



Visuo-haptic object-related activation in the ventral visual pathway

Amir Amedi¹, Rafael Malach², Talma Hendler³, Sharon Peled³ and Ehud Zohary¹

¹ Neurobiology Department, Life Science Institute and Center for Neural Computation, Hebrew University, Givat Ram, Jerusalem 91904, Israel

² Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel

³ Wohl Institute for Advanced Imaging, Tel-Aviv Sourasky Medical Center, Israel

Correspondence should be addressed to E.Z. (udiz@lobster.ls.huji.ac.il)

The ventral pathway is involved in primate visual object recognition. In humans, a central stage in this pathway is an occipito-temporal region termed the lateral occipital complex (LOC), which is preferentially activated by visual objects compared to scrambled images or textures. However, objects have characteristic attributes (such as three-dimensional shape) that can be perceived both visually and haptically. Therefore, object-related brain areas may hold a representation of objects in both modalities. Using fMRI to map object-related brain regions, we found robust and consistent somatosensory activation in the occipito-temporal cortex. This region showed clear preference for objects compared to textures in both modalities. Most somatosensory object-selective voxels overlapped a part of the visual object-related region LOC. Thus, we suggest that neuronal populations in the occipito-temporal cortex may constitute a multimodal object-related network.

When searching for your flashlight in a tent at night, you must rely on tactile information to identify objects. The visual representation of the shape of your flashlight might facilitate your search. A lifelong experience shapes this correspondence between the tactile sensation of an object and the way the object looks. Although similar associations are formed between vision and other modalities, an intrinsic similarity exists between visual and tactile object recognition. Both are based on the extraction of basic features (such as contours) and their spatial arrangement, which together define an object. This raises the possibility that object recognition benefits from multimodal integration of information. However, our current understanding of the brain mechanisms responsible for such convergence of multimodal information is sparse.

A central theme in sensory neurophysiology is that information processing in early sensory areas is strictly modality specific. This division of labor is also seen within modalities, with different cortical areas specializing in processing different aspects of the physical stimulus (such as motion, depth, color, shape and texture of an object)^{1–4}. Indication for convergence of information from different visual sub-modalities can be seen in the responses of neurons in higher-order visual areas, such as inferotemporal (IT) cortex. These neurons respond to objects, irrespective of the visual cues that define them⁵. Similarly, fMRI studies found that object-related areas in the occipito-temporal part of human cortex (LOC) are activated when object shape is inferred from motion, texture or luminance differences⁶.

Can this convergence of information from multiple sources leading to cue invariance be observed across modalities as well? To test this issue, we mapped regions that were similarly activated by objects (versus textures) grasped either haptically or visually. We found somatosensory object-selective activity in the

occipito-temporal region. Its anatomical location (overlapping part of LOC), and its selective pattern of activation suggest that this region of the human brain, which has been considered strictly visual, is indeed a multimodal (at least, visuo-haptic) information processing region devoted to aspects of object recognition.

RESULTS

Previously, we found that areas in the ventral stream are differentially activated by visual objects compared to textures and scrambled images^{7–10}. Can this selectivity be observed if objects are touched rather than seen? To address this question, we conducted MRI scans under four different experimental conditions: seeing visual objects, seeing visual textures, touching somatosensory objects and touching somatosensory textures (Fig. 1a).

First, we asked whether areas commonly considered strictly visual are activated by somatosensory stimuli. To test this directly, we did two statistical tests searching for voxels that were preferentially activated by touch. One test was for voxels activated by somatosensory objects compared to the rest condition (all other epochs, including the visual epochs, were ignored). The other test was for voxels activated by somatosensory textures compared to the rest condition. Voxels above criterion threshold (linear regression, $r > 0.33$, $p < 0.005$) responding to at least one of the two somatosensory stimulus types are shown in Fig. 1b–d, in the left hemisphere, contralateral to the hand performing the task. We found a robust somatosensory activation in a ventral region anterior to retinotopic visual areas. Similar somatosensory activation patterns were seen at this location in all subjects. Eight subjects showed bilateral activation with stronger activation in the contralateral hemisphere (the last subject had only ipsilateral activation). Across subjects, the region of somatosensory acti-

