

What vs. where in touch: an fMRI study

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Two streams have been identified in cortical visual processing: a ventral stream for form, color, and features, and a dorsal stream for spatial characteristics and motion. We investigated whether similar “what” and “where” dissociations of function exist for human somatosensory processing. Using identical stimuli and hand movements, subjects either performed tactile object recognition (TOR) and ignored location or performed tactile object localization (LOC) and ignored identity. A matched-movement control task separated activation associated with sensorimotor input from higher-level cognitive contributions. Results confirmed separate processing streams for TOR and LOC. TOR activated the frontal pole as well as bilateral inferior parietal and left prefrontal regions involved in tactile feature integration and naming. LOC activated bilateral superior parietal areas involved in spatial processing. The dissociation of object and spatial processing streams appears to be a modality general organizational principle in the brain.

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Introduction

The cortex is divided into multiple regions and distinct streams of information processing are defined by connections and operations within and between subsections of these areas (Caminiti et al., 1996). Two streams in cortical visual processing have been identified: a ventral stream for fine analysis of the visual scene into form, color, and features, and a dorsal stream for the coding of

spatial characteristics of the visual scene and motion (e.g., Ungerleider and Mishkin, 1982). Recently, investigators have shown that the auditory system also has distinct object and spatial processing streams (e.g., Anourova et al., 2001; Kaas and Hackett, 1999; Maeder et al., 2001). In this study, functional magnetic resonance imaging (fMRI) was used to investigate whether an analogous “what” vs. “where” dissociation exists for the human somatosensory system.

In the visual system, the ventral “what” system pathway connects striate, prestriate, and inferior temporal cortical regions. The dorsal “where” or “how” system connects striate, prestriate, and superior parietal cortical regions (Goodale and Milner, 1992). Support for the two visual processing streams comes from patient and neuroimaging research (e.g., Farah, 1990; Haxby et al., 1991; Newcombe et al., 1987).

Relatively little research has compared neural pathways for object and spatial processing in the human somatosensory system. Evidence in support of a somatosensory object-processing stream in ventrolateral somatosensory cortex can be found in primate (Friedman et al., 1986; Mishkin, 1979; Murray and Mishkin, 1984), neuropsychological (Caselli, 1991, 1993; Reed and Caselli, 1994; Reed et al., 1996), and neuroimaging studies (Amedi et al., 2001; Bonda et al., 1996; Reed et al., 2004). The inferior parietal areas of macaques appear to be somatosensory equivalents of visual inferotemporal cortices because each region connects its respective sensory modalities to mesial temporal paralimbic and limbic structures (Friedman et al., 1986). Research with brain-injured humans also supports a distinct neural pathway for tactile object recognition (TOR). Caselli (1991, 1993) examined patients with focal lesions involving the ventrolateral somatosensory association cortices (SII, inferior parietal, parietal insula) and sparing SI. Unilateral lesions of the inferior parietal region selectively impaired TOR contralaterally without commensurate impairments of basic or intermediate tactile functions, spatial, or language functions. Circumscribed damage to the inferior parietal area also produced TOR deficits separate from low-level tactile perception and supramodal spatial processing deficits, thereby demonstrating a dissociation of tactile “what” from “where” (Reed et al., 1996). In addition, neuroimaging data from tactile shape memory and recognition tasks have implicated the ventrolateral somatosensory

Abbreviations: LH or L, left hemisphere; RH or R, right hemisphere; BA, Brodmann's Area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; mFG, medial frontal gyrus; SFG, superior frontal gyrus; prCG, precentral frontal gyrus; poCG, postcentral gyrus; SM1, primary sensorimotor cortex (pre- and post-central gyrus); IPL, inferior parietal lobule; SPL, superior parietal lobule; SII, secondary somatosensory cortex; MTG, middle temporal gyrus.

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Table 1
Brain areas activated during TOR conditions compared to MOV conditions

Hemisphere, Gyrus, Area	BA	Talairach coordinates at peak activation			Cluster level	
		x	y	z	No. of voxels	t*
R IFG/Frontal operculum	13/45/47	33	27	−3	91	1.77
R IFG/Frontal operculum	44/45	63	18	21	15	0.74
R prCG, poCG, IPL	1/2/3/4/6/40	57	−21	30	123	1.48
R Precuneus	39	27	−69	36	46	1.19
L Precuneus/SPL	7	−9	−72	54	21	1.38
L Precuneus	7/19	−21	−57	33	33	1.24

* $T^2(1449) = 0.32$, $P_{\text{uncorrected}} < 0.001$. Clusters restricted to a minimum of 8 voxels in extent.

stream concerned with object recognition and tactual learning (e.g., Bonda et al., 1996; Ginsburg et al., 1987; Mishkin, 1979; Roland et al., 1998).

