

Beyond sensory images: Object-based representation in the human ventral pathway

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We investigated whether the topographically organized, category-related patterns of neural response in the ventral visual pathway are a representation of sensory images or a more abstract representation of object form that is not dependent on sensory modality. We used functional MRI to measure patterns of response evoked during visual and tactile recognition of faces and manmade objects in sighted subjects and during tactile recognition in blind subjects. Results showed that visual and tactile recognition evoked category-related patterns of response in a ventral extrastriate visual area in the inferior temporal gyrus that were correlated across modality for manmade objects. Blind subjects also demonstrated category-related patterns of response in this “visual” area, and in more ventral cortical regions in the fusiform gyrus, indicating that these patterns are not due to visual imagery and, furthermore, that visual experience is not necessary for category-related representations to develop in these cortices. These results demonstrate that the representation of objects in the ventral visual pathway is not simply a representation of visual images but, rather, is a representation of more abstract features of object form.

haptic perception | fMRI | supramodal cortex

In the human brain, the ventral object visual pathway can generate distinct representations for a virtually unlimited number of objects or faces. Using functional MRI (fMRI), we have shown that visual perception of faces and other object categories evokes distinct patterns of neural activation in ventral temporal cortex that are widely distributed and overlapping (1). The topographic organization of these representations of faces and objects in ventral temporal cortex, which we have called object form topography, may reflect how the attributes of visual appearance that underlie object and face recognition are related visually, structurally, or semantically. The present study was designed to test the hypothesis that the representations of object categories in these cortical regions are not simply visual but, rather, are representations of more abstract, supramodal aspects of object form. Recently, Amedi *et al.* (2, 3) and James *et al.* (4) have shown that both visual and tactile recognition of objects activate a part of object-responsive cortex, the dorsal part of the lateral occipital complex or LO proper. However, they did not show whether the information carried by activity during visual and tactile recognition, as reflected in topographic patterns of response, are correlated. Such crossmodal correlation of patterns of response would suggest that a common representation is activated by these two sensory modalities. Moreover, neural responses during tactile recognition of objects could be due to visual imagery of these objects (5, 6) rather than to the activation of a supramodal representation of object form. Therefore, we decided to investigate whether the category-related patterns of response to visually presented objects are also found for tactile processing of the same object categories and the extent to which these patterns are correlated across modalities, which affords a direct test of whether the representations of objects evoked by visual and tactile recognition are related. In addition, we studied blind subjects, who were either congenitally blind or had become blind at an early age and

reported no visual memories, to rule out that category-related patterns of response in visual cortex during tactile processing are due to visual imagery and to test whether visual experience is required for category-related patterns of response to develop in these “visual” cortices.

We conducted two experiments. In the first experiment, we used fMRI to measure regional brain activity in sighted subjects during tactile and visual recognition of different categories of objects, specifically human faces, bottles, and shoes. In the second experiment, we studied tactile recognition of the same object categories in subjects who were congenitally blind or who became blind early and reported no visual memories. Bottles and shoes were selected as categories of nonface objects because they are common objects that blind subjects typically recognize tactilely on a daily basis. For tactile recognition of faces, we used life masks made with a soft skin-like material over a hard backing. The study of tactile and visual recognition of different object categories in the same sighted subjects allowed us to examine whether the category-related patterns of response we have described for visual perception (1) are found also for tactile recognition and whether these patterns are crossmodal.

Materials and Methods

Subjects. Five sighted subjects (two females and three males, mean age = 33 ± 6 years), two congenitally blind subjects, and two early blind subjects with no recollection of any visual experience (two females and two males, mean age = 53 ± 14 years; cause of blindness: one with congenital glaucoma, one with retrolental fibroplasia, one with acquired glaucoma at age five, one with spinal meningitis at age four) were studied. All subjects received medical, neurological, and psychiatric examinations and a structural MRI brain scan to exclude disorders that could affect brain function (other than blindness in the congenitally blind individuals). No subject was taking any psychotropic medication. All subjects gave their written informed consent after the study procedures and risks were explained.

Image Acquisition. fMRI was used to examine neural activity elicited by tactile and visual recognition of objects. Images were acquired by using gradient echo echoplanar imaging on a GE 3T scanner (General Electric, Milwaukee, WI) [repetition time = 2,500 ms, 40 3.5-mm-thick sagittal images, field of view = 24 cm, echo time = 30 ms, flip angle = 90°]. High-resolution T1-weighted spoiled gradient recall images were obtained for each subject to provide detailed anatomy (124 1.2-mm-thick sagittal images, field of view = 24 cm). For tactile recognition, 8 time series, each consisting of 174 brain volumes, were obtained for each subject. For visual recognition in

Abbreviations: fMRI, functional MRI; VOI, volume of interest.