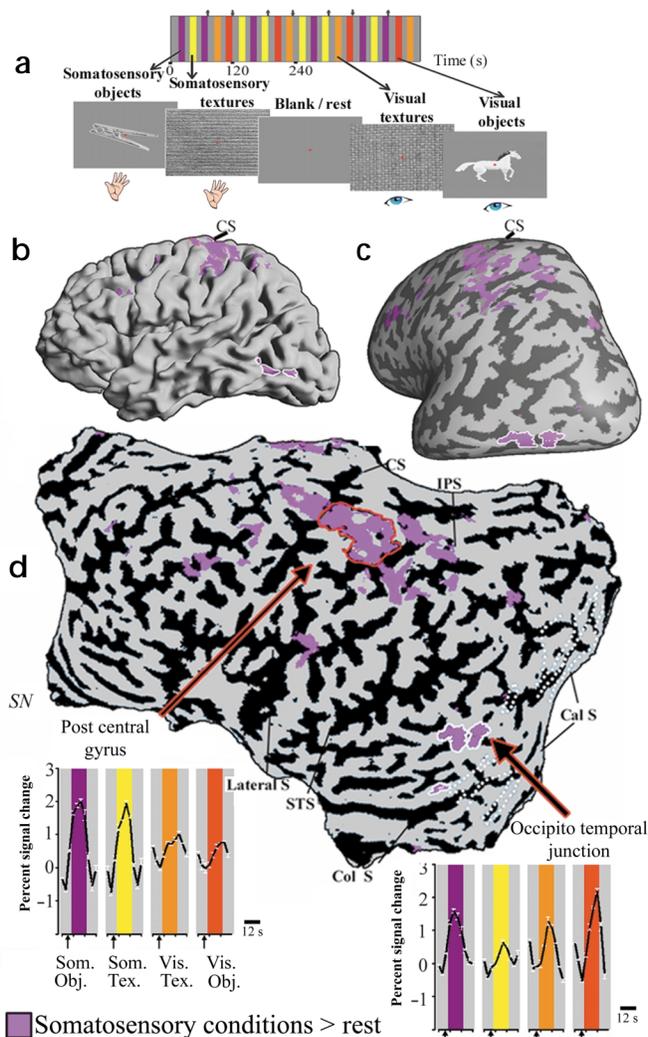


Fig. 1. Somatosensory clusters in the occipito-temporal region showing multimodal (visuo-haptic) object selectivity. **(a)** The experimental protocol used in the main experiment. Four conditions were interleaved in a block design: somatosensory objects, somatosensory textures, visual textures and visual objects. In the first two conditions, subjects touched the objects or textures with their eyes closed; in the second two conditions, subjects viewed the stimuli. Upward- and downward-pointing arrows denote times of eyes opening or closing, respectively. **(b–d)** Activation maps for somatosensory objects and textures, and average time course in two regions of interest (ROIs; the occipito-temporal region and post central gyrus). Two linear correlation tests were used to reveal all somatosensory activation: somatosensory objects compared to the rest condition, and somatosensory textures compared to the rest condition. Voxels activated by either one or both tests are shown in purple. The clusters are presented on a three-dimensional folded reconstruction of the contralateral hemisphere **(b)**, on an inflated brain of the same hemisphere **(c)** and on the unfolded hemisphere **(d)**, enabling inspection of the activation patterns across the entire cortical hemisphere of one subject (SN). Dotted white lines indicate borders of retinotopic areas. Occipito-temporal region (corresponding to the somatosensory activation clusters between the posterior inferior-temporal sulcus in the most dorsal part to the posterior fusiform gyrus ventrally), encircled by white contours; post-central gyrus, encircled by red contours. Below, average time course across all repetitions of the same condition for the clusters in the two ROIs. Error bars, standard error of the mean across repetitions. Upward-pointing arrows, beginning of each block. A 3-s rightward shift in the time of each block onset was introduced to account for the lag in the hemodynamic response. There is somatosensory and visual activation in the occipito-temporal region, although there was no requirement in the statistical tests for these voxels to be visually active. Furthermore, this region shows object preference, irrespective of the modality used. In contrast, the activation pattern in the post central gyrus is dominated by touch, with no preference for objects over textures, when the overall activation pattern is considered. Cal S, calcarine sulcus; CS, central sulcus; STS, superior temporal sulcus; IPS, intraparietal sulcus; Col S, collateral sulcus.

vation stretched from the posterior fusiform gyrus in the most ventral part, to the posterior inferior temporal sulcus, in the most dorsal part. We will refer to this region throughout the following text as the occipito-temporal region.

To inspect the time course of activation in more detail, we focused on two regions of interest: the somatosensory activated area in the occipito-temporal region, and the post central gyrus, which contains the primary somatosensory areas (Fig. 1d). The occipito-temporal region showed clear somatosensory preference for objects compared to textures, although this selectivity was not included in the statistical test. Furthermore, this region showed a similar object preference in the visual modality, although the visual epochs were ignored in the statistical tests. This suggests that the occipito-temporal region might integrate information about objects from both modalities. In contrast, the activation pattern in the post-central gyrus was generally limited to the somatosensory epochs.