Likewise, neuropsychological support exists for a distinct somatosensory spatial pathway. One patient exhibited a dissociation between a ‘where’ system and a ‘how’ system for tactile and proprioceptive stimuli; he could not localize or interact with felt objects but could recognize them (Rossetti et al., 1995). Patients with dorsomedial lesions associated with a dorsal stream in somatosensory cortices (premotor area, Brodmann areas (“BA”) 5 and 7) present transitory impairments in tactile spatial functions, including sensorimotor integration and the spatiotemporal organization of touch and movement (Caselli, 1993).

This study documents a somatosensory “what–where” division of function in the intact human cortical system. Using the same objects and movement sequences, subjects either recognized objects while ignoring location or localized objects while ignoring identity. The neural activity generated by TOR and tactile object localization (LOC) was compared to determine if ventrolateral somatosensory regions were more active for TOR and dorsal, superior parietal regions were more active for LOC.

Materials and methods

Subjects

Seven, healthy, right-handed male subjects (mean age = 24.7; range 22–29 years) were paid to participate in this study. Each had normal brain structure as established using an MRI scan. All subjects gave informed consent for a protocol approved by the Human Subjects Review Board of the University of Utah, School of Medicine.

Stimuli

Stimuli were six, real, multidimensional objects glued in one of six positions on a long foam-core board. The six, real objects were easily named, nonmagnetic, small objects typically found around the house: a whistle, a die, a marble, a pencil-tip eraser, a button, and a spool of thread. The board was 12.7 cm wide and 50.8 cm

long so that it could be placed under the subject’s hand in the scanner. A raised reference point was provided at the center bottom edge of the board. Objects were placed in one of six possible locations on the board. The locations were 5.08 cm apart horizontally and 6.35 cm apart vertically. Catch trials were included to ensure accurate task performance: a plastic letter “X” or “O” was placed in one of three positions that did not correspond to any target location. Catch trials occurred on 6% of the trials. The objects and locations were pretested to make the object recognition and localization tasks as similar in difficulty as possible. Pilot subjects could reliably recognize all objects and locations in approximately the same time. The Movement and Rest control conditions used boards with a reference point and no object.

Procedure

Subjects participated in five 4.5 min sessions. A pseudo-randomized, blocked design was used. Each subject performed four tasks while lying supine in the MR scanner with their eyes closed: tactile object localization (LOC), tactile object recognition (TOR), movement alone (MOV), and rest with attention on the hand (REST). In each session, four task conditions were presented three times each, for a total of 12 blocks (i.e., REST, MOV, TOR, LOC, MOV, TOR, REST, LOC, TOR, MOV, and REST). Each 24-s epoch included eight, 3-s trials.

In the LOC task, subjects localized the object in one of six numbered locations (e.g., response “3”), ignoring identity. For each trial, subjects began with their right hand on the board with their middle finger on the reference point. Then, they performed a hand-movement sequence in which they moved their hand along the surface of the board to the object, grasped it, and released it. Pilot testing confirmed that subjects could consistently recognize the current set of stimuli and locations using this sequence. Subjects lifted the left index finger when they recognized the specific location (e.g., 1, 2, 3, 4, 5, or 6) in which the object was presented. For correct performance, subjects should have lifted their left finger on 94% of the trials because 6% of the trials were catch trials in which the object was not in any of the six identified locations. The locations to be identified were presented in random order.

