal gyrus and the lateral occipital complex more than palpation of nonsense objects made of balsa wood (Reed et al., 2004). Pietrini et al.’s results (2004) also showed involvement of ventral occipital and inferior temporal areas during haptic recognition of common man-made objects and facemasks. Finally, occipital areas, including ventrolateral occipital regions, were also more highly activated when participants haptically explored unfamiliar 3-D nonsense objects relative to baseline (fixation of a blue cross) (James et al., 2002). Collectively, these results suggest that ventral occipital and temporal cortex are commonly activated by haptic recognition of familiar and unfamiliar objects relative to baseline (i.e., textures; rest). Moreover, the tasks typically require haptic object processing at the basic level of classification Rosch, Mervis, Gray, Johnson, and Boyes-Braem (1976). Both sets of studies implicate ventral occipital and temporal regions, which may also underlie LH’s difficulty in haptically differentiating faces. Accordingly, we hypothesize that these regions may further play an important role in the haptic *identification* of facemasks by neurologically intact participants.

The final set of studies speaks more directly to the specific neural mechanisms that underlie face processing. As mentioned earlier, visual neuroscience has implicated the right fusiform gyrus in visual face processing (Gauthier et al., 1999; Kanwisher et al., 1997; Rhodes et al., 2004). Pietrini et al. (2004) showed that haptic and visual face-specific activation patterns did not overlap along the fusiform gyrus. This finding explicitly rules out a small multisensory face-specific processing region; however, it does not reject the possibility that the right fusiform gyrus as a whole mediates face recognition with subregions specialized for particular sensory input modalities.

We selected an identification task for two reasons. First, it encourages haptic processing of objects explicitly as faces. Second, it requires participants to specifically differentiate faces at the exemplar or subordinate level (Rosch et al., 1976), in keeping with the nature of LH’s specific impairment in both visual and haptic face perception. Finally, to avoid confounding the contributions of material versus geometric cues, which might have occurred in some of the studies that used common objects, we choose to present rigid facemasks that clearly provide only geometric information.

Using functional magnetic resonance imaging (fMRI) to measure brain activity, we predict that in the posterior brain, haptic identification of facemasks may activate ventral occipital and temporal regions, specifically the right fusiform gyrus, more strongly than do carefully controlled sensorimotor nonsense objects. Like the facemasks, the rigid control objects are made of clay and vary three-dimensionally. They are deliberately constructed so that they are similar to the masks in external size and shape; however, their internal features (i.e., protruberances and depressions) are randomly positioned so as to elicit the same kinds of exploratory hand movements as the facemasks. Finally, to equate the familiarity of face and control objects, we provide substantial training to participants in order to achieve comparably high levels of performance prior to the fMRI task.

2. Methods

2.1. Participants

Seven healthy right-handed volunteers (4 males, 3 females), aged 21–29 years (mean = 27.6; $SD = \pm 3.1$), participated in the fMRI study. All were right-handed as defined by a version of the Edinburgh Inventory (Oldfield, 1971). The ethical review boards of the University of Western Ontario and Queen’s University both approved a protocol for the procedure. None of the volunteers had any history of symptoms requiring neurological, psychological, or other medical care.

2.2. Stimuli

A set of 36 3-D clay facemasks employed in previous research (Kilgour & Lederman, 2002; Kilgour et al., 2004) served as face stimuli. Each facemask was constructed from a human model by molding plaster strips to the model’s face, allowing holes for the model to breathe. When the plaster strips dried, the cast was removed from the face. Clay was then molded to the interior of the cast, resulting in a mask of the face that was identical in size and spatial proportion to the model’s face, with their features preserved. The masks

were air dried, then baked in a kiln to produce a rigid surface that was uniformly rough to the touch.

Additionally, 36 3-D sensorimotor control objects were created from Cone 6–8 stoneware clay, the same clay from which the facemasks were made. The plaster casts from which the facemasks were made were also used to create the control objects. That is, clay was applied to the interior surface of the plaster casts of the faces such that the control objects would be the same size and of similar curvature as the facemasks. However, the clay was not molded into the eye area or the noses as we were not making faces. Although we would have preferred to produce facemasks with facial features scrambled, this was not technically feasible. Accordingly, varying numbers of depressions, bumps and raised lines (2–8 per mask) were spatially distributed randomly over the object's surface, as shown in Fig. 1. The control objects required exploratory hand movements that were very similar to those used to explore the facemasks, as confirmed by the first author's observations during training and from videotapes of a post-imaging session described in Section 3.1. Complexity was not explicitly controlled because our primary goal was to configure the internal features of the control objects randomly within an exterior shape and size that were both similar to those of the facemasks.