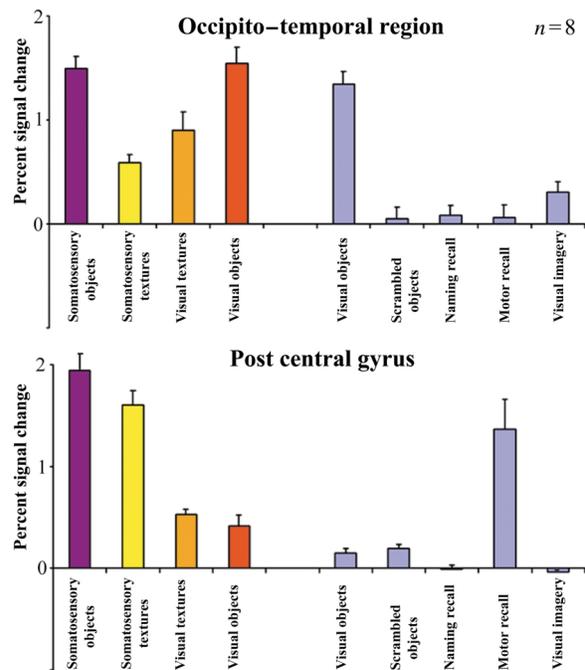
The results shown in Fig. 1 are typical of the data obtained across subjects. When the average activation level across all subjects showing contralateral somatosensory activation in the occipito-temporal region (eight of nine subjects) was examined, the occipito-temporal region showed a clear object preference, irrespective of the modality used to identify the object (Fig. 2). To

address this quantitatively, we used a two-way ANOVA using two independent factors: stimulus type (objects/textures) and modality type (visual/somatosensory). The only statistically significant factor in the occipito-temporal region of interest was the stimulus type, confirming that this was the main factor governing the level of activation in this region ($F_{1,28} = 35.169, p < 0.0001$). In contrast, the only significant factor in the post central gyrus was the modality type ($F_{1,28} = 85.365, p < 0.0001$). The overall activation pattern in the post central gyrus was dominated by touch, with no clear preference for objects over textures. In both regions, the interaction term was not statistically significant.

In a control experiment, done immediately after the main experiment, we tested the possible contribution of other factors to the putative somatosensory activation seen in the occipito-temporal region (Fig. 2, blue bars). We designed three conditions: 'naming recall,' 'motor control recall,' and visual imagery' (see Methods). In addition, we remapped the visual object related areas using a standardized set of visual objects and highly scrambled images of the same objects. The results of the control experiment replicate the visual object selectivity of the somatosensory-activated voxels, using the standardized set. The results also show that the somatosensory activity could not have resulted from the different confounding factors (motor, naming



Fig. 2. The magnitude of activation reveals multimodal (visuo-haptic) object selectivity in the occipito-temporal region. Average percent signal change is shown for the different conditions across subjects, in the occipito-temporal region and, for comparison, the post central gyrus. Left, conditions in the main experiment, somatosensory objects, somatosensory textures, visual textures and visual objects. The voxels were chosen in the two ROIs according to the same anatomical and threshold criteria as in the parametric map presented in Fig. 1. Voxels in the occipito-temporal region were activated by objects, irrespective of the modality in which they were sensed (visual or somatosensory). Right, magnitude of response of same voxels determined from the control experiment (blue bars). The control experiment included epochs of naming recall, motor movements imitating object palpation, and visual imagery, as well as epochs of viewing visual objects and their scrambled versions. This experiment verified that the occipito-temporal region was not activated to any extent by motor movements and covert naming of objects. Small activation was observed in the occipito-temporal region during the imagery blocks, but its magnitude was significantly lower than the activation in response to somatosensory objects and visual objects. This possibly reflects a modulatory top-down effect of visual imagery. In contrast, activation in the post central gyrus was present in both the somatosensory and the motor conditions, but there was no indication of a differential response to objects versus textures.



and visual imagery), although visual imagery may have had a small modulatory role in this region.

The somatosensory evoked region in the occipito-temporal cortex was preferentially activated by objects, whether they were touched or seen. Thus, we next asked to what extent the somatosensory object-specific voxels overlapped the visual object-related LOC. To test this directly, we did two independent tests. The first was to find voxels showing somatosensory object specificity, and the second was to delimit LOC, the visual object selective region.