Data deposition: The neuroimaging data have been deposited with the fMRI Data Center, www.fmridc.org (accession no. 2-2004-115Y8).

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the sighted subjects, 12 time series, each consisting of 125 brain volumes, were obtained. Voxels were $3.75 \times 3.75 \times 3.5$ mm for both the tactile and the visual recognition studies.

Tactile Recognition Stimuli and Tasks. Tactile stimuli were life masks of faces, plastic bottles, and shoes made with no metal. The objects in the nonface category were selected because they were common objects that were close to the same size as faces and because blind subjects would recognize them tactilely on a daily basis. Each object was presented to the subjects with a wooden pole with a Plexiglas platform on one end upon which the object was attached with Velcro. The subjects had their forearms comfortably resting on a wooden table positioned over their stomach. Subjects' arms were restrained at the elbow to avoid movement of the upper arm. Subjects explored each object using both hands. Sighted subjects were blindfolded during the tactile recognition tasks. Subjects performed two tactile recognition tasks: one-back repetition detection and simple tactile exploration. During the one-back task, subjects indicated whether each object was the same or different as the previous one by pressing foot pedals with the right ("same") or left ("different") foot. During the simple exploration task, subjects explored each object but made no responses. Based on behavioral pilot studies, presentation times for the one-back task were varied by category to make performance accuracies more equivalent. Faces were presented for 15 s, shoes for 10 s, and bottles for 5 s. All subjects could achieve better than 90% accuracy for all categories with these presentation times. Subjects could respond at any time between initial presentation of a stimulus object and the presentation of the next stimulus. For the simple exploration task, which was included to control for the effect of unequal presentation times in the one-back task, all stimuli were presented for 5 s. Stimulus presentations were separated by 5 s. Each time series consisted of three stimulus blocks, one for each category, in counterbalanced order. Each block was 2 min, and 30-s rest intervals separated blocks. One-back repetition and simple exploration tasks were presented on alternating runs, with approximately half of the subjects in each group performing the simple exploration task on the odd-numbered runs and vice versa.

Subjects were instructed to try to form a representation of the whole object, rather than relying on isolated details for identification. Subjects wore surgical cotton gloves to minimize the use of surface clues such as the texture of the material for matching. Furthermore, objects were presented alternately at 45° and 315° angles (relative to the vertical axis of the Plexiglas platform) because pilot studies indicated that rotation of objects increased task difficulty and required subjects to form a more holistic representation of the objects.

Before fMRI scanning, subjects received five 1-h training sessions on consecutive days to become familiar with the objects and the task procedure.

Tactile Recognition Data Analysis. Image data were analyzed with multiple regression by using 36 regressors to model hemodynamic changes associated with our tactile recognition tasks. For each category in each task, the following effects were modeled by separate regressors: 1, mean response to each stimulus; 2, linear changes in responses to stimuli within blocks; 3, quadratic changes in responses to stimuli within blocks; 4, mean response during delays between stimuli; 5, linear changes within blocks of responses during delays; 6, quadratic changes within blocks of responses during delays. In addition to these 36 regressors of interest, 8 regressors of no interest were included to factor out signal changes due to head movement, namely the six movement parameters derived from the motion correction postprocessing analyses and the residual mean squares of the fit of each unaligned scan to the base scan and of each realigned scan to the base scan. Beta weights for the regressors that modeled the mean responses to each category in each task were used as estimates of the strength of response relative to rest in each

voxel. The remaining regressors for each category and task accounted for temporal changes within blocks related to temporal variations in responses to stimuli and responses during delays. These regressors were treated as regressors of no interest.

Cortex that responded significantly during tactile recognition was identified on the basis of the omnibus effect of all regressors of interest ($P < 10^{-8}$). For the analysis of neural responses in visual extrastriate cortex during tactile and visual recognition, anatomically defined volumes of interest (VOI) were drawn on the high-resolution structural images to identify ventral temporal, inferior temporal, ventral occipital, and dorsal occipital cortex. The VOI for ventral temporal cortex extended from 70 to 20 mm posterior to the anterior commissure in Talairach brain atlas (7) coordinates and consisted of the lingual, parahippocampal, and fusiform gyri. The VOI for inferior temporal cortex also extended from 70 to 20 mm posterior to the anterior commissure and consisted of the inferior temporal gyrus, excluding the occipitotemporal sulcus. The VOI for ventrolateral occipital cortex extended from the occipital pole to 70 mm posterior to the anterior commissure and consisted of the lingual, fusiform, inferior occipital, and middle occipital gyri. VOIs also were drawn to identify the dorsal occipital cortex, the intraparietal sulcus, sensorimotor cortex (defined as the pre- and postcentral gyri), and the cerebellar hemispheres to describe the activations seen in these structures during tactile recognition. Voxels within these VOIs that responded significantly during tactile recognition were used for an analysis of correlations between category-related patterns of response to the same category ("within-category") and between patterns of response to different categories ("between-category"). Because these voxels were selected based on their inclusion in nonoverlapping, anatomically defined VOIs, results from different VOIs do not overlap.