The clay facemasks and sensorimotor control objects were used during both the training and scanning phases of the experiments. The complete set of 72 stimulus objects was used across participants. However, each participant was presented with a different reduced subset for training (i.e., 18 faces and 18 sensorimotor control objects), which was further reduced for the fMRI task (i.e., 12 of the original 18 faces and 12 of the original 18 sensorimotor control objects).

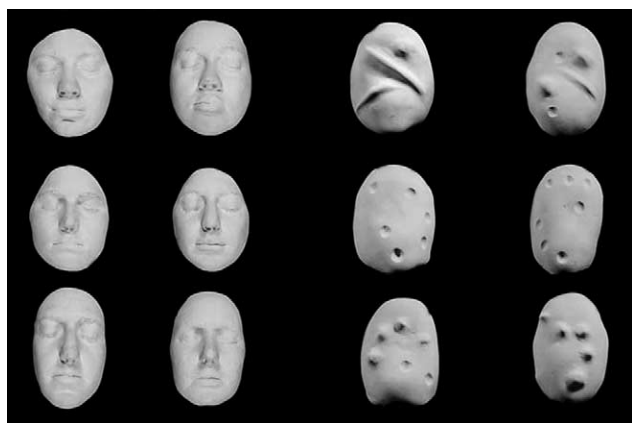


Fig. 1. Examples of 3-D facemasks and 3-D sensorimotor control objects, which were all made of clay. Each control object was approximately the same size and general shape as the facemasks. Bumps and pits were applied to the surface of the objects in a random fashion—the objects were not symmetrical. During the training phase, participants learned 18 facemasks by name (all female) and 18 sensorimotor control objects by letter.

2.3. Training procedure

Each participant was individually trained at Queen's University to identify a set of 18 facemasks by name (all female) and 18 sensorimotor control objects by letter. During training, the participant lay blindfolded on a bench in a supine position and the stimuli were presented at approximately abdomen level. To minimize movement artefacts, he or she explored the stimuli with only one hand. We selected the left hand because the left hand/right hemisphere may have an advantage in a variety of haptic tasks, as indicated by split-brain research, research with patients and evidence from neurologically intact observers (Banich, 2004; Kolb & Whishaw, 2003; Summers & Lederman, 1990). In addition, using the left hand maximized the chances of observing right-hemisphere fusiform activation (e.g., Kanwisher et al., 1997).

Each participant began by learning four facemasks, selected and presented randomly. A facemask was presented with the associated name.² The observer freely explored the facemasks manually. This was repeated several times until the participants indicated they were ready to be tested. During testing, they were presented with a facemask and required to name it correctly. They were required to identify each facemask correctly on two trials, before the training session was ended. The next training session was identical, except that two additional facemasks were added. This procedure continued until all the faces were learned. The control objects were learned in the same manner, using letters for purposes of identification.

Participants were required to identify facemasks and control objects with 100% accuracy in about 7–8 s (on average) to ensure that observers were highly proficient at this task while ensuring that the identification process took up most of the manual exploration period. On average, it took 10–12 h of training to satisfy the demanding criteria for acceptable haptic identification.

2.4. fMRI procedure

The fMRI phase of the study was performed using the MRI facility at the Robarts Research Institute in London, Ontario. For each participant, a different subset of the 18 facemasks and 18 sensorimotor control objects used originally in training was presented in the magnet (12 facemasks and 12 control objects). Participants were not told which of the objects they had previously learned would be presented during the fMRI task. They lay blindfolded in the magnet with their head secured in the

² We employed the actual names of the people whose faces were used to produce the molds from which the facemasks were created. We did not believe it was necessary to control for the familiarity of the names or letters because each observer was so highly practiced, ultimately recognizing all objects perfectly, and within only about 7 s.

head coil with foam padding. Their left shoulder and upper arm were also supported with foam padding to minimize movement. A Plexiglas table placed over the lower half of the body, with the front edge at about the level of the abdomen, allowed each participant to explore the stimuli in roughly the same position as during the training phase, again using only their left hand. Participants rested their right hand/arm on their abdomen or straight down by their side. The stimuli were presented to the participants on the Plexiglas table with the sliding platform. Two experimenters were used to speed the stimulus presentation process. One experimenter presented the other with two stimulus objects at a time, who in turn presented them in proper sequence to the subject, as shown in Fig. 2.

In the fMRI phase, the observers were instructed to explore and silently name facemasks and control objects within each 10 s presentation interval. The entire schedule of the fMRI study was guided by a very short beep that was audible to both the participant and the experimenter.