We found voxels that were preferentially activated by somatosensory objects compared to somatosensory textures (visual epochs were ignored). The largest and most significant cluster of somatosensory object-selective voxels was found in the occipito-temporal region, although some activation was also found in the parietal cortex (Fig. 3a, left, statistically significant voxels; Fig. 3a, right, average time course). We then searched for voxels that were significantly activated by visual objects compared to scrambled versions of the same objects (Fig. 3b), and determined the overlap between the maps in Figs. 3a and b (Fig. 3c). The voxels of preferential somatosensory object activation overlapped with part of the visual object selective LOC. Almost all the somatosensory object-selective voxels were located inside LOC. The activation time courses demonstrate that, on average, LOC shows strong object selectivity only in the visual modality (time course, Fig. 3b). However, there is a sub-region within LOC that is selective to objects in both modalities, and to the same extent (time course, Fig. 3a; maps, Fig. 3c).

We determined whether these results were repeatable by viewing the pattern of activity across subjects. In all the presented cases (and, in total, in eight of nine contralateral hemispheres), we found somatosensory object-specific voxels in the occipito-temporal region (Fig. 4a). Some activation was also found in the parietal cortex, but this was variable across subjects. Hardly any preferential object activation occurred in primary motor and primary somatosensory areas, or in typical language areas. We then checked if the somatosensory object-specific voxels were consistently located within LOC, using the two independent tests (as in Fig. 3, for subject QE). We found voxels showing both somatosensory and visual object selectivity in the contralateral

hemisphere of eight of nine subjects (Talairach coordinates¹¹, averages \pm s.d., -45 ± 5 , -62 ± 6 , -9 ± 3). Figure 4b presents the average time course (across subjects) of the activation in somatosensory object-selective voxels in the occipito-temporal region. The hemodynamic signal shows a robust activation in response to both visual and somatosensory objects, demonstrating the multimodal (visuo-haptic) characteristics of this sub-region. In comparison, the average time course across all LOC voxels (Fig. 4c) was specific only to visual objects.

DISCUSSION

Multimodal activation in the ventral stream

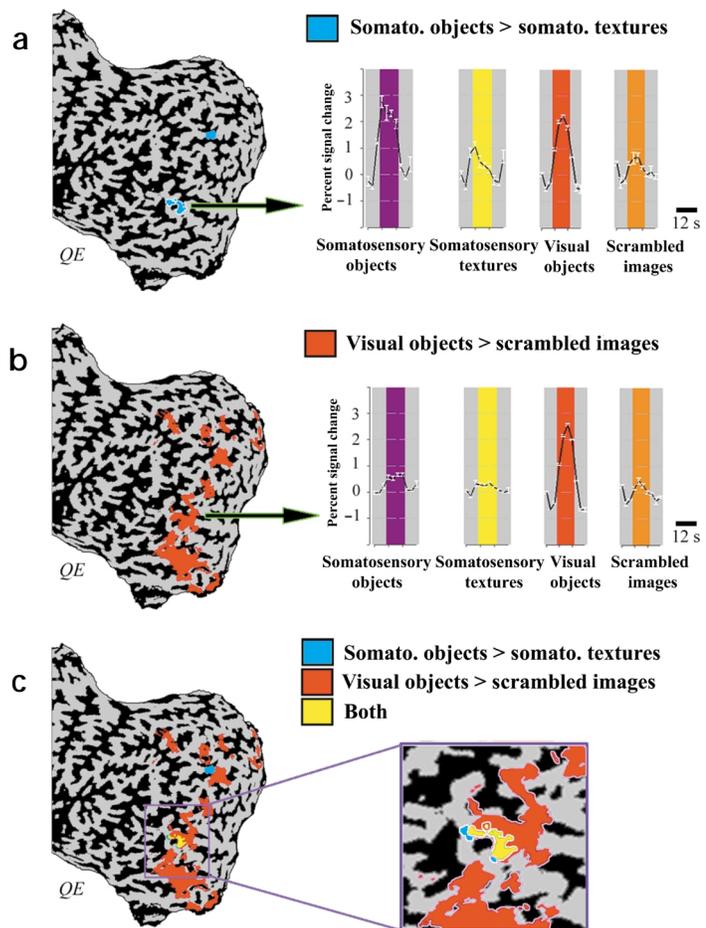
In this study we found robust and consistent somatosensory activation in the occipito-temporal region, previously considered strictly as part of the visual ventral pathway. We showed somatosensory activation within the human ventral visual areas in a coherent and consistent anatomical location. Moreover, this haptic activation was specific; on average, tactile objects elicited greater activation than tactile textures. Analogous object specificity occurs for visual objects versus textures in similar cortical regions⁶⁻¹⁰. In seven of nine subjects, most of the somatosensory object-specific voxels in the occipito-temporal region overlapped a subregion of the visual object-selective complex (LOC), and the rest of the voxels were abutting LOC. These results suggest that cortical populations in the occipito-temporal region may function as multimodal object-selective networks in humans.