Correlations between patterns of response in voxels that responded significantly during tactile recognition were analyzed to determine whether these patterns were category-related by using the methods we used in a previous study of patterns of response during visual recognition (1). This analysis determines whether the patterns of response during the one-back tactile recognition task are most similar to patterns of response to the same category during the simple exploration tactile recognition task. For each subject, correlations were calculated between patterns of response to the same category and between patterns of response to different categories. Correlations between patterns of response were calculated based on pairs of observations defined by the strengths of response in each voxel to the two conditions being compared. Response strengths were normalized as differences from the mean response to all categories in each voxel. We then compared the strength of within-category correlations to the strength of between-category correlations with matched-pair t tests.

Visual Recognition Stimuli and Task. The location of cortex that responds during visual recognition of faces and other objects and category-related patterns of response during visual recognition was determined in all sighted subjects by using the stimuli and task procedures from a previous fMRI study of visual recognition (1). Visual and tactile recognition studies were conducted on separate days. Visual stimuli were photographic images, presented for 500 ms with 2-s intervals between stimuli, and subjects performed a one-back repetition task in which they indicated their responses by pressing buttons with the right thumb. In addition to the categories used in the current study of tactile recognition, patterns of response to houses, chairs, cats, scissors, and scrambled pictures were also measured, but these results were not used in the current analysis. For a detailed description of stimuli, task procedures, and methods of analysis, see Haxby *et al.* (1).

Analysis of Overlap Between Visually and Tactilely Responsive Cortices. Object-selective visual cortex was defined by using our previous criteria, based on an omnibus test of differential response to

categories ($P < 10^{-6}$). Overlap between cortex that responded during tactile and visual recognition was quantified for each anatomically defined VOI and expressed as a percentage of visually responsive cortex. This crossmodally responsive cortex was then divided according to whether it responded maximally to faces, bottles, or shoes during visual recognition to determine which subset of visually responsive cortex was more involved in tactile recognition.

Analysis of Category-Related Responses Across Tactile and Visual Modalities. Correlations between patterns of response during tactile and visual recognition were calculated for crossmodally responsive cortex to analyze whether category-related patterns were similar across these modalities. Brain images from the separate tactile and visual recognition scanning sessions were aligned by using the program 3DVOLREG in AFNI (R. W. Cox, Bethesda; afni.nimh.nih.gov/afni). Voxels were selected that met criteria for being re-

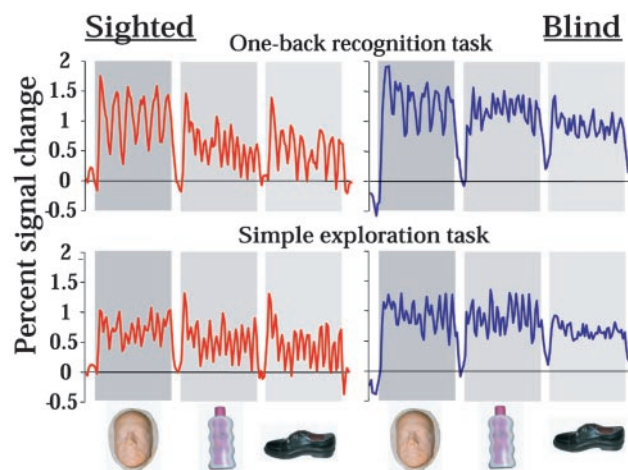


Fig. 2. Mean time series, averaging across subjects, voxels, and blocks, for the response in inferior temporal cortex during the one-back repetition detection and simple tactile exploration tasks in sighted and blind subjects.

sponsive to both visual and tactile stimuli (see above). For each subject, crossmodal correlations were calculated both within and between categories. The strengths of within- and between-category correlations were compared with matched-pair t tests.

Results

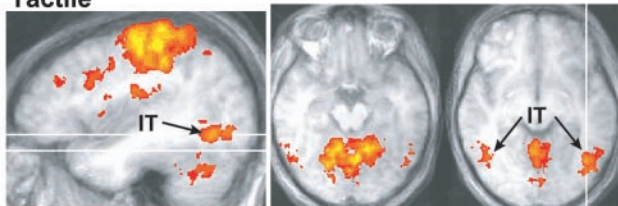
Areas Activated During Tactile Recognition. We measured patterns of neural response with fMRI while subjects performed two object tactile recognition tasks: one-back repetition detection and simple tactile exploration. Both tactile tasks evoked activity in ventral extrastriate cortex in both sighted and blind subjects. The most consistent areas of activation were in the posterior inferior temporal sulcus bilaterally (Figs. 1 and 2). Other visual areas activated during tactile recognition were observed in ventral temporal, and inferior occipital and dorsal occipital extrastriate visual cortices. In addition, tactile recognition evoked activity in large bilateral areas in the hand region of sensorimotor cortex, in the intraparietal sulcus, and in the cerebellum (Table 1). Note that the inferior and ventral temporal areas, which were based on anatomically defined VOIs (see *Materials and Methods*), differ from each other primarily in the lateral-medial dimension: the center of mass for the inferior temporal activation lies 14–22 mm lateral to that for the ventral temporal activation. The inferior temporal activations in sighted and blind subjects were in essentially the same locations, with a separation of only 8 mm, center to center, in Talairach (7) stereotaxic space.