All participants began by exploring two control objects, each for 10 s and separated by a 5-s inter-stimulus interval during which the experimenter replaced the current object with the second object (1.5 s per image). After the 30-s control-object interval, participants explored a pair of facemasks with the same two 10-s stimulus presentation separated by a 5-s inter-stimulus interval. Each participant repeated this 30-s cycle for both sensorimotor control objects and facemasks six

times, resulting in 360 s (30-s cycle \times 2 object types \times 6 times, 240 functional images), as shown in Fig. 3. The stimuli were blocked in pairs with each presented for 10 s as the most efficient procedure for obtaining adequate brain activation within the necessary time constraints.

2.5. MRI acquisition

Images were acquired using a 4T, whole body MRI system (Varian/Siemens) and a quadrature head coil. We collected functional images using a T2*-weighted, segmented (navigator corrected), gradient echo EPI acquisition (TE = 15 ms, TR = 750 ms, flip angle = 40°, 2 segments) for BOLD-based imaging. The field of view was 19.2 cm \times 19.2 cm \times 6.6 cm, with an in-plane resolution of 64 \times 64 pixels and 15 contiguous coronal slices, resulting in a voxel size of 3.0 mm \times 3.0 mm \times 6.0 mm. Each volume (15 planes) required 1.5 s to acquire and spanned a volume of cortex from the occipital pole to the central sulcus. Functional activation data were superimposed onto high-resolution T1-weighted anatomical images covering a whole brain (voxel size of 0.75 mm \times 0.75 mm \times 1.5 mm).

2.6. MRI analysis

Image processing and statistical analysis were performed using the Statistical Parametric Mapping package (SPM99, <http://www.fil.ion.ac.uk/spm>, Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Mathworks, Sherborn MA, USA) (Friston, Ashburner, Frith, Heather, & Frackowiak, 1995; Friston, Holmes, et al., 1995; Worsley & Friston, 1995).

Each scan was begun with four “dummy” volumes to bring the tissue to stable state. These four volumes were then eliminated during pre-processing. All images within each run were realigned to the second scan. Then, the T1-weighted anatomical images were co-registered to the second scan in the functional images using the similarity measure, Mutual Information. Each co-registered T1-weighted anatomical image was normalized to a standard T1 template involving a linear and nonlinear spatial transformation. The first step of the normalization involved determining the optimum 12-parameter affine transformation by minimizing the sum of squares difference between the image to be normalized and the template image. The affine transformation was followed by estimating nonlinear deformations with a linear combination of three dimensional discrete cosine transform (DCT) basis functions. The template image was defined by the Montreal Neurological Institute (MNI) and closely approximates the space described in the atlas of Talairach and Tournoux (1988). The parameters from this normalization process were then applied to each functional image. High-resolution anatomical images

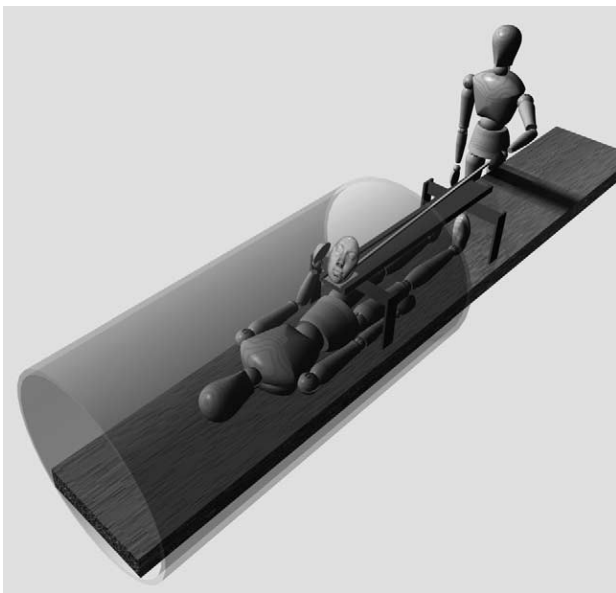


Fig. 2. The set-up used to present stimuli to a participant in the fMRI scanner. The experimenter used the rod to change the position of the moveable table. In the “in” position, the participant could reach the stimulus; in the “out” position, the experimenter could reach the stimulus. A second experimenter (not shown) handed the stimuli to the first experimenter.