Controls for possible confounding factors

In principle, the somatosensory activation reported here could have resulted from other confounding factors, including effects due to naming or motor responses. Regarding the naming issue, we confirmed before the scan that the subjects could recall more object names during the naming epochs compared to the maximal names they could give while palpating three objects during the somatosensory object conditions. In spite of this, there was hardly any activation in the somatosensory vox-



Fig. 3. Cortical maps and time course of regions showing preferential somatosensory, visual and multimodal (visuo-haptic) object activation in one subject (QE). (a) Somatosensory object-selective voxels. The statistical test highlighted voxels with preferential somatosensory object activation compared to textures (somato. objects > somato. textures, cyan blobs). Right, average time course of activation (across repetitions of the same condition) in these voxels. These voxels have strong preference for both somatosensory and visual objects, although the visual epochs were ignored in the statistical test. (b) Visual object-selective voxels. Voxels that were activated by visual objects compared to scrambled images of the same objects (visual objects > scrambled images, red blobs). Right, time course of activation (averaging across all LOC voxels). In general, LOC is selective to visual objects, but not to somatosensory objects. (c) The overlap between the somatosensory and visual object-selective voxel maps reveals a subregion within LOC that is activated by objects in both modalities (yellow). Right, magnified version of this subregion. Most voxels showing somatosensory and visual object preference also show visual object preference, which explains why the average time course for the somatosensory object selective voxels shown in (a) also show visual object selectivity.



els in the occipito-temporal region during the naming condition. Similarly, this region was not activated by motor movements imitating those done when subjects explored the objects haptically. However, these control conditions were effective, because the same finger movements strongly activated typical motor areas and the post central gyrus (Fig. 2), whereas naming activated typical language areas in the frontal and parietal lobes (data not shown).

Naming and motor components also cannot explain the preferential somatosensory activation for objects versus textures (Figs. 3 and 4) because the experiment was designed so that naming requirements were equal in the object and texture conditions (three names in each). Similarly, in both conditions, the subjects handled three items in the same hand position using characteristic hand movements. The only difference between the two conditions was in the type of somatosensory input they evoked. Finally, if the naming recall and motor components were similarly engaged during the two somatosensory conditions, no activation would be observed in strictly motor or language areas when testing for preferential activation by somatosensory objects compared to textures. Indeed, when performing the above test, no activation was found in primary motor and somatosensory areas, or in language areas. To conclude, our results indicate that activation in the occipito-temporal region is related to somatosensory object recognition rather than to language or motor functions.

Another possible explanation for the somatosensory activation in visual areas could be visual imagery. This implies that the activation in the occipito-temporal region stemmed from top-down visual imagery signals triggered by somatosensory input. Indeed, a recent report found that visual imagery affects the activation profile in the posterior fusiform gyrus¹². Although we cannot rule out some modulatory contribution by visual imagery, a number of reasons suggest that visual imagery could not be the sole factor responsible for the pattern of activation in the occipito-temporal region. First, we got a significantly lower signal in epochs of visual imagery compared to epochs of somatosensory object palpation (paired *t*-test, $p < 10^{-4}$, $n = 8$; Fig. 2). This