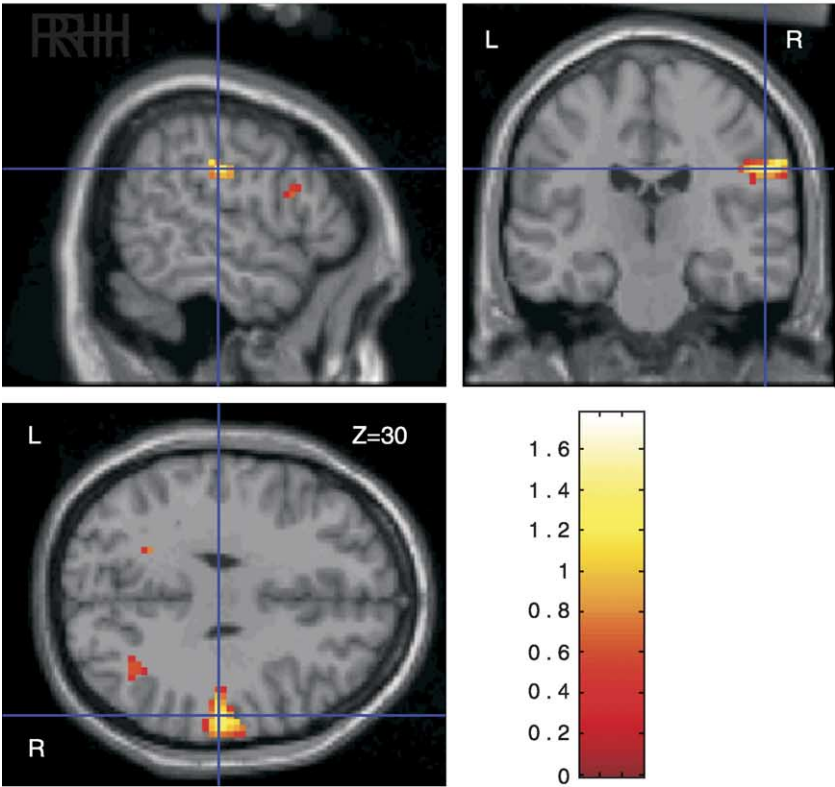
In the TOR task, subjects recognized the object (e.g., response “whistle”), ignoring its location. Subjects used the hand-movement

Table 2
Brain areas activated during LOC conditions compared to MOV conditions

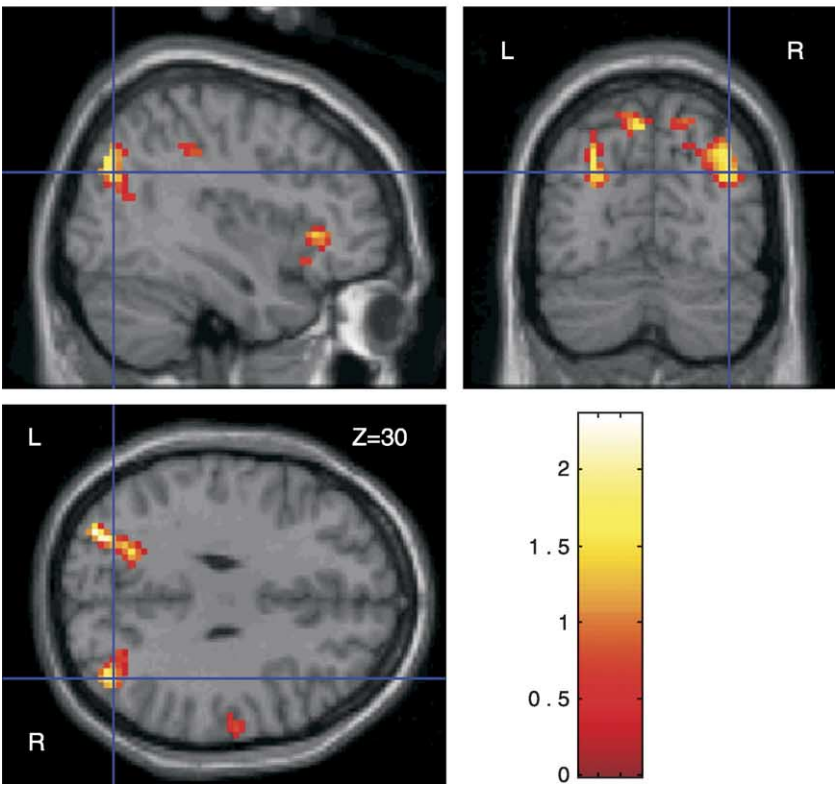
Hemisphere, Gyrus, Area	BA	Talairach coordinates at peak activation			Cluster level	
		x	y	z	No. of voxels	t*
R IFG, MFG, Frontal operculum	47	33	27	0	47	2.02
R poCG, prCG	3/4/6	66	−15	33	18	1.17
R MTG, IPL, Precuneus	19/39	39	−72	30	149	1.94
R IPL, poCG	2/40	45	−33	42	29	1.28
R poCG	7	12	−57	69	12	1.06
R SPL	7	21	−69	57	35	1.20
L Precuneus	7/19	−27	−75	33	110	2.35
L Precuneus/SPL	7	−6	−75	51	33	2.07