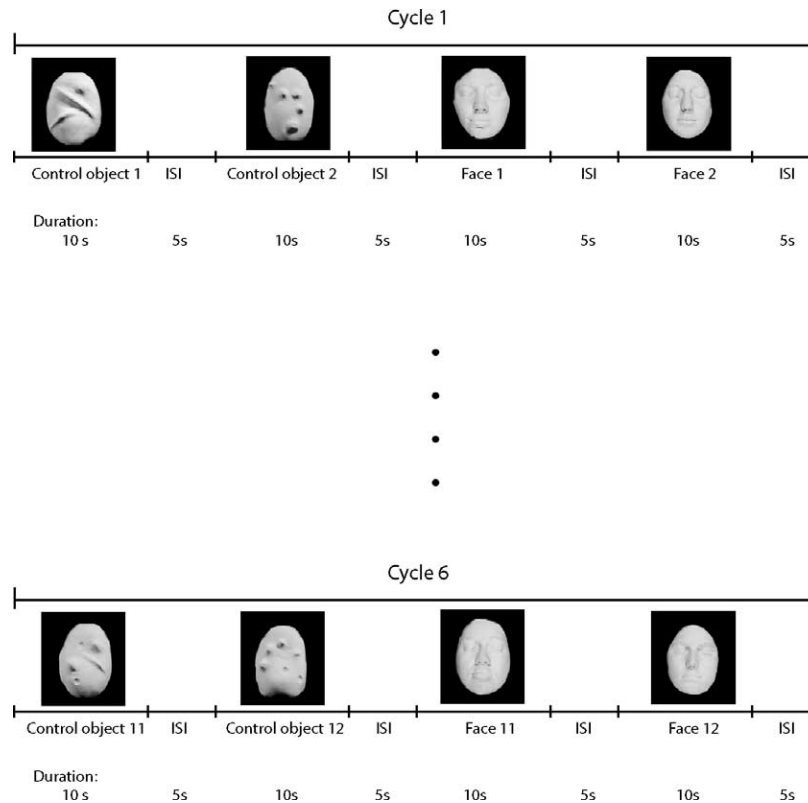


Fig. 3. Experimental design for the fMRI experiment. Participants were told to explore and silently name the control and facemask objects presented within each 10-s presentation interval. Participants explored two control objects, each for 10 s followed by a 5-s interstimulus interval. After this 30-s control-object cycle, subjects explored a pair of facemasks with the same presentation and inter-stimulus intervals, constituting a second 30-s cycle. The sensorimotor control and facemask cycles were repeated six times for a total of 360 s.

were also normalized by the same procedure. Finally, these spatially normalized functional images were resampled to a voxel size of $2 \times 2 \times 2$ mm and smoothed using an 8-mm FWHM Gaussian kernel in the $/x/$, $/y/$, and $/z/$ axes.

2.7. Statistical analysis

We fitted a general linear model (GLM) to the pooled data from all observers, using a fixed-effect model to increase the sensitivity of the analysis (Friston, Ashburner, et al., 1995; Friston, Holmes, et al., 1995). The time series for each voxel was high-pass filtered to 1/120 Hz and low-pass filtered by a canonical hemodynamic response function. The neural activities for each of the 10-s periods (i.e., 6.67 scans) were modeled with each box-car function convolved with a canonical hemodynamic response function. The design matrix consisted of seven sessions, each of which included two regressors for facemasks and sensorimotor control objects for each participant. We implemented two linear contrasts involving 10-s exploration of facemasks vs. 10-s exploration of control objects (facemasks vs. control objects) and vice versa. The resulting SPM $\{T\}$ for these contrasts was thresholded at $T_{411,9} = 3.75$ ($p < .0001$, uncor-

rected for multiple comparisons). We report brain regions with a significant $p < .05$ cluster level (i.e., volume $> 632 \text{ mm}^3$) corrected for multiple comparisons over the whole functional brain image (Friston, Holmes, Poline, Price, & Frith, 1996).

2.8. VOI-based group analysis

To confirm that the group main effect obtained with the fixed-effect model generalized to the population, we subsequently implemented a volume-of-interest (VOI) statistical analysis using a random-effect model (see e.g., Friston, Holmes, Price, Buchel, & Worsley, 1999; Saito, Okada, Morita, Yonekura, & Sadato, 2003). The data were extracted as filtered raw data from areas significantly activated by the contrast of facemasks vs. control objects.

To calculate relative percent signal change, we first calculated the mean signal value of all data for each participant in each area. Then, the relative percent signal change was calculated for each participant as follows: (mean signal in 30-s experimental block – mean signal of all data)/(mean signal of all data). The first four scans from each 30-s were excluded from this analysis. The relative percent signal change in each VOI was statistically

evaluated between facemasks and control objects using the SPSS software package (Version 10.0J, SPSS Japan, Tokyo, Japan).

3. Results

3.1. Training results

By the end of the training period, participants recognized both facemasks and control objects with 100% accuracy. The mean response time for facemasks was 7.2 ± 1.5 s (mean \pm 1 SD) and for sensorimotor control objects was 8.4 ± 1.5 s. A paired-samples *t* test showed that the response time for facemasks was not significantly different from that for the control objects, $t_6 = -1.57$, $p = .17$. The results confirm that the facemasks and control objects were of comparable difficulty and familiarity.

