Abstract

We used functional magnetic resonance imaging (fMRI) to investigate the neural substrates involved in haptic processing of texture, shape, and hardness. Subjects performed haptic classification tasks on a set of 27 silicone objects having parametrically defined shape, texture, and hardness. The objects were ellipsoids of revolution in which the ratio of the long to the short axis was varied, producing three different shapes. Three surface textures and three hardness levels were used. In three separate experiments, the same subjects classified each object along the three levels of one of the object properties (shape, texture, or hardness). Texture, shape, and hardness processing led to contralateral activation in the postcentral gyrus (PCG). A common region located within relatively posterior portions of the PCG was observed during shape and texture identification whereas a separate and more anterior region was activated during the hardness identification task. The hardness identification task also produced bilateral activation within the parietal operculum. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Sensory systems

Topic: Somatosensory cortex and thalamocortical relationships

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1. Introduction

Whenever we grasp an object, information from a variety of sources is potentially available to the somatosensory system including texture, hardness, thermal properties, weight, shape, and size. Little is known about the cortical representations that underlie the processing of these properties during simple grasping movements in humans. In this paper we focus on three prominent object properties: shape, texture, and hardness.

Early lesion work in the monkey suggested that different cortical regions might be responsible for the processing of shape and texture. Working in SI, Randolph and Semmes [14] found that whereas area 3b lesions impaired monkeys’ shape and texture discriminations, area 2 lesions only impaired shape discriminations and area 1 lesions only impaired texture discriminations. Unit recording in the monkey has confirmed and extended these findings. Darian-Smith et al. [3] found that area 3b and area 1 cells are sensitive to 2-D textured surfaces. Sinclair and Burton [16] also found texture-sensitive cells in area SII (a region which receives inputs from area 3b).

Other single-cell recording work has examined the role of somatosensory cortex in the processing of the shape and texture of 3-D objects. For example, Koch and Fuster [8] found area 2 and area 5 cells that discriminated between various 3-D shapes. Iwamura and his colleagues have conducted the most extensive studies on single-cell SI responses to the shape and texture of 3-D objects. In their processing scheme, Iwamura and colleagues [6] suggest that area 3b provides information about fine features of objects which can be perceived at the level of the fingertips (e.g. fingertip-sized stimuli such as raised 2-D patterns). In contrast, area 2 provides information about object properties useful for manipulation (i.e., the global features of objects, such as size, shape, and texture, which are perceived across relatively large finger/hand skin areas).

Although little work has been done elucidating the neural substrates of hardness processing in the monkey,
behavioural evidence, in conjunction with what is known about receptor inputs to somatosensory cortex, suggests that the critical cortical maps for the coding of the hardness of relatively compliant surfaces might lie in areas 3b and 1 [17]. In their monkey lesion study, Randolph and Semmes [14] found that area 3b lesions and possibly area 1 lesions impaired hardness discrimination.

More recently, the cortical substrates of haptic shape and texture have been examined in neurologically intact humans with functional neuroimaging. O’Sullivan, Roland, and Kawashima [13] had subjects make texture and length discriminations, and found that length discriminations produced contralateral PCG activation in a more inferior region than that produced by texture discriminations. In related work, Roland, O’Sullivan, and Kawashima [15] identified an area in the parietal operculum that was sensitive to texture and a region in the intraparietal sulcus that was sensitive to shape. Burton, Sinclair, Lin, and MacLeod [2] observed activation in several parietal regions including the PCG during a texture discrimination task. Finally, Deibert, Kraut, Kremen, and Hart [4] report inferior parietal activation during a tactile object identification task.

In the present fMRI study we expand on this work by having subjects judge shape, texture, and hardness using a single set of objects that vary simultaneously along these three dimensions. Each dimension of this set of custom-made, parameterized objects was selected such that shape, texture, and hardness were perceptually equivalent [9].