Category-Related Patterns of Response During Tactile Recognition.

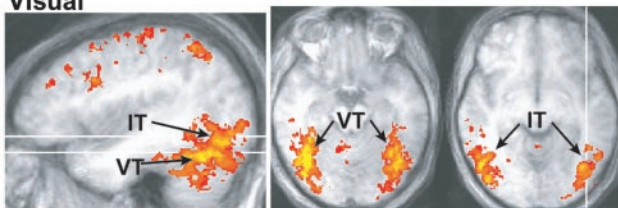
Patterns of response in extrastriate cortices were analyzed to determine whether they were category-related. These analyses examined correlations between the patterns of response evoked during the one-back repetition detection task and the patterns evoked during simple tactile exploration. Stronger within-category correlations across task, as compared to between-category correlations, indicate the existence of category-related patterns of response (1). In sighted subjects, within-category correlations were greater than between-category correlations in inferior temporal, but not in ventral temporal, cortex (Fig. 3). These differences were significant for comparisons of within-bottles or within-shoes correlations and within-faces to correlations between bottles or shoes and faces ($P < 0.05$). Within-category correlations for bottles or shoes and for faces were nearly identical. In blind subjects, within-category correlations were significantly greater than between-category correlations in ventral temporal cortices ($P < 0.05$). In inferior temporal cortex, this comparison was in the expected

Sighted Subjects

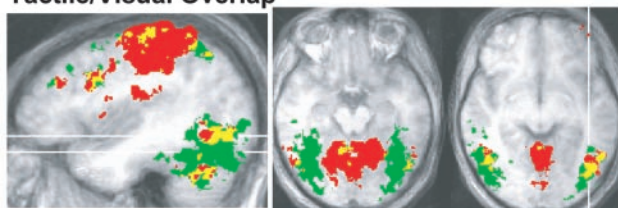
Tactile



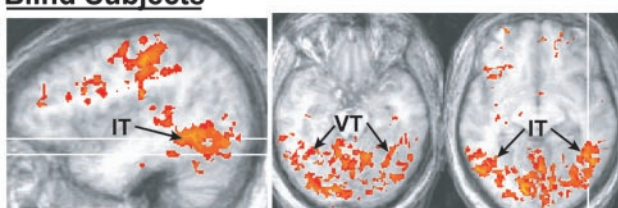
Visual



Tactile/Visual Overlap



Blind Subjects



x = -42 mm z = -16 mm z = -6 mm

Fig. 1. Brain areas that responded during tactile and/or visual object perception in sighted subjects and during tactile perception in blind subjects. Sagittal and axial images from group Z-score maps of activated areas are shown for the sighted and blind subjects. The inferior temporal (IT) and ventral temporal (VT) regions activated by tactile and visual object perception are indicated. The tactile/visual overlap map shows the areas activated by both tactile and visual perception (shown in yellow), as well as the areas activated only by tactile (red) and visual (green) perception. The white lines in the sagittal images correspond to the locations of the axial slices and, similarly, the white line in the axial slice indicates the location of the sagittal section.

Table 1. Volumes and Talairach atlas coordinates for the centers of mass for regions that responded during tactile recognition

Region	Group	Volume (mean ± SE), cc	Left			Right		
			x	y	z	x	y	z
Inferior temporal	Sighted	3.8 ± 0.4	-46	-58	-11	48	-55	-10
	Blind	6.3 ± 1.1	-46	-55	-4	54	-52	-5
Ventral temporal	Sighted	3.9 ± 0.7	-24	-55	-14	28	-49	-18
	Blind	7.3 ± 1.8	-32	-61	-7	32	-54	-11
Ventral occipital	Sighted	3.3 ± 1.1	-31	-80	-12	26	-77	-12
	Blind	10.7 ± 2.9	-21	-84	-6	28	-83	-6
Dorsal occipital	Sighted	4.4 ± 1.2	-8	-83	5	18	-80	10
	Blind	13.7 ± 3.5	-24	-81	15	18	-83	17
Somatosensory	Sighted	30.4 ± 3.8	-35	-27	49	33	-28	49
	Blind	27.9 ± 4.8	-31	-19	48	39	-19	45
Intraparietal sulcus	Sighted	4.1 ± 1.4	-21	-64	42	25	-64	43
	Blind	5.2 ± 1.5	-25	-60	43	28	-62	43
Cerebellum	Sighted	21.0 ± 1.2	-14	-52	-32	17	-58	-43
	Blind	18.8 ± 5.4	-15	-54	-31	22	-62	-31

direction but did not reach statistical significance ($P = 0.12$) (Fig. 3). These results demonstrate in both sighted and blind subjects that tactile recognition of life masks of faces and of small manmade objects evokes distinct patterns of response in ventral visual extrastriate cortex.