In addition, the hand movements used to explore both types of object were comparable, consisting of enclosure (i.e., grasp) and contour following (i.e., edge following) exploratory procedures (Lederman & Klatzky, 1987). This was ascertained in three different ways. First, the first author observed this behavioral pattern during the extensive training phase. Second, the ways in which participants subsequently described their manual exploration immediately after the imaging to the first author were very similar to how they had manually explored the stimulus objects during training. Third, in a post-imaging phase conducted 1–2 weeks after imaging, the same participants performed a haptic match-to-sample face recognition task with their left hand to confirm their high level of competence. A set of facemasks never presented during those two phases was used. The sessions were videotaped and subsequently examined informally by the authors. Once again, the exploratory hand movements were similar across the face stimuli, consisting primarily of contour-following, and less frequently, enclosure exploratory procedures (Lederman & Klatzky, 1987). Overall, the similarity in hand movements is to be expected, given the considerable practice our partici-

pants received and the fact that facemasks and control objects alike varied only in their geometric properties. These results are important because they allow us to minimize the possibility that differences in activation between the facemasks and the control objects were not due to differences in the hand movements used to explore the two sets of objects.

3.2. fMRI results

Table 1 shows the coordinates of foci in the contrast of facemasks vs. sensorimotor control objects. In accord with our hypothesis, the facemask vs. sensorimotor control objects contrast significantly activated the left fusiform gyrus and the right parahippocampal/hippocampal area (Fig. 4). In addition, the facemask task significantly activated the left cingulate area, the left inferior parietal lobe, and two clusters of the right cerebellum (Table 1, Fig. 4). There was no notably different activity in the vicinity of the postcentral gyrus. The contrast of control objects vs. facemasks failed to yield any significant activity.

3.3. VOI analyses

The Volume of Interest (VOI) analyses were performed to test the generality of the results of the fixed-effect group analyses. The mean value of the relative signal change was 0.11 ± 0.08 (mean \pm 1 SD) for facemasks and -0.11 ± 0.11 for sensorimotor control objects in the left fusiform gyrus, and 0.07 ± 0.04 for facemasks and -0.08 ± 0.05 for sensorimotor control objects in the right parahippocampal/hippocampal area. Other corresponding control results included 0.08 ± 0.07 and -0.07 ± 0.09 for the left inferior parietal lobe, 0.10 ± 0.05 and -0.07 ± 0.06 in the left cingulate region, 0.09 ± 0.04 and -0.06 ± 0.08 in one cluster in the cerebellum (26, -66, -26), and 0.08 ± 0.05 , and -0.07 ± 0.07 in the other cerebellar cluster (16, -80, -36). Pairwise *t* tests showed a significant difference in signal change between the two object sets for the left fusiform area ($t_6 = 3.53$, $p < .01$) and for the right

Table 1
Significantly activated foci in the contrasts of facemasks vs. sensorimotor control objects (fixed effect)

Anatomical region	BA ^a	Side	x ^b	y ^b	z ^b	t _{411,9} ^c	Cluster volume (mm ³)
Fusiform area	37	L	-48	-40	-18	5.05	736
Parahippocampal/hippocampal	35	R	28	-20	-18	4.94	784
Cingulate	23	L	-4	-14	28	5.59	7240
Inferior parietal area	40	L	-50	-46	38	4.71	736
Cerebellum		R	16	-80	-36	5.01	1520
		R	26	-66	-26	4.83	4528

^a BA = Brodmann area.

^b x, y, z are stereotaxic coordinates (mm).

^c *t* scores are peak activations within a significant cluster of activated voxels; $t_{411,9} > 3.75$ corresponds to $p < .0001$ uncorrected for multiple comparisons; $p < .05$ corrected.