2. Method

2.1. Objects

The set of 27 objects were ellipsoids of revolution, formed by rotating an ellipse around the longer axis (see [9]). The ratio of long-to-short axis was varied, producing three different shapes each given a descriptive name: ‘cigar’ (11.8 cm/4.2 cm), ‘egg’ (8.8 cm/4.8 cm), and ‘ball’ (7.0 cm/5.5 cm). Texture was varied by changing the microstructure of the surface, which was composed of small, contiguous four-sided pyramids. By changing the size of these pyramids, three texture types were created: ‘smooth’ (1 mm pyramid sides), ‘medium’ (2 mm pyramid sides), and ‘rough’ (3 mm pyramid sides). Three hardness levels were produced by altering the durometer value of the silicone used to make the objects: ‘soft’ (10), ‘firm’ (25), and ‘hard’ (70).

2.2. Procedure

Subjects: Seven healthy right-handed (as established by a modified version of the Oldfield [12] inventory) adult volunteers participated in the study (age range 22–30 years; 4 males and 3 females). Pre-Imaging Training: Prior to the fMRI experiments, the subjects were trained to classify each object along the three levels of each object property (shape, texture, and hardness). Subjects lay on the bed of the scanner (outside of the bore of the magnet) with their right arm propped up in a position similar to the position adopted during the actual MRI experiments. The subject’s right hand was held open, palm facing down. For a given classification task, a series of objects was placed on the palm of the subject’s right hand. The subject was trained to perform a stereotyped ‘gripping’ movement for all trials. When the object was placed on the palm of the hand, the subject curled his or her fingers around the contours of the object, squeezing it once and then reopening their hand and releasing the object into the experimenter’s hand. As soon as the object was released the subject verbally classified it into one of the three levels by name. After each trial subjects were given feedback. Training continued until accuracy reached a 90 percent criterion. This type of training was used for each of the classification tasks. Additionally, subjects were trained to perform a control task in which the palm of their right hand was tapped with a small wooden probe (2 mm diameter). This tap signaled the subject to perform a single ‘grasp’ movement with their right hand. In this ‘grasp’ movement, the subject simulated the gripping of an object by curling the fingers of their right hand inward stopping before their fingers touched the palm of the hand, and then reopening their hand. The ‘grasp’ used in the control task simulated the sort of grasp that was made in the classification task but minimized tactile stimulation. Subjects kept their eyes closed throughout the training, so that visual cues could not be used to make the classifications. The pre-imaging training required approximately 20 min to complete.

2.3. MRI experiment

After training, subjects performed each classification task in the fMRI imager. The order of the classification tasks was counterbalanced. In three separate functional scans, subjects classified each object along the three levels of one of the object properties (shape, texture, or hardness). Each classification task took 6 min, with four alternating 90 s cycles. Each of the cycles consisted of the classification of the stimulus objects (45 s) alternating with the control task (45 s). For a given classification task, objects were placed in the subject’s right hand — approximately one every 5 s. Subjects gripped the object once and then classified it. For the control task, the palm of the subject’s right hand was tapped with a small probe — again approximately once every 5 s. This tap signaled the subject to perform a single ‘gripping’ movement with the right hand. On average, 8–9 stimuli were presented during each half cycle. Before each functional scan several practice trials were presented to reacquaint the subject with the particular classification task that would subsequently follow. Subjects kept their eyes closed during the 6 min
experiment and generated the classification name ‘in their head’ immediately following the release of the object. Identical procedures were used for the shape and hardness classification tasks.