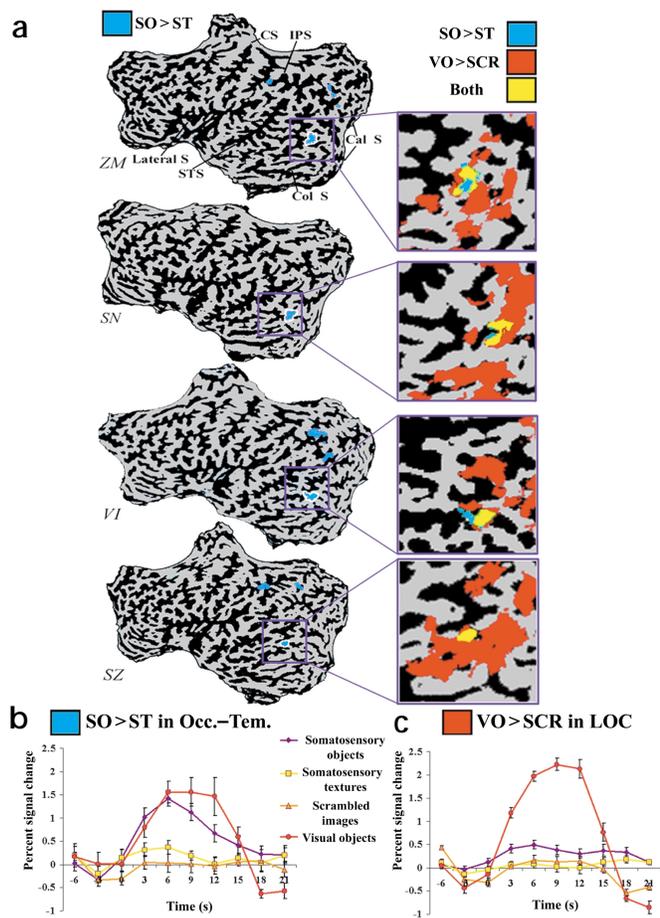
occurred despite the fact that subjects explored haptically the same number of objects during the somatosensory epochs as they were asked to imagine. Second, a direct test for voxels preferentially activated by visual imagery (compared to blank trials), revealed that in six of nine subjects, the 'imagery' voxels partly overlapped with the visual object-related complex LOC. These voxels also showed some overlap with the occipito-temporal region. However, even in these cases, we had to adopt a lower threshold ($r > 0.22$) to observe the putative imagery-evoked activation. Finally, preliminary results (Pietrini *et al.*, *Soc. Neurosci. Abstr.* 26, 686.2, 2000) reported somatosensory activation in the congenitally blind and in sighted subjects, in the same general anatomical location as reported here (inferior-temporal and fusiform gyrus, Talairach coordinates unavailable). Because the blind subjects have never experienced objects visually, it is unlikely that they engage in visual imagery.

To conclude, we suggest that activation in the occipito-temporal region is related to somatosensory object recognition rather than to other confounding factors, although visual imagery may have had a small modulating effect.

Connection to other works and possible interpretations
Previous studies on tactile object recognition found somatosensory object-related activity mainly in the intraparietal sulcus (IPS) and neighboring cortical areas in the parietal lobule, such as the supramarginal and angular gyri¹³⁻¹⁴. Consistent with these studies, we found parietal activation in



Fig. 4. Voxels showing multimodal (visuo-haptic) object selectivity and averaged time course across subjects. **(a)** Voxels showing preferential somatosensory object activation and their overlap with visual object-selective voxels of the LOC. The statistical test highlighted clusters with preferential somatosensory object activation, compared to textures (SO > ST, cyan blobs, left). In all subjects shown and, in total, in 8/9 contralateral hemispheres, we found somatosensory object-selective activation in regions that were referred to as non-retinotopic visual areas. No preferential activation occurred in primary motor and somatosensory areas (rolandic cortex around the CS), and typical language areas. This indicates that the motor components as well as the basic somatosensory components were comparable in the two conditions, and thus were canceled out. The same logic applies to the naming requirements in both conditions. Insets, magnified occipito-temporal region. As in Fig. 3c, voxels that are activated by visual objects compared to scrambled images of the same objects (VO > SCR, red blobs) are part of LOC. Superimposed are voxels activated by somatosensory objects versus textures (identical to the voxels in the left panel). Yellow blobs, voxels activated independently by both tests. Cyan blobs in insets, voxels activated only by somatosensory objects. Most somatosensory object-related activation is inside LOC. **(b)** Average time course (across subjects) showing the somatosensory object-selective activation in the occipito-temporal region. Time zero, beginning of the epoch. The average activation profile demonstrates the multimodal (visuo-haptic) characteristics of this region. The hemodynamic signal follows an identical onset to both somatosensory and visual objects. No activation is seen for the somatosensory textures or the scrambled images conditions. **(c)** In comparison, the average hemodynamic response in LOC (across subjects) is specific to visual objects.



response to somatosensory objects compared to textures in most of our subjects. Further studies are needed to determine the critical features of, and the possible relationship between, somatosensory activation in the parietal cortex and the occipito-temporal region.

