Tactile processing of different object categories involves extrastriate visual cortical areas in the human brain

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Abstract. Functional magnetic resonance imaging (fMRI) studies demonstrated that tactile discrimination evokes patterns of neural response in the extrastriate ventral temporal cortical areas similar to those induced by the visual percept of the same category of objects. These findings strongly indicate that object representation in the ventral visual pathway is not simply a representation of visual images but quite a representation of more abstract features of object form.

1 Introduction

Visual processing of faces and different object categories in the human brain occurs mostly in the ventral extrastriate visual cortex. Specifically, we have demonstrated that processing of different object categories is associated with distinct patterns of response in ventral temporal extrastriate visual cortex that are widely distributed and overlapping: we named this organization of different object representations in the visual extrastriate cortex Object Form Topography (1), referring to the topographically organized representation of the attributes of a form that underlie face and object recognition.

Recently, both tactile perception and recognition of objects have been shown to activate the dorsolateral part of visual object-responsive occipital cortex (2,3). Therefore, we developed a series of studies to determine whether visual and tactile recognition of different object categories share common patterns of neural response. In particular, we investigated whether the representation of objects in these visual extrastriate regions is a more abstract representation of object form, independent from the sensory modality that carries the information to the brain. To address this question, we examined the patterns of response elicited by visual and tactile recognition of distinct categories of objects (faces and small manmade objects, specifically plastic bottles and shoes) in sighted and congenitally blind subjects (4,5,6).

2 Methods

We used functional magnetic resonance imaging (fMRI; Gradient echo EPI, GE 3T scanner) to examine neural activity elicited by tactile recognition of faces (life masks) and other objects (shoes and bottles) in four congenitally blind adults and five blind-folded sighted subjects. In alternating runs, subjects performed a one-back repetition tactile detection task or a simple tactile exploration task. 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 behavioural 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 separated by 5 s of rest. Each time series consisted of three 2 min-stimulus and 30-s rest blocks, one for each category, in counterbalanced order. One-back repetition and simple exploration tasks were presented on alternating runs.

In the sighted subjects only, we also measured neural responses during visual recognition of the same categories of objects, using an experimental procedure similar to that employed in our previous fMRI study (1). The brain regions that showed significantly increased neural activity during tactile and visual recognition were identified in each subject. The category-specificity of patterns of response within ventral temporal cortical regions was analyzed by examining between and within category correlations between the patterns of response during tactile repetition detection and the patterns of response during simple tactile exploration, and during visual one-back repetition task (for a more detailed description, refer to the Materials and Methods section of reference 6).

3 Results

Both in the sighted and in the blind subjects, both tactile tasks evoked activity in ventral extrastriate cortex, specifically in the posterior inferior temporal sulcus bilaterally (Figure 1). Additional visual cortical areas that were activated also during tactile tasks were observed in ventral temporal and occipital extrastriate visual cortices. Tactile perception and recognition activated large bilateral areas in the sensorimotor cortex, in the intraparietal sulcus, and in the cerebellum. Earlier visual areas in occipital cortex also were activated during tactile recognition (Figure 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 individuals ($P<0.05$ for both temporal and occipital cortices). 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.

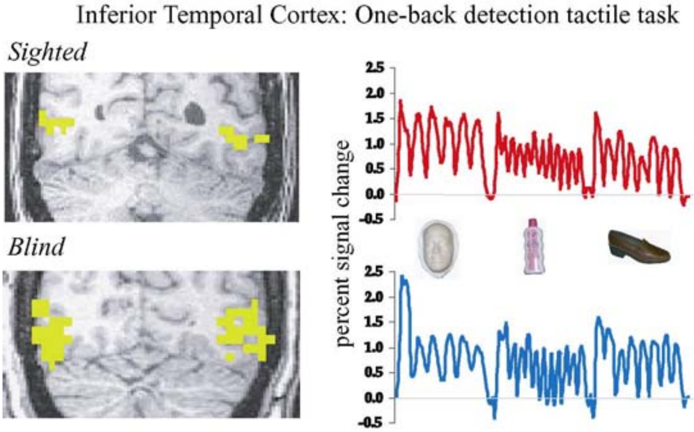

Fig. 1. On the left side, coronal images from *F*-score maps of activated areas during the one-back detection tactile recognition task in a sighted individual and a blind individual are shown. The right side of the figure shows mean time series, averaging across subjects, voxels, and blocks, for the response in inferior temporal cortex during the one-back repetition detection task in sighted and blind subjects. The three different categories presented for the tactile task (face masks, plastic bottles and shoes) are symbolized with small icons at the bottom of the graph.