2.4. MRI system

fMRI was performed on a Siemens/Varian 4 T whole body imager (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) using a purpose-built head coil. After a global shim, anatomic imaging allowed delineation of the area of interest (central sulcus and PCG). A bite bar was used for head stabilization. T1-weighted sagittal scout images were acquired to select 10 contiguous 5 mm slices in a coronal orientation across the brain. Each functional volume was acquired using a navigator echo corrected, interleaved all three tasks. Orientation across the brain. Each functional volume was comparable absolute areas of activation were observed for acquired to select 10 contiguous 5 mm slices in a coronal The signiﬁcance level was selected such that relatively head stabilization. T1-weighted sagittal scout images were posed on a normalized (Talairach) anatomical 3-D data set. The Tournoux atlas [18] using an afﬁne transformation. Within regions within the PCG are active for hardness identiﬁcation task. Figs. 1±2 highlight one of the this representation, 3-D statistical maps were generated by tion relative to shape and texture identiﬁcation. The latter to time series of task-related functional activation [5]. General linear models (multi-subject design) were computed for each of the three experiments from 7 volume time-courses (7 subjects) with 120 points each. The identiﬁcation of task-related activity was based on group correlation maps (7 subjects and 120 time points per condition) thresholded at P<0.005, which were superimposed on a normalized (Talairach) anatomical 3-D data set. The signiﬁcance level was selected such that relatively comparable absolute areas of activation were observed for all three tasks.

3. Analyses

In each experiment, 120 fMR images were acquired, comprising a timeseries of images at each voxel. Using Brain Voyager 3.9 [19], the 2-D functional data sets were incorporated into the 3-D anatomical data sets through interpolation to the same resolution (voxel size: 1×1×1 mm). Because the 2-D functional and 3-D anatomical data sets were collected within the same scanning session, co-registration of the two data sets could be computed directly based on the Varian slice position parameters for the T1- and T2*-weighted images. For each subject the anatomical data sets were transformed into Talairach space. The 3-D data set for each subject was rotated such that it was aligned with the stereotaxic axes. For this, the locations of the anterior commissure, posterior commis- sure, two rotation parameters for mid-sagittal alignment, and the extreme points of the brain volume acquired had to be speciﬁed manually in the 3-D anatomical data set. These points were then used to scale the 3-D data sets into the dimensions of the standard brain of the Talairach and Tournoux atlas [18] using an afﬁne transformation. Within this representation, 3-D statistical maps were generated by ﬁrst removing any linear drifts over time from each voxel’s time course, applying a spatial ﬁlter with a Gaussian kernel of 4 mm (full width half-maximum), and then cross-correlating each voxel’s time course with a reference sinusoid at the stimulus alternation frequency of 1/90 Hz with a lag of 4 s to account for the hemodynamic delay [1]. The statistical analyses of the changes in the BOLD signal were based on the application of the general linear model to time series of task-related functional activation [5].

4. Results

As Fig. 1 (panels A–C) shows, contralateral PCG activation was observed in the shape, texture, and hardness identiﬁcation tasks. The shape and texture tasks appear to activate overlapping portions of the PCG, although it appears that the shape task activated a slightly more lateral and anterior region of the PCG (panel B) relative to the texture task (panel A). In contrast, the hardness identiﬁcation task activated a more anterior portion of PCG (see panel C) that was separate from the regions activated by the shape and texture identiﬁcation tasks. Interestingly, the hardness identiﬁcation task also produced bilateral activation of the parietal operculum (see panel D). Fig. 2 shows the degree of overlap between the cortical regions activated in the three tasks. Based on its relatively anterior location within the PCG, the region involved in hardness identiﬁcation likely corresponds to Brodmann’s areas 3a–3b, whereas the more posterior regions of the PCG that were activated during the shape and texture tasks likely correspond to Brodmann’s areas 1–2. Table 1 summarizes the Talairach and Tournoux stereotaxic coordinates for the aforementioned regions.

5. Discussion

Much like earlier functional work, we observed con- tralateral activation in the PCG during shape and texture identiﬁcation [2,4,15]. In addition, we also demonstrate contralateral PCG activity when subjects perform a hard-
Fig. 1. GLM maps of the cortical regions activated for shape (panel A), texture (panel B), and hardness (panel C) identification. Note activation in contralateral PCG. Panel D shows the bilateral activation within the parietal operculum observed during the hardness identification task.

portions of the PCG relative to texture identification (see Table 1). Our work provides evidence that the critical region within the PCG involved in hardness identification is located in a relatively anterior region of the PCG relative to the regions recruited for shape and texture identification.