Studies in macaque monkeys support our finding of somatosensory activation in the ventral pathway. About 20% of the neurons in area TE show stimulus-selective responses to objects grasped haptically (K. Tanaka, T. Hasegawa and K. Matsumoto, *IBRO* 5, 22, 1999). Area TE in the inferotemporal cortex is considered the final visual stage of the ventral pathway, which is essential for pattern recognition. Neurons in this area respond to moderately complex images, and are characterized by their general invariance to changes in stimulus size or position within their large receptive fields^{15–20}. Furthermore, area TE is directly connected with the superior temporal polysensory area²¹ (STP), which contains both visual, auditory and somatosensory unimodal neurons and multimodal neurons²².

Human fMRI shows that a putative homologue of monkey IT is a non-retinotopic occipito-temporal region termed the lateral occipital complex (LOC). This region is preferentially activated by visual objects^{6–10}, and shows similar invariant properties in response to changes in size and position²³. The haptic neuronal sensitivity we found in the occipito-temporal region may reflect a bimodal (visuo-haptic) representation of basic features and their spatial relationships, both of which are essential for identifying objects. According to this interpretation, the area of overlap between the visual and somatosensory object activation is a bimodal convergence association zone of the two separate pathways. Another possible interpretation of these results is that the activation in the occipito-temporal region reflects stored

object-related visual information that can be accessed via cues from the somatosensory modality, and possibly from other modalities. This view argues that direct interactions among modality-specific sensory pathways underlie a multimodal representation of objects. According to this view, the bimodal activation occurred in the visual cortex rather than somatosensory areas because object recognition relies primarily on vision.

Relationship to plasticity in V1 of the blind

Somatosensory activation of an area in the ventral stream may help explain the issue of cross-modal plasticity. Both primary and secondary visual cortices are activated by high-level somatosensory tasks (such as Braille reading) in blind subjects²⁴. Furthermore, trans-magnetic stimulation of the occipital cortex leads to disruption of Braille reading, demonstrating the functional relevance of these areas in the blind²⁵. Because the visual and somatosensory inputs are segregated at the thalamic level, it was proposed that this plasticity was established through the parietal cortex. In humans and monkeys, the anterior regions of the parietal cortex are generally dedicated to somatosensory processing, whereas the more posterior parts are dedicated to visual processing. However, in macaque monkeys, the anatomical connections between the anterior parietal (7a) and posterior (7b) areas are sparse^{26–28}. Our results in sighted subjects raise another possibility, that in blind subjects, the somatosensory activity in the occipito-temporal region expands to the rest of LOC and then to earlier retinotopic areas such as V2 and V1 in the absence of stronger visual input. This pattern of plasticity between neigh-



boring areas has been demonstrated in previous studies^{29–33}. One certain example is the cross-modal visuo-haptic plasticity found in neighboring and partly overlapping areas of the anterior ectosylvian cortex of the cat following eyelid suture³⁴. Further studies in sighted and blind subjects at different stages and periods of blindness will shed light on this issue.

Multimodality in single neurons?

To what extent does the apparent multimodal activation in individual voxels within the occipito-temporal region represent cross-modal integration at the single neuron level? The limited spatial resolution of fMRI (at about 3 mm)³⁵ precludes us from making a firm conclusion regarding this question. Thus, 'multimodal' activation could be recorded even if the occipito-temporal region contained interdigitated or abutting maps of purely visual and purely somatosensory representations. One approach to resolve this problem is through repetition-related adaptation²³. As a first step, we divided the somatosensory object epochs into those in which objects were touched after they were seen earlier in the experiment (three epochs), and epochs using objects not yet seen (three epochs). We found that the somatosensory object signal produced after objects were seen was slightly reduced compared to the unseen objects (paired *t*-test, $p < 0.05$, $n = 8$). This preliminary result suggests that the relevant voxels may show cross-modal adaptation, hinting that neurons in the occipito-temporal region may be activated both by somatosensory and visual objects. However, this issue should be tested more rigorously in a separate experiment.

METHODS

MRI acquisition. The BOLD fMRI measurements were done in a whole-body, 1.5-T, Signa Horizon LX8.25 General Electric scanner, located at the Wohl Institute for Advanced Imaging in the Tel-Aviv Sourasky Medical Center. The MRI system was equipped with 22 mT/m field gradients with a slew rate of 120 T/m/s (Echospeed). Three-dimensional anatomical volumes were collected using a T1 SPGR sequence. The functional MRI protocols were based on a multi-slice gradient echo, echo-planar imaging (EPI) and a standard head coil. The functional data were obtained under the following optimal timing parameters: TR, 3 s; TE, 55 ms; flip angle, 90°; imaging matrix, 80 × 80; FOV, 24 cm. The 17 slices with 4-mm slice thickness and 1-mm gap were oriented approximately in the axial position, covering the brain except the most dorsal and ventral tips.