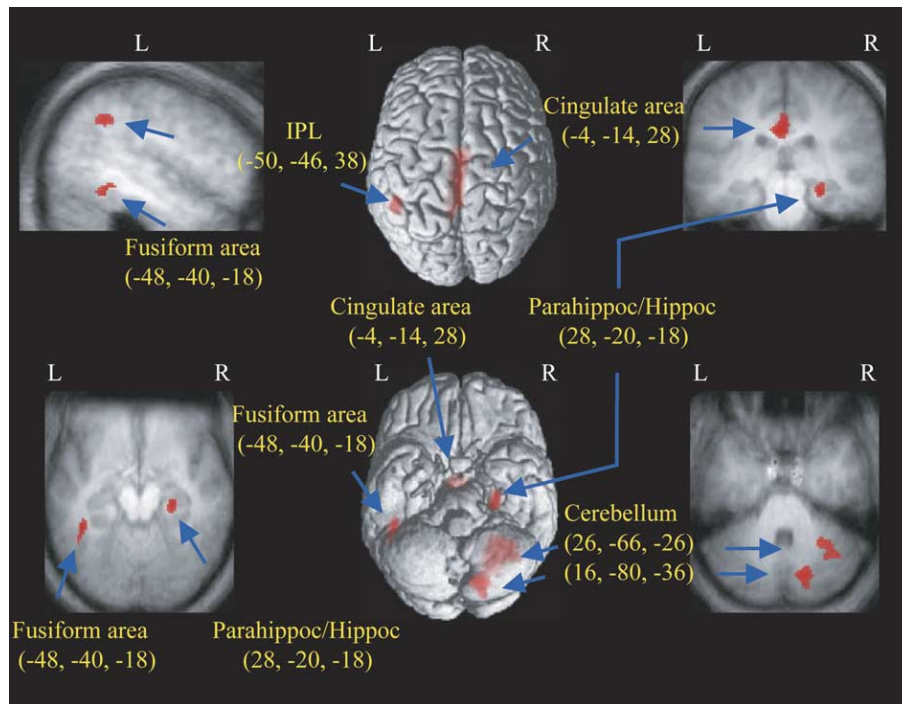


Fig. 4. Significantly activated brain areas. The contrast of facemasks vs. control objects significantly activated the left inferior parietal lobe, the left fusiform gyrus, the right hippocampal/parahippocampal area, the left posterior cingulate area, and two clusters of the right cerebellum. Control objects did not yield any activity significantly more than facemasks. Brain activity was superimposed on the group mean T1 image or on surface-rendered T1 image unrelated to the participants of the present study. $T_{411,9}$ value was thresholded at 3.75, corresponding to $p < .0001$ uncorrected for multiple comparisons. $p < .05$ corrected at cluster level. L = left; R = right.

parahippocampal/hippocampal area ($t_6 = 4.58$, $p < .001$); in addition, significant differences were obtained in the left inferior parietal lobe ($t_6 = 3.00$, $p < .05$), the left cingulate area ($t_6 = 4.68$, $p < .01$), and in two clusters in the cerebellum (i.e., for $[26, -66, -26]$: $t_6 = 3.51$, $p < .05$, and for $[16, -80, -36]$: $t_6 = 4.39$, $p < .01$). These results confirm that there was a greater signal change for facemasks than for control objects in the two predicted brain regions, as well as in the left inferior parietal lobe, left cingulate area, and two regions of the cerebellum.

4. Discussion

In the absence of vision, haptic identification of facemasks activated left fusiform and right parahippocampal/hippocampal regions more than did the haptic identification of control objects. In contrast, the identification of sensorimotor control objects showed no differential activity in the posterior brain. These results suggest that ventral occipital and temporal areas, such as the fusiform and parahippocampal/hippocampal regions, may play an important role in haptic face identification. In addition, we obtained similar results for left cingulate, left inferior parietal, and right cerebellar regions.

4.1. Task considerations and implications

Previous studies have shown that both neurologically intact, sighted observers (e.g., Kilgour & Lederman, 2002; Kilgour et al., 2004; Pietrini et al., 2004) and blind observers (Pietrini et al., 2004) are capable of recognizing faces by touch alone with above-chance performance. Unfortunately, it is possible that these individuals might not have treated the stimulus objects as faces per se. Therefore, we used an identification task in the current study as a means of enhancing the possibility that participants would process the objects as faces. In addition, we provided substantially more training with the facemasks than in the previous studies. Despite the absence of all material cues, our observers learned to perform the task perfectly within only ~ 7 s. Therefore, the current results clearly confirm that people are indeed capable of recognizing faces by touch alone.

Participants were trained to perform both tasks with comparably high speed and accuracy; moreover, as the facemask and control objects were similar in overall size and shape (Fig. 1), they required similar forms of manual exploration. There was no conspicuously different activity between the types of stimuli in the vicinity of the postcentral gyrus. Therefore, it is unlikely that other factors, such as movement, differential cognitive demands, or level of object familiarity, produced the disparate

activity patterns produced by the facemasks and sensorimotor control objects.

4.2. fMRI results and implications

The prediction that ventral temporal and occipital areas are involved in haptic face identification derives from the fact that these areas were impaired in the first documented case of haptic prosopagnosia (Kilgour et al., 2004), as well as by studies involving the haptic recognition of familiar and unfamiliar objects relative to baseline (i.e., textures; rest) in neurologically intact individuals (Amedi et al., 2001, 2002; Deibert et al., 1999; James et al., 2002; Pietrini et al., 2004; Reed et al., 2004) and in a case study involving an individual with damage to the areas of interest (Feinberg et al., 1986). The current results support our hypothesis that ventral occipital and temporal regions, which are damaged in a haptic prosopagnosic individual (LH), are crucial for haptic face recognition and identification. Our results also extend those of Pietrini et al. (2004) by showing that parahippocampal/hippocampal areas are important as well for haptic face identification. Although not part of the original hypothesis, we further note that the predicted difference in activation patterns occurs too in several other areas, including left cingulate area, left inferior parietal lobe and right cerebellum. These other activated areas may be involved in haptic face identification.