Although we do not have direct cytoarchitectonic evi-
Fig. 2. GLM maps of the relative overlap of cortical regions involved in shape, texture, and hardness identification. Note in panel A the high degree of overlap between the PCG region sensitive to shape and the region sensitive to texture. Panels B and C show the pronounced activation in the more anterior portion of PCG during hardness identification relative to shape and texture identification.
dence, the fact that a relatively more anterior PCG region was activated during the hardness task is consistent with monkey lesion work showing that area 3b is important for hardness discrimination [14]. In addition, the relatively more posterior region of PCG that was active during the shape and texture identification tasks is consistent with monkey lesion work suggesting that area 2 plays a role in shape processing [14] and is also consistent with monkey lesion and electrophysiological work showing that area 1 plays a role in texture processing [3,14].

In addition to the expected contralateral PCG activation during the hardness identification task, we also observed contralateral activation within the parietal operculum. This suggests that the parietal operculum plays an important role in hardness processing whereas it appears to play a far smaller role in shape or texture processing. This region likely corresponds to area SII [15].

The ipsilateral activation we observed within the parietal operculum during a hardness identification task seems somewhat surprising. However, neurophysiological work in the monkey has also provided evidence for bilateral representation of the hand in somatosensory cortex. Iwamura and his colleagues report cells along the area 2–5 border that have bilateral receptive fields [7] (conveyed via callosal connections) and are active during the palpation of hand-held objects [6]. At least one other functional neuroimaging paper in humans has also shown the possibility of bilateral processing of haptic information. Using PET, O’Sullivan, Roland, and Kawashima [13] found bilateral activation in the supramarginal and angular gyri during a haptic length discrimination task whereas for a texture discrimination task they did not.

The present results are generally consistent with the few functional neuroimaging studies that have examined shape and/or texture processing [2,4,15]. There are some differences between our findings and other work in the literature; however, it should be noted that even within the existing literature there is not a complete consensus about the cortical substrates of texture and shape processing. For example, Burton et al. [2] observed activation within the intraparietal sulcus during a passive texture discrimination task, in addition to PCG activation; in contrast, Roland, O’Sullivan, and Kawashima [15] observed activation within the parietal operculum during their texture discrimination task. Our texture identification task led to activation within a region of the PCG which appears to border on the intraparietal sulcus — consistent with the findings of Burton et al. [2]. We were unable, however, to confirm the findings of Roland, O’Sullivan, and Kawashima [15] who found that a shape discrimination task activated a region centered around the intraparietal sulcus, and who observed parietal operculum activation during a texture identification task.

The selection of an appropriate motor control condition for a somatosensory task is always a challenge. Our use of a simulated gripping movement as a control task might have caused subjects to produce slightly different gripping movements as compared to the gripping movements they produced during the haptic task. Thus, some of the effects we observed might have also been due to slight differences between the gripping movements produced in the two tasks. One advantage of our approach was that we used the identical set of target objects for all three of our identification tasks. Thus, any differences between the three identification tasks (i.e., shape, texture, and hardness) in terms of cortical activation can be attributed to differences in the way that these three attributes are processed.

At present, there are few functional neuroimaging studies that have looked at both shape and texture processing — and to our knowledge, none that has also examined hardness processing within the same study. Moreover, the handful of existing studies have all used different methodologies: different tasks (passive vs. active palpation; identification vs. discrimination), different stimuli (2-D vs. 3-D objects), and different control conditions. In addition, with the exception of our study, the experiments that have examined more than one characteristic (e.g., texture and shape) have used different objects in each of the tasks. Future neuroimaging studies will hopefully continue to tease apart these various factors so that we can arrive at a satisfactory understanding of the cortical substrates involved in shape, texture, and hardness processing in humans.

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References