Within the domain of small manmade objects, however, the patterns of response to bottles and shoes during tactile recognition did not differ significantly from each other. The mean within-category correlations for bottles and shoes did not differ significantly from the mean correlations between bottles and shoes, although the differences were in the expected direction (sighted subjects: $r = 0.23$ vs. $r = 0.00$, $P = 0.12$; blind subjects: $r = 0.19$ vs. $r = 0.07$, $P = 0.26$). The patterns of response to bottles and shoes during visual recognition showed the smallest difference of all pairwise comparisons in our previous study (1) ($P = 0.04$), but the patterns of response to faces differed greatly from the responses to both bottles and shoes ($P < 0.001$ in both cases). In that study (1), the mean for within-category correlations for bottles and shoes in cortex that responded maximally to visually presented manmade objects was 0.33, which is only slightly higher than the corresponding within-category correlations for tactile perception found in the

current study. Thus, in both the visual and tactile modalities, the patterns of response evoked by bottles and shoes in temporal cortex clearly differ from the patterns of response to faces but are hard to distinguish from each other.

Cortex Activated by both Tactile and Visual Recognition. In the sighted subjects, we also measured patterns of neural response to visually presented objects by using the same methods as in our previous study (1). Thus, we could identify the regions of ventral and inferior temporal cortex that participate in both tactile and visual recognition of these object categories. Most of the visually responsive cortex in these areas that was also active during tactile recognition was in inferior temporal cortex (Fig. 4). Whereas $19 \pm 4\%$ (mean ± SE) of inferior temporal visually responsive cortex also was activated during tactile recognition, a significantly smaller proportion of ventral temporal visually responsive cortex was activated during tactile recognition ($8 \pm 4\%$; $P < 0.001$). Moreover, most of the inferior temporal visually responsive cortex that was activated during tactile recognition responded more to bottles or shoes than to faces during visual recognition ($25 \pm 5\%$ of cortex that responded maximally to bottles or shoes vs. $5 \pm 2\%$ of cortex that responded maximally to faces, $P < 0.01$).

Crossmodal Correlations Between Category-Related Responses. Finally, we analyzed whether the patterns of response evoked by these categories in sighted subjects during tactile recognition were correlated with the patterns of response evoked during visual recognition. Reliable category-related patterns of response during tactile

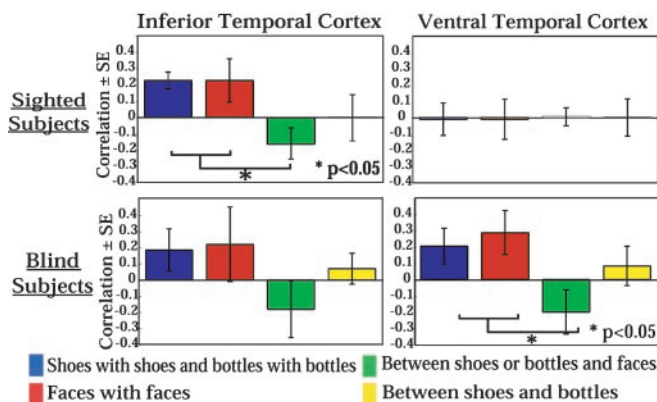


Fig. 3. Correlations between patterns of neural response evoked by two tactile recognition tasks (one-back repetition task and simple exploration) in sighted and blind subjects. Each bar represents the mean correlation across subjects ± SE. Blue and red bars depict the mean within-category correlations, separating correlations for manmade objects (shoes and bottles) from correlations for faces. Green and yellow bars depict the mean between-category correlations, separating correlations between patterns of response to faces as compared to manmade objects for correlations between patterns to the two categories of manmade objects.

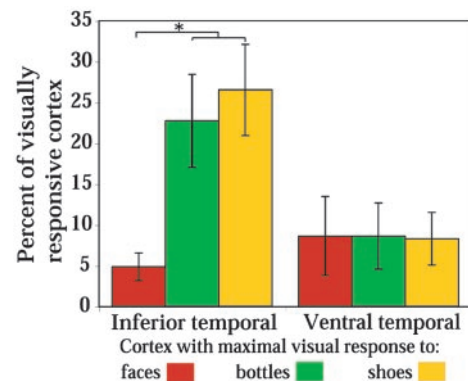


Fig. 4. Proportion of visually responsive cortex with maximal responses to faces, bottles, or shoes that was also activated by tactile recognition of objects.