Our prediction concerning the specific involvement of the right fusiform gyrus derives from neuroimaging studies of visual face recognition, which implicate this region (Gauthier et al., 1999; Kanwisher et al., 1997; Rhodes et al., 2004). In our study, participants received considerably greater training in a haptic identification task to increase the likelihood that observers would process the facemasks as faces per se. The results confirm involvement of the fusiform gyrus in haptic face recognition and identification, although the activation is in the left hemisphere. We will consider possible reasons for left- as opposed to right-hemisphere fusiform involvement in later sections.

We have focused on the neural network that mediates haptic face identification in the posterior brain. As mentioned in the introduction, at such an early stage in our neural investigation, rather than attempting to dissociate haptic face processing from memory processes, we regard memory as an important component of haptic face identification. Nevertheless, data exist that are relevant to the current study. Our subjects were instructed to associate facemasks with their names, while control objects were associated with letters. It is known that the left temporal lobe is crucial for lexical retrieval (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996). The left temporal lobe was activated when subjects named persons, animals and tools (Damasio et al., 1996). In addition, retrieving people's names from face

cues activated the left temporal pole more than did retrieval of their occupations (Tsukiura et al., 2002). However, the current task activated ventral and temporal regions that are more ventral and posterior than the temporal regions reported by both Damasio et al. (1996) and Tsukiura et al. (2002). Hence, it is unlikely that the occipito-temporal regions were primarily activated by the difference in category names between the facemasks and control objects.

4.3. Activation of fusiform regions

The current results only partially support our hypothesis concerning the involvement of the *right* fusiform gyrus. Although the fusiform gyrus was activated more strongly by faces than by control stimuli, the greater activation was on the *left* side, despite the fact that we used left-hand exploration to maximize the chances of seeing right-hemisphere fusiform activation. The left hemisphere has been implicated in sequential processing (Kolb & Whishaw, 2003). Therefore, it is possible that the greater left-hemisphere fusiform activation observed in this study occurs because the haptic system must gather information about facial features in a predominantly sequential fashion during manual exploration. In contrast, the need for sequential processing during visual face recognition is less obvious inasmuch as the visual system can examine the entire face simultaneously.

Researchers such as Amedi et al. (2001) and James et al. (2002) have suggested that for object recognition, the occipitotemporal region may serve as a multisensory shape-recognition area by receiving sensory inputs about objects from earlier sensory stages of somatosensory and visual processing. As explained earlier, it was not our goal to draw comparisons with visual face recognition in this fMRI study on haptic face identification. Thus, we chose not to include a visual control.

Activity in the fusiform gyrus (and possibly other areas) may have occurred alternatively as a result of participants using a visual-mediation heuristic to haptically process faces (e.g., Lederman, Klatzky, Chataway, & Summers, 1990). That is to say, they may have translated the haptically derived inputs into a visual image, and subsequently processed the visual image using visual mechanisms. In contrast to the right-hemisphere dominance observed in the fusiform gyrus during visual face perception, it is known that visual imagery of faces evokes a stronger response in the left ventral temporal cortex (Ishai, Ungerleider, & Haxby, 2000; Ishai, Haxby, & Ungerleider, 2002). Might left fusiform gyrus activation in the current study (Table 1; Fig. 4) be the result of participants using a temporally based visual-mediation heuristic during haptic exploration of faces? We note that at the end of the experiment half of the participants volunteered that they had used visual imagery. The remaining half indicated they did not. It is also possible,

therefore, that adopting a visual-mediation heuristic during haptic exploration activated a network of brain areas that has been previously implicated in visual face imagery.

A visual-mediation heuristic would seem to be a viable option inasmuch as the visual system is generally far superior to the haptic system when processing the complex geometric features that differentiated facemasks and sensorimotor control objects. Lederman et al. (1990) confirmed the use of visual mediation when participants were required to haptically identify common objects represented in 2-D raised-line drawings. They showed strong correlations between rated ability to form visual images [Visual Vividness Imagery Questionnaire (VVIQ); Marks, 1973] and their identification accuracy and response times. However, the behavioral study on haptic face matching (Kilgour & Lederman, 2002) failed to confirm similar significant correlations between VVIQ scores and either face-matching accuracy or response time. Given the current ambiguity concerning the use of visual mediation in haptic object recognition, we plan to continue exploring this issue in additional behavioural and fMRI studies. The success with which two congenitally blind subjects, as well as two others blinded at an early age, haptically recognized facemasks (Pietrini et al., 2004) provides preliminary evidence that neither visual experience nor visual imagery is necessary, although it may still be sufficient. Clearly additional research is needed to resolve the controversy between multisensory and visual-mediation interpretations of haptic face processing.