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. In sighted subjects, within-category correlations were greater than between-category correlations in inferior temporal, but not in ventral temporal, cortex. 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 direction but did not reach statistical significance ($P=0.12$). These results demonstrate that in both sighted and blind subjects tactile recognition of life masks of faces and of small manmade objects evokes distinct patterns of response in ventral visual extrastriate cortex. However, 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 were hard to distinguish from each other.

In the sighted subjects, we compared patterns of neural response to visually presented objects as we did in our previous study (1). We identified the regions of ventral and inferior temporal cortex that participated 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 (Figure 1). Whereas 19 ± 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 ± 4%; $P<0.001$). 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 ± 5% of cortex that responded maximally to bottles or shoes vs. 5 ± 2% of cortex that responded maximally to faces, $P<0.01$).

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, that is, whether they correlated *across modalities*. Reliable category-related patterns of response during tactile recognition were found in the inferior temporal but not in the ventral temporal cortex of sighted subjects. 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. In contrast, the pattern of neural response during visual recognition of faces did not correlate with the pattern evoked by tactile discrimination of life masks of faces. The results of these cross-modal comparisons of patterns of response indicate that 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, while tactile recognition of life masks of faces evokes representations that are unrelated to those evoked during visual face recognition.

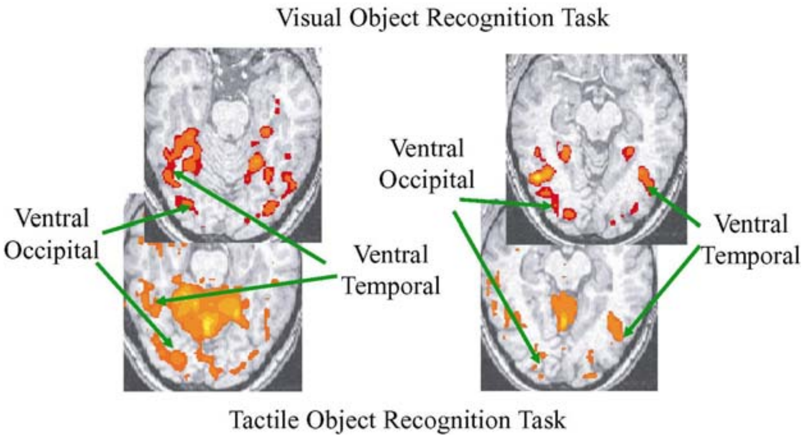

Fig. 2. Axial images from single sighted subject *F*-score maps of activated areas during tactile and visual object recognition task are shown Tactile/visual overlap map shows the areas activated by both tactile and visual perception (shown in yellow), as well as the areas activated only by tactile (red) and visual (green) perception.

4 Conclusions

These results demonstrate that the visual ventral extrastriate cortex is activated also by tactile modality, not only in sighted individuals, but also in subjects who have had no visual experience.

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 these extrastriate regions the patterns of neural response 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.

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.

In blind subjects, tactile recognition of faces and common objects also activated occipital, as well as temporal visual areas. Furthermore, 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.

By studying blind individuals who have no visual memories for faces and objects, we were able to rule out that the responses evoked by tactile recognition in visual areas were merely the result of visual imagery. Also, we could examine whether the development of category-related patterns of response in the object pathway requires visual experience or simply requires experience with objects independent from the sensory modality. Our findings 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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References

1. Haxby, J., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., & Pietrini, P. (2001) Science 293, 2425-2430.

2. Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001) Nat. Neurosci. 4, 3243-30.
3. James, T.W., Humphrey, G.K., Gati, J.S., Servos, P., Menon, R.S., & Goodale, M.A. (2002) Neuropsychologia 40, 1706-1714.
4. Pietrini P., Furey M.L., Ricciardi E., Gobbini M.I., Wu W.C., Cohen L., Guazzelli M., Haxby JV. Neural Activity in Ventral Extrastriate Cortex during Tactile Discrimination of Faces and Other Objects in Congenitally Blind and Sighted Subjects. Presented at the 8th International Conference on Functional Mapping of Human Brain Mapping, June 2-6, 2002 Sendai, Japan. NeuroImage 658
5. Pietrini P., Furey M.L., Gobbini M.I., Ricciardi E., Wu W.C., Cohen L., Guazzelli M., Haxby JV. Ventral extrastriate visual cortex is activated during tactile discrimination of faces and objects: a fMRI study in congenitally blind and sighted subjects. Proceedings of the XII ESCOP and XVIII BPS Cognitive Section Conference, Edimburgh, UK, September 2001
6. Pietrini P., Furey M.L., Ricciardi E., Gobbini M.I., Wu W.C., Cohen L., Guazzelli M. & Haxby JV. Beyond sensory images: Object-based representation in the human ventral pathway. (2004) Proc Natl Acad Sci USA 101, 5658–5663.