* $T^2(1449) = 0.32$, $P_{\text{uncorrected}} < 0.001$. Clusters restricted to a minimum of 8 voxels in extent.

a) TOR vs. MOVt



b) LOC vs. MOVt



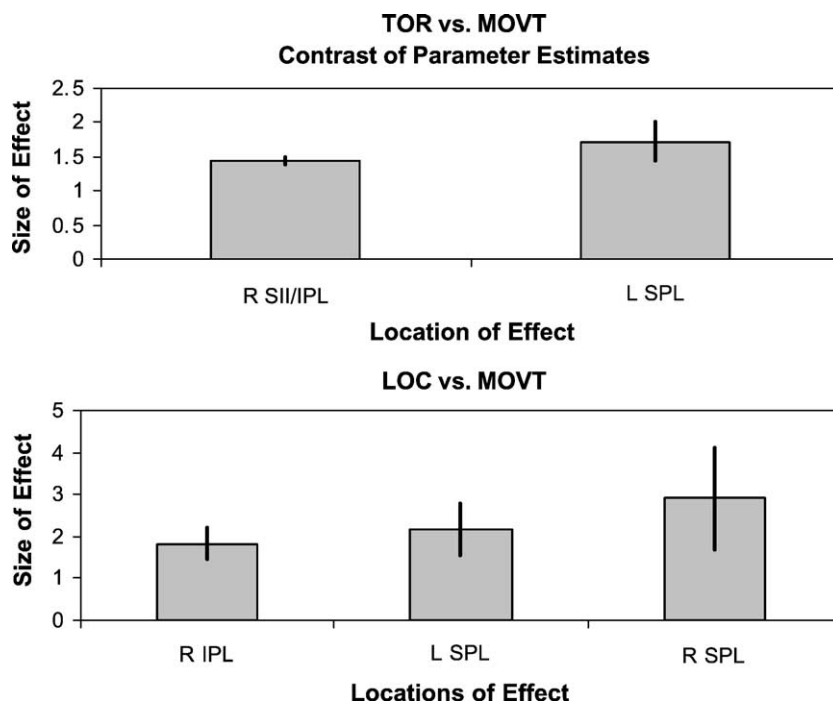


Fig. 2. Contrast of parameter estimates for TOR vs. MOV and LOC vs. MOV contrasts. The mean size of effect and its standard deviation are illustrated for significant IPL and SPL areas. IPL and SPL were defined as the significant peak voxel coordinates for IPL and SPL areas reported in Tables 1 and 2.

sequence to recognize the objects and lifted their left index finger to indicate recognition. They did not lift their finger if they did not recognize the object (i.e., catch trial or did not recognize the object). The objects to be recognized were presented in random order.

There were two control conditions. The movement (MOV) task provided a robust signal associated with sensorimotor aspects of the tasks (i.e., the purely motoric and sensory activity) without object recognition or localization. Subjects executed the hand-movement sequence on a board that had no object and lifted the left index finger. In the REST task, subjects put their right hand down on a blank board and focused their attention on their hand.

Prior to scanning, subjects received practice on the TOR and LOC tasks until they achieved a criterion of 90% accuracy. During each session, the experimenter told subjects which task to perform before each epoch. Three experimenters monitored the subject for correct executions of the movement sequence and accurate recognition responses. All subjects achieved 90% accuracy and above for both TOR and LOC tasks. After the experiment was completed, subjects reported that the two tasks felt similar in difficulty.

Functional imaging

Data were acquired with a Picker 1.5 T Eclipse System whole body MRI system (Picker Inc., Cleveland OH) with echo speed gradients and a local gradient coil. T1-weighted anatomical images (7-mm thickness (skip 0 mm), FOV = 26 cm, 256 × 256

pixel matrix) and contiguous multislice T2*-weighted echo-planar images (flip angle = 90°, T_E = 40 ms, 64 × 64 pixels, FOV = 26 cm, voxel size = 3.67 mm × 3.67 mm × 7 mm) were obtained. Volumes were obtained continually every 3 s. Each volume comprised 16 slices (slice thickness of 7 mm). Five sessions of four 4.5 min were recorded. For each session, 99 volumes were acquired with three “dummy” volumes acquired at the start of each session to allow for T1 equilibration effects. Thus, 480 volumes of data were acquired for each subject.