4.4. Activation of inferior parietal, parahippocampal/hippocampal, cingulate gyrus, and cerebellar regions

A lesion to the inferior parietal lobe has previously been associated with an inability to recognize or name common objects (tactile agnosia) (Gerstmann, 1918; Reed, Caselli, & Farah, 1996). Gerstmann's patient showed normal haptic processing of the objects' physical attributes (e.g., roughness, shape, and temperature) and could select an object that had been previously explored. Perhaps the inferior parietal lobe contributes to the process of binding sensory attributes into a representation of objects for memory retrieval. In support of this suggestion, Reed et al.'s patient seemed to show such deficits in binding shape features. The patient failed to recognize half of the common objects with her agnostic hand. She was able to extract the basic contour of the object (e.g., could roughly draw the bottle), but could not correctly perceive the internal details (e.g., drew 12 holes for a two-hole cassette tape).

Previous research has speculated that the hippocampal/parahippocampal and posterior cingulate regions may be part of a memory retrieval network for visual face recognition (Leveroni et al., 2000). Kim et al. (1999)

have suggested that the cerebellum may perform the role of integrating and coordinating recognition memory processes for visual face recognition. Hence, one can speculate that haptic information about faces may be transformed into an integrated representation in the inferior parietal cortex and fusiform gyrus, while the hippocampal/parahippocampal regions, posterior cingulate region, and the cerebellum may contribute to retrieving the memory trace related to the representation.

Memory is likely to have played an important and highly complex role in the current haptic face-identification task. Recall that prior to the fMRI phase of the experiment, participants were trained over a period of several weeks to successfully identify both facemasks and sensorimotor control objects. Therefore, during the subsequent fMRI phase, participants were required to use long-term memory to retrieve the identity of each face. Leveroni et al. (2000) have shown that a network of bilateral brain activation involving the prefrontal, lateral temporal, and mesial temporal (hippocampal and parahippocampal regions) is activated by recognition of visual famous faces compared to unfamiliar faces or faces that had only recently been encoded. In addition, the contrast between famous faces and newly learned faces shows significant activity in a number of areas, including the right fusiform and parahippocampal/hippocampal regions in the temporal lobe, and bilateral posterior cingulate and right inferior parietal regions in the parieto-occipital lobe. Although that study is not directly comparable to the current one, which compared haptic identification of facemasks versus sensorimotor control objects, it may be worth exploring further whether similar areas are activated during long-term memory of faces that are haptically identified.

Unlike visual face processing, the highly sequential nature of manual exploration demands that the haptic system integrate successively acquired inputs into an overall representation of the object using short-term memory. To the extent that visual mediation is used with faces to recode the haptically derived inputs into a visual representation, brain areas activated during visual short-term memory for faces may also be involved during haptic face identification. Ishai et al. (2002) showed that visual imagery of famous faces activated a network that included bilateral calcarine, hippocampus, precuneus, intraparietal sulcus (IPS), and the inferior frontal gyrus (IFG). In all regions, images generated from short-term memory (subjects memorized specific pictures of famous faces just before the imagery task) produced greater activation than images generated from long-term memory (i.e., subjects imagined famous faces without learning specific pictures of the people). In the current study, short-term memory would be used in the fMRI task during the face-encoding stage. While the Ishai et al. study and the current one are not directly equivalent, it is not unreasonable to speculate that this visual-imagery

short-term memory network might be involved in haptic face identification.

4.5. Summary

Haptic identification of rigid 3-D facemasks significantly activated left fusiform, right hippocampal/parahippocampal, left cingulate, left inferior parietal, and right cerebellar regions more than sensorimotor control objects, also made of clay and matched for difficulty, familiarity, and manual exploration. The haptic identification of the control objects did not show any additional significant activity in posterior brain regions beyond those produced by the facemasks. This result suggests that ventral occipital and medial temporal areas may play an important role in the neural network that mediates haptic face identification at the subordinate level. When considered along with the results from other studies discussed in the introduction, these regions would appear to constitute part of a neural network that subserves haptic processing of common objects—including faces—and nonsense shapes at both basic and subordinate levels. We further speculate that the left fusiform region may mediate the temporal processing of sequentially explored facial features, as is more commonly required during haptic as opposed to visual face processing.

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