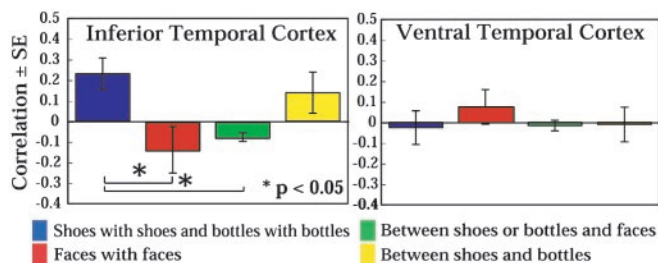


Fig. 5. Crossmodal correlations between category-related patterns of response during visual and tactile recognition. Each bar represents the mean correlation across subjects \pm SE. Blue and red bars depict the mean within-category correlations, separating correlations for manmade objects (shoes and bottles) from correlations for faces. Green and yellow bars depict the mean between-category correlations, separating correlations between patterns of response to faces as compared to manmade objects from correlations between patterns to the two categories of manmade objects.

recognition were found in the inferior temporal cortex of sighted subjects but not in their ventral temporal cortex (as discussed above). In the inferior temporal cortex that was active during both tactile and visual recognition, the patterns of response to bottles and shoes during tactile recognition were significantly correlated with the patterns of response to the same categories during visual recognition (Fig. 5). The within-category correlations for bottles and shoes were significantly greater than correlations between bottles or shoes and faces ($P < 0.05$). The within-category correlations for faces, however, were actually negative and nonsignificantly lower than correlations between faces and bottles or shoes. The results of these crossmodal comparisons of patterns of response indicate that, whereas tactile recognition of bottles and shoes evokes representations in the ventral object vision pathway that are closely related to the representations evoked during visual recognition of these objects, tactile recognition of life masks of faces evokes representations that are unrelated to those evoked during visual face recognition.

Earlier visual areas in occipital cortex were also activated during tactile recognition (Table 1 and Fig. 1). The volumes of temporal and occipital cortices that were tactilely responsive in blind subjects were greater than the volumes of tactilely responsive occipitotemporal cortices in sighted subjects ($P < 0.05$ for both temporal and occipital cortices), consistent with previous reports (8, 9). By contrast, the volume of sensorimotor and cerebellar cortex that was activated during tactile recognition tended to be greater in sighted than in blind subjects (Table 1), indicating that the larger occipital activation in blind subjects was not simply due to difficulty or global activity level.

Discussion

This study was designed to test whether the information about faces and object categories that is represented in the ventral visual pathway by distinct patterns of neural activity is strictly visual or a more abstract, supramodal representation of object form. To investigate this hypothesis, we studied the neural response elicited by tactile recognition of life masks of faces and two categories of common manmade objects, namely bottles and shoes. We have shown previously that visual perception of faces and these two categories of manmade objects evoke distinct patterns of response in temporal extrastriate cortex (1). In this study, we investigated whether a similar category-related organization is associated with tactile recognition of the same object categories. Specifically, we tested whether the patterns of response elicited by tactile recognition of faces and manmade objects are distinct and to what extent these differential patterns of response during tactile recognition are similar to the patterns of response elicited by visual recognition of the same categories.

We studied tactile recognition in both sighted and blind individuals. By studying sighted individuals, we could determine whether the locations and patterns of response evoked by tactile recognition are related to the responses evoked by visual recognition. By studying blind individuals who have no visual memories for faces and objects, we could rule out that the responses evoked by tactile recognition in visual areas are merely the result of visual imagery. The study of blind subjects also allowed us to examine whether the development of category-related patterns of response in the object pathway requires visual experience or simply requires experience with objects independent of sensory modality.

Tactile recognition activated a large distributed network of cerebral and cerebellar cortical regions that included visual extrastriate regions in inferior temporal and ventral temporal cortex. In sighted subjects, the temporal areas activated by tactile recognition were also activated by visual recognition of the same object categories. Interestingly, the portion of visually responsive cortex activated by tactile recognition was greater in inferior temporal cortex, and within inferior temporal cortex, tactilely responsive cortex came predominantly from areas that responded more during visual recognition of bottles and shoes than during visual recognition of faces.