Image preprocessing

Image and statistical analyses were performed using statistical parametric mapping and the SPM99 software package (Wellcome Department of Cognitive Neurology, University College, London, 2000). All volumes were realigned to the first volume to correct for interscan movement and then resliced using a sinc interpolation in space (Friston et al., 1995a,b). Each volume was normalized (Friston et al., 1995a,b) to a standard EPI template volume, based on the Montreal Neurological Institute (MNI) reference brain (Evans et al., 1993, 1994), in the standardized space of Talairach and Tournoux (1988) using nonlinear basis functions. Finally, the data were smoothed with a Gaussian kernel of 8 mm full width at half-maximum to compensate for residual variability after spatial normalization. Smoothing also improves the applicability of the Gaussian random field theory used in the subsequent statistical inferences.

Fig. 1. Across-subject conjunction activation for TOR vs. MOV and LOC vs. MOV. Areas of significant activation are overlaid on normalized brain slices based on the MNI brain presented in neurological orientation (i.e., left hemisphere is on the left). Sagittal, coronal, and horizontal sections are illustrated. (a) For TOR vs. MOV, activated regions included right somatosensory cortex (BA 1/2/3), inferior parietal somatosensory association areas, and SII (BA 40). The right inferior frontal gyrus/prefrontal cortex (BA 13/45/47) and premotor areas (BA 4/6) may be part of an attention network. Limited activation was found in bilateral precuneus (BA 7/19/39) and right superior parietal cortex (BA 7). (b) For LOC vs. MOV, the activated regions included bilateral superior parietal cortex and precuneus, associated with spatial processing. The right inferior frontal gyrus and the right middle frontal gyrus (BA 47) and premotor areas (BA 4/6) may be associated with an attention network.

Table 3

Brain areas activated during TOR conditions compared to LOC conditions

Hemisphere, Gyrus, Area	BA	Talairach coordinates at peak activation			Cluster level	
		x	y	z	No. of voxels	t*
RL SFG, mFG	9/10	0	60	27	129	1.24
R MFG, prCG	4/6	42	−9	45	81	1.12
RL cingulate	6/24/31/32	3	−3	45	784	2.07

* $T^7(1449) = 0.32$, $P_{\text{uncorrected}} < 0.001$. Clusters restricted to a minimum of 8 voxels in extent.

Statistical analysis

The data were analyzed using an across-subject conjunction implemented in SPM99. The statistical analysis of each effect of interest had two stages. In the first stage, activation maps for each task-pair contrast and each subject were calculated. In the second conjunction stage, areas of common activation for all subjects were identified for each effect of interest. Six effects of interest were studied separately in this manner: TOR vs. REST, LOC vs. REST, TOR vs. MOVIT, LOC vs. MOVIT, TOR vs. LOC, and LOC vs. TOR. Our analysis follows closely the method discussed in Friston et al. (1999), which formalizes the calculation of statistical thresholds corrected for a conjunction across a population of subjects.

Analysis stage I

The expected responses were modeled in an experimental design matrix by convolving a box-car function with a standard hemodynamic response function (HRF). The temporal derivative of the expected hemodynamic response was also added as a regressor, allowing compensation for response-delay variations. Low frequency artifacts, corresponding to aliased respiratory and cardiac effects and other slow variations in signal intensity, were removed by high-pass filtering (>96 s period) the time series, and a low-pass filter based on the HRF was used to remove transients. In addition, whole volume signal changes were removed by global scaling. Using the experimental design matrix and standard linear estimation, session-specific t statistical maps (SPM {t}) pertaining to each effect of interest were calculated for each subject (Friston et al., 1995a,b).

Analysis stage II

An across-subject conjunction was calculated by finding the minimal t value (at each voxel) across all subjects (Friston et al., 1999). An uncorrected $P < 0.001$ threshold was applied. Areas of activation that survived the statistical threshold were characterized in terms of their peak heights (t value maxima) with their positions specified in coordinates (x , y , and z) in stereotactic space defined by the MNI (Evans et al., 1993). We report cluster activations with a minimum extent of 4 voxels. The activation maps were then superimposed on high-resolution MR scans of the standard MNI brain. Locations of peak activation were associated with their corresponding Brodmann areas using the MNI Space Utility (http://www.ihb.spb.ru/~pet_lab/) and by neuroanatomical analysis of the sulci and gyri.