Experimental procedure. The stimulus sequences were generated on a PC, and projected via a LCD projector (Epson MP 7200, Japan) onto a tangent screen located inside the scanner and in front of the subject. During the experiment, the subjects kept their right arm on a custom-made table, and touched the objects and textures in the somatosensory epochs with their right hand.

Subjects. Volunteers without neurological or psychiatric problems (27–50 years old; four women, five men; six right-handed, three left-handed, as assessed by the Edinburgh test) participated in the experiments. The Tel-Aviv Sourasky Medical Center Ethic Committee approved the experimental procedure. A written informed consent was obtained from each subject.

Stimuli and experimental design. We used 18 objects and 18 textures. The objects were three-dimensional solid bodies of a convenient size to grasp with one hand. The textures were 18 × 18 cm amorphous sheets. All objects and textures were photographed at a typical angle, to allow easier visual recognition. The subjects knew in advance the names of all items, from a list given to them a week before the scan, but they did not see or touch the items before the scan. Typical names were given to the objects (syringe, fork etc.) and to the textures (sandpaper, fur etc.).

Subjects did the control experiment immediately after the main exper-

iment, during a single scan. The experiment was run in a block design format (Fig. 1a). Block types consisted of somatosensory objects and somatosensory textures for six blocks each, and visual objects and visual textures for four blocks each. Each block lasted 12 s, followed by a blank (rest) period of 9 or 12 s. The first and last blank periods were longer (27 and 15 s, respectively). The touched objects or textures were presented to the subjects by the experimenter for 4 s (3 in each block). Visual images were shown for 1.33 s each (9 in each block). In all cases, the subjects were required to covertly name the objects or textures. The subjects got a short auditory cue (lasting about one second) three seconds before each somatosensory block, and immediately at the end of the block, to assure that they touched the objects only during the appropriate period.

In the control experiment, we remapped the visual object-related areas, using a standardized set of visual objects and highly scrambled images of the same objects. In addition, there were three types of blocks: 'naming recall', 'motor recall' and 'visual imagery' (four blocks each, all were done with eyes closed, as in the somatosensory blocks). In the naming recall block, subjects were asked to covertly recall the names of the objects from the list. The items presented matched the ones presented in the main experiment. We confirmed before the scan that each subject could name at least 80% of the items from the list. On average, the subjects could name seven objects in a naming epoch. In the motor recall task, the subjects made hand movements imitating the grasping and exploration of objects. In the visual imagery condition, the subjects were orally asked to visually imagine three objects they saw in the previous experiment. The objects to be imagined were changed across the six epochs, so that, altogether, subjects were asked to imagine all the objects. All subjects were acquainted with the various conditions of the main and control experiments before the scan, using a different set of stimuli.

Data analysis. Data analysis was done using the BrainVoyager 3.9 software package (Brain Innovation, Maastricht, the Netherlands). For each subject, the two-dimensional functional data were aligned to two-dimensional anatomical slices of the same subject. Before statistical analysis, raw data were examined for motion and signal artifacts. If necessary, head-motion correction and temporal smoothing in the frequency domain were applied to remove drifts, and to improve signal-to-noise ratio. The data were analyzed using a linear correlation test. The signal time course was correlated with a reference function, shifted by three seconds to account for the hemodynamic response. Only voxels with a correlation coefficient above 0.33 ($p < 0.005$, not corrected for multiple comparisons) were included in the statistical map. The obtained maps were superimposed on three-dimensional anatomical reference scans. The three-dimensional recordings were used for surface reconstruction. This procedure included the segmentation of the white matter using a grow-region function. The cortical surface was then unfolded, cut along the calcarine sulcus and flattened. The obtained activation maps were superimposed on the inflated and unfolded cortex for each subject, and the Talairach coordinates were determined for each region of interest. The borders of retinotopic visual areas were determined based on mapping the vertical and horizontal visual field meridians for each subject^{36–37}. This map was obtained in a separate scan, when the subject viewed triangular wedges either containing natural grayscale images or flickering black-and-white random dots, as described previously³⁸. Areas of activation were depicted in a pseudo-color map according to the significance level, and overlapped with high-resolution anatomical images of the same slice. Time courses were obtained from the statistically significant voxels. The subject's average signal intensity was estimated by averaging across all the voxels in the region of interest. Then, the average signal intensity across all subjects was calculated, pooling over the different individual average signal intensities.

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