The patterns of response in these extrastriate regions were category-related. The category-related nature of these patterns was demonstrated by examining whether the pattern of response evoked by faces was reproducible across two tactile recognition tasks and distinct from the patterns of response evoked by the manmade objects and vice versa. The patterns of response in inferior temporal cortex evoked by tactile recognition of faces and objects were significantly category-related in sighted subjects and showed a trend toward being category-related in the blind subjects. The patterns of response in ventral temporal cortex during tactile recognition were significantly category-related in only the blind subjects. In sighted subjects, the patterns of response to bottles and shoes in inferior temporal cortex were similar for visual and tactile recognition, suggesting that the representation of manmade objects in this area is supramodal. The pattern of response during tactile recognition of faces, however, was not related to the pattern of response evoked by visual recognition of faces.

These results indicate that tactile recognition of manmade objects evokes representations in a posterior inferior temporal region of visual extrastriate cortex, and that these representations are similar to those evoked by visual recognition of the same objects. We and others have shown previously that cortex in the inferior temporal gyrus tends to respond more strongly to small, manmade objects, such as chairs and shoes, than it does to faces, animals, or houses (10, 11), and the cortex in this region that responded during both visual and tactile recognition was predominantly from regions that responded more to bottles and shoes than to faces. This region is part of a larger region that Malach *et al.* (12) have called LO (lateral occipital area), that responds more to meaningful stimuli than to nonsense images. They have shown further that this region contains cortex that responds during both visual and tactile recognition of meaningful objects as compared to tactile or visual textures (2, 3), and the location of this crossmodal region, which they named LOTv, is essentially identical to the region of overlap between visual and tactile activation in our study [differences in Talairach (7) stereotaxic locations were 5 mm for the sighted subjects and 9 mm for the blind subjects]. Furthermore, Amedi *et al.* (3) showed that the cortex in LOTv responds more to the visual presentation of small, graspable objects as compared to faces or scenes, consistent with our results. This region also responds during tactile exploration of novel, meaningless three-dimensional clay objects, suggesting that it responds more to object form than to other semantic features of objects (4).

Our results also showed that tactile object perception also evokes category-related patterns of response in temporal extrastriate cortex of blind subjects. The patterns of response in blind subjects were

significantly category-related in ventral temporal cortex and showed a nonsignificant trend toward being category-related in inferior temporal cortex. Although the crossmodal patterns of response in the sighted subjects may reflect mediation of tactile recognition by visual imagery (4–6, 13), such an explanation cannot account for the use of these cortices in blind individuals who report no visual memories. A role for visual imagery in the sighted subjects cannot be ruled out, but a parsimonious account would attribute the participation of extrastriate visual cortices during tactile recognition to the same process in both subject groups, which we propose is a representation of more abstract, supramodal aspects of object form. Furthermore, the findings in blind subjects suggest that the development of topographically organized, category-related representations in extrastriate visual cortex does not require visual experience. Experience with objects acquired through other sensory modalities also appears to be sufficient to support the development of these patterns.

Tactile recognition of faces, however, does not appear to evoke the same representations evoked by visual recognition of faces. Ventral and inferior temporal cortex that responded maximally to faces during visual recognition tended not to be activated during tactile recognition of faces or other objects. The activity evoked by tactile face recognition was not related to the pattern of response during visual face recognition. Subjects reported that they found it difficult to form an image of the whole face during tactile recognition. Instead, they tended to focus on single features, such as the chin or nose, to perform the one-back repetition detection task, despite the task manipulations designed to induce the formation of a representation of the whole object. Subjects also reported that they made no use of the eye region for tactile recognition. These subjective reports and the imaging results suggest that during tactile recognition of faces, subjects processed the faces more like other objects than like holistic face configurations (14). Even within the visual modality, face inversion impedes configural face processing (15) and results in increased activity in extrastriate cortical regions that respond more to nonface objects than to faces (16).

Two potential confounds in our experiments concerned the possible effects of stimulus and experimenter movement while presenting the objects and the differential difficulty of face, shoe, and bottle tactile recognition. The introduction of objects into the magnet bore and related movement by the investigator could lead to artifactual signal changes in the brain due to alteration of the magnetic field (17). A separate experiment that we conducted earlier, however, demonstrated that experimenter and stimulus movement, in the absence of tactile stimulation, did not cause signal change in the areas that responded during tactile stimulation.^{††}

Because of the differential difficulty associated with tactile recognition of the three stimulus categories, we decided to have two tactile tasks: one with different stimulus presentation durations to

allow accurate performance and one with equal stimulus presentation directions and no performance requirement. This manipulation also allowed us to examine whether the neural responses showed similar category-related patterns that were independent of task parameters. Previously, we and others have shown that category-related patterns of response during visual recognition are independent of task (passive vs. delayed matching) and stimulus quality (photographs vs. drawings) (1, 10). The faces, shoes, and bottles were of roughly equivalent lengths and all had an elongated shape. However, because the shapes of shoes and bottles differ more from the shapes of faces than from each other, simple shape differences could play a role in the observed category-related patterns. The extent to which category-related patterns of response in object-responsive extrastriate cortex are related to object form or semantic associations remains to be established.