Table 4

Brain areas activated during LOC conditions compared to TOR conditions

Hemisphere, Gyrus, Area	BA	Talairach coordinates at peak activation			Cluster level	
		x	y	z	No. of voxels	t*
R IPL, SPL, Precuneus	7/40	42	−60	48	47	0.80
L SPL	7	−27	−69	48	18	0.72
L Precuneus	7	−6	−75	48	29	1.02
L Precuneus	19	−30	−78	36	8	0.77

* $T^7(1449) = 0.32$, $P_{\text{uncorrected}} < 0.001$. Clusters restricted to a minimum of 8 voxels in extent.

www.ihb.spb.ru/~pet_lab/) and by neuroanatomical analysis of the sulci and gyri.

Results

Six contrasts were performed using across-subjects conjunction analyses that revealed common activated brain regions for all seven subjects. First, TOR and LOC were compared to REST to confirm that the experiment activated contralateral primary sensorimotor cortex (e.g., left SM1). Second, TOR and LOC were compared with MOVIT to eliminate activation associated with sensorimotor inputs and to examine the cognitive substrates associated with tactile object recognition and spatial localization. Last, TOR and LOC were directly compared to reveal distinct activation patterns consistent with the function of each task.

Paradigm confirmation

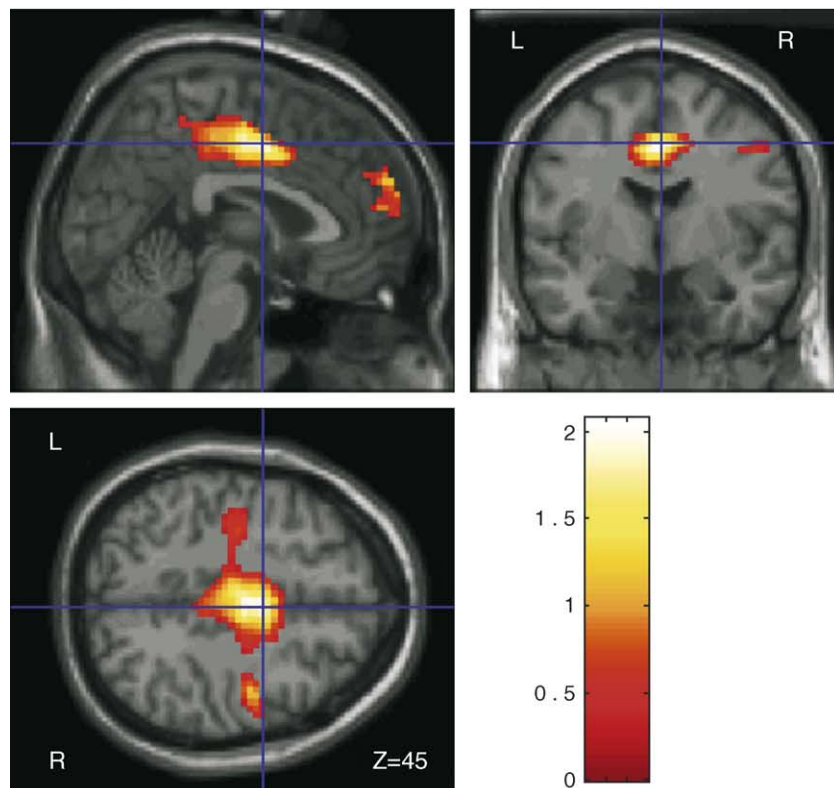
When TOR and LOC were each compared to REST, the cortex adjacent to the central sulcus in the LH (i.e., contralateral to the hand used for palpation) was strongly activated. This activation was most significant in the contralateral primary sensorimotor cortex: the largest and most extensive cluster was evident near the central fissure in left hemisphere, spreading both anteriorly to motor cortex and posteriorly to parietal cortex. These activated areas are consistent with sensation and movement of the right hand. For the TOR vs. REST comparison, the contralateral SM1 cluster (Brodmann areas “BA” 2/3/4/40) had Talairach space coordinates of $x = -36$, $y = -36$, and $z = 66$ ($T^7(1449) = 0.32$, $P < 0.001$ uncorrected, $t = 6.12$). For the LOC vs. REST comparison, the contralateral SM1 cluster (BA 2/3/4/40) had Talairach space coordinates of $x = -36$, $y = -36$, and $z = 66$ ($T^7(1449) = 0.32$, $P < 0.001$ uncorrected, $t = 5.79$).

Comparisons of TOR and LOC to MOVIT

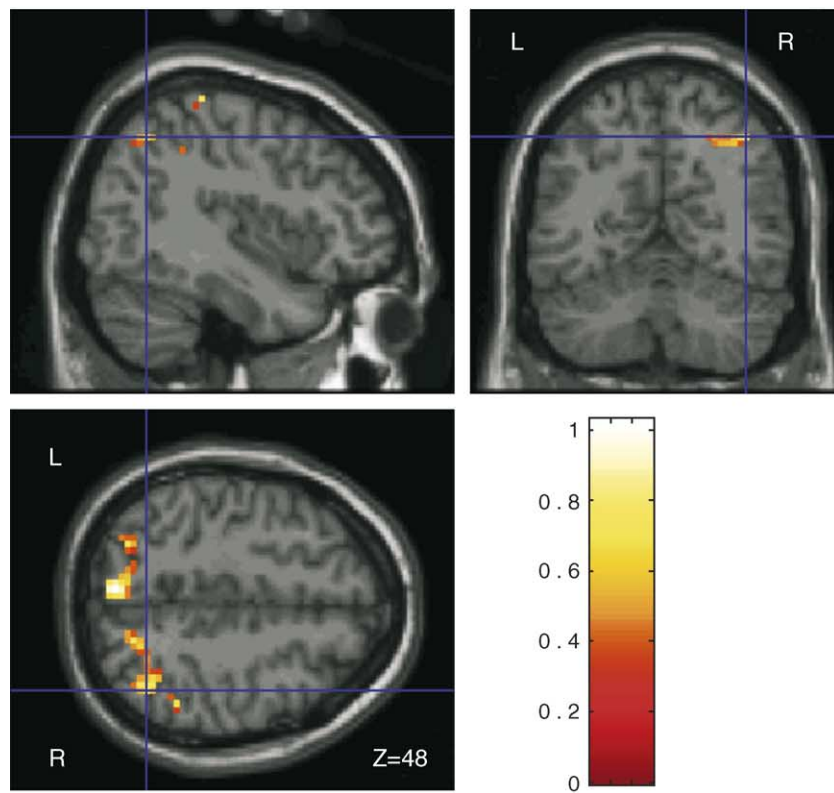
TOR and LOC were each compared to MOVIT. The Talairach space coordinates and sizes of the activated clusters, their extent, and their significant t values ($T^7(1449) = 0.32$, $P < 0.001$ uncorrected) are shown in Tables 1 and 2. Fig. 1 shows clusters

Fig. 3. Across-subject conjunction activation for TOR vs. LOC and LOC vs. TOR. Areas of significant activation were overlaid on normalized brain slices based on the MNI brain presented in neurological orientation (i.e., left hemisphere is on the left). Sagittal, coronal, and horizontal sections are illustrated. (a) The TOR vs. LOC comparison shows increased BOLD signal in the frontal pole, motor cingulate, and premotor/prefrontal areas associated with motor attention and the integration of object features. (b) LOC vs. TOR comparison shows increased BOLD signal in the left and right superior parietal and precuneus regions associated with multimodal spatial processing.

a) TOR vs. LOC



b) LOC vs. TOR



of activation as labeled color overlays on normalized anatomical MRI slices.

Areas showing significantly increased BOLD signal during TOR vs. MOV'T were similar to TOR vs. REST, but without the contralateral primary somatosensory and motor components. The right (ipsilateral) somatosensory cortex (BA 1/2/3) as well as inferior parietal somatosensory association areas and SII (BA 40) was activated. These regions have been associated with the TOR process (Reed et al., 2004). In addition, the right inferior frontal gyrus/frontal operculum (BA 13/45/47) and premotor areas (BA 4/6) were activated. These regions may also reflect the TOR process or a more general process such as attention (Reed et al., 2004). The activation in the contralateral primary sensorimotor cortex (SM1) that was observed when TOR was compared to REST was absent, indicating that the MOV'T condition provided an effective control for sensorimotor activation. Finally, more limited clusters of activation were found in the bilateral precuneus (BA 7/19/39) and in the right superior parietal cortex (BA 7) that may be associated with spatial processing. The location of the left superior parietal cluster is very close to the left superior parietal cluster activated for the LOC vs. MOV'T comparison reported below. To provide additional confirmation of the consistent activation across subjects of our specific areas of interest, namely inferior parietal somatosensory association areas and left superior parietal cortex (BA 7 or SPL), we conducted a contrast of parameter estimates for the peak voxel location of each area (see Table 1) for each subject. Fig. 2 illustrates the size and variability of the effect across subjects in each area.