Previous studies have shown that another form of tactile recognition, Braille reading, activates ventral temporal areas in subjects with both congenital and acquired blindness and that subjects with acquired blindness also show activation of primary visual cortex during tactile Braille reading (8, 9, 18, 19). In the current study, we found that tactile recognition of faces and common objects also activated occipital, as well as temporal visual areas and, furthermore, that the volumes of occipital and temporal cortices that were tactilely responsive were greater in the blind than in the sighted subjects. We also found significant category-related patterns of response in the ventral temporal cortex in the blind but not in the sighted subjects. These results suggest some plastic functional reorganization of these visual cortices in blind subjects that enables them to use more of these cortices to support tactile recognition of objects (8, 9, 20–22), but the small sample sizes and the difference in age between the sighted and blind subjects limit the conclusions that can be drawn from group differences. Other studies have shown that visual cortex in blind subjects is also recruited for auditory processing and for nonvisual cognitive functions (23, 24), providing further demonstrations that visual cortices can be reorganized to mediate nonvisual functions in the blind.

Our findings, however, show that sighted subjects also make use of visual cortices during tactile recognition, in particular in the inferior temporal gyrus, suggesting that plastic reorganization due to sensory deprivation is not the necessary precondition for the participation of cortex in the ventral object vision pathway during tactile recognition. The supramodal nature of the representation of object form in inferior temporal cortex may explain how individuals who have had no visual experience are able to acquire normal knowledge about objects and interact effectively with their external world.

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^{††}Pietrini, P., Furey, M. L., Gobbini, M. I., Ricciardi, E., Wu, H.-H. C., Cohen, L., Guazzelli, M. & Haxby, J. V. (2000) *Soc. Neurosci. Abstr.* **26**, 686.2.

- Haxby, J., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L. & Pietrini, P. (2001) *Science* **293**, 2425–2430.
- Amedi, A., Malach, R., Hendler, T., Peled, S. & Zohary, E. (2001) *Nat. Neurosci.* **4**, 324–330.
- Amedi, A., Jacobson, G., Hendler, T., Malach, R. & Zohary, E. (2002) *Cereb. Cortex* **26**, 1202–1212.
- James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S. & Goodale, M. A. (2002) *Neuropsychologia* **40**, 1706–1714.
- Ishai, A., Ungerleider, L. & Haxby, J. (2000) *Neuron* **28**, 979–990.
- O'Craven, K. & Kanwisher, N. (2000) *J. Cognit. Neurosci.* **12**, 1013–1023.
- Talairach, J. & Tournoux, P. (1988) *Co-planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An approach to Cerebral Imaging* (Thieme, Stuttgart).
- Sadato, N., Pascual-Leone, A., Grafman, J., Deiber, M. P., Ibanez, V. & Hallett, M. (1996) *Nature* **380**, 526–528.
- Sadato, N., Okada, T., Honda, M. & Yonekura, Y. (2002) *Neuroimage* **16**, 389–400.
- Ishai, A., Ungerleider, L., Martin, A., Schouten, J. & Haxby, J. (1999) *Proc. Natl. Acad. Sci. USA* **96**, 9379–9384.
- Hasson, U., Harel, M., Levy, I. & Malach, R. (2003) *Neuron* **37**, 1027–1041.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R. & Tootell, R. B. (1995) *Proc. Natl. Acad. Sci. USA* **92**, 8135–8139.
- Sathian, K. & Zangaladze, A. (2002) *Behav. Brain Res.* **135**, 127–132.
- Külour, A. R. & Lederman, S. J. (2002) *Perception Psychophys.* **64**, 339–352.
- Yin, R. K. (1969) *J. Exp. Psychol.* **81**, 141–145.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A. & Martin, A. (1999) *Neuron* **22**, 189–199.
- Birn, R., Bandettini, P., Cox, R. & Shaker, R. (1999) *Hum. Brain Mapp.* **7**, 106–114.
- Büchel, C., Price, C. & Friston, K. (1998) *Nature* **394**, 274–277.
- Büchel, C., Price, C., Frackowiak, R. S. & Friston, K. (1998b) *Brain* **121**, 409–419.
- Cohen, L., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catala, M. D., et al. (1997) *Nature* **389**, 180–183.
- Cohen, L., Weeks, R. A., Sadato, N., Celnik, P., Ishii, K. & Hallett, M. (1999) *Ann. Neurol.* **45**, 451–460.
- Röder, B., Rösler, F. & Hennighausen, E. (1997) *Psychophysiology* **34**, 292–307.
- Röder, B., Stock, O., Bien, S., Neville, H. J. & Rösler, F. (2002) *Eur. J. Neurosci.* **16**, 930–936.
- Amedi, A., Raz, N., Pianka, P., Malach, R. & Zohary, E. (2003) *Nat. Neurosci.* **6**, 758–766.