Areas showing significantly increased BOLD signal during the LOC condition compared to the MOV'T condition also eliminated the SM1 components, indicating that the MOV'T condition provided an effective control for sensorimotor activation. Activation was found in bilateral superior parietal cortex and precuneus (LH: BA 7 and 19, RH: BA 7) and extended into the right middle temporal gyrus and inferior parietal cortex (RH: BA 19/39). The cluster in the inferior parietal cortex is superior to the region associated with SII (e.g., $(\pm 53.3, -20.3, 22.4)$; Moore et al., under review; Reed et al., 2004). These regions have previously been associated with spatial processing (e.g., Haxby et al., 1991). To provide additional confirmation of the consistent activation across subjects of our specific areas of interest, namely inferior parietal somatosensory association areas and bilateral superior parietal cortex (BA 7 or SPL), we conducted a contrast of parameter estimates for the peak voxel location of each area (see Table 2) for each subject. Fig. 2 illustrates the size and variability of the effect across subjects in each area. In addition, activation was found in the right inferior frontal gyrus/frontal operculum, the right middle frontal gyrus (BA 47), and premotor areas (BA 4/6). These areas may be associated with attentional processing (Reed et al., 2004). In sum, these activation patterns are consistent with multimodal spatial localization.

The above analysis indicates some overlap in neural activation for the present TOR task with areas associated with visual localization, and likewise the LOC task overlaps with visual object recognition areas. For example, LOC-MOV'T analysis activated the middle temporal gyrus, part of the ventral object recognition stream. Likewise, the TOR-MOV'T analysis activated the superior parietal lobe, part of the dorsal spatial stream. To identify those regions that were active in both LOC and TOR conditions irrespective of their shared motor and lower-level sensory demands, we performed an inclusive mask of LOC-MOV'T with

the contrasts comprising TOR-MOV'T. Confirming the separate analyses, common areas of activation for LOC and TOR included right inferior frontal gyrus (BA 47), right pre- and post-central gyrus (BA 3/4/6), right precuneus (BA 39), left precuneus (BA 7/19), right inferior parietal lobule (BA 40), and left superior parietal lobe (BA 7).

Direct comparisons of TOR and LOC

For TOR vs. LOC and LOC vs. TOR, the Talairach space coordinates and sizes of the activated clusters, their extent, and their significant t values ($T^7(1449) = 0.32$, $P < 0.001$ uncorrected) are shown in Tables 3 and 4. Fig. 3 shows clusters of activation as labeled color overlays on normalized anatomical MRI slices. The TOR vs. LOC contrast revealed significantly increased BOLD signal in the frontal pole (BA 9/10), motor cingulate (BA 6/24/31/32), and right premotor areas (BA 4/6). The converse contrast of LOC vs. TOR revealed increased BOLD signal bilaterally in superior parietal cortex (BA 7) and the precuneus (BA 7 and 19). Thus, TOR differentially activates areas thought to be involved in feature integration as well as motor planning and attention, and LOC differentially activates areas thought to be involved in spatial localization.

Discussion

The present results are the first neuroimaging data to provide direct evidence that neural regions for somatosensory “what” are different from “where.” Separate neural substrates for tactile object localization (LOC) were distinguished from those for tactile object recognition (TOR). Because subjects performed TOR and LOC on the same stimuli using the same hand movements, TOR and LOC tasks activated some overlapping regions of cortex. Subjectively, it is difficult to recognize an object without localizing it and vice versa. Nonetheless, the task comparison revealed task-specific differences. When sensorimotor components were removed from TOR, activation remained in a ventrally directed pathway. In contrast, when sensorimotor components were removed from LOC, activation in superior parietal areas remained. This activation supports the dorsal pathway implicated for tactile spatial processing by patient data (Caselli, 1993). These regions are also similar to those activated by visual spatial processing (Clark et al., 1994; Haxby et al., 1991), but the primary visual cortex was not differentially activated by these tactile tasks.

A direct comparison of TOR to LOC revealed differential activation of the frontal pole and a motor attention network. Activation in the frontal pole may indicate the integration of multimodal feature information and abstract thinking (O'Reilly et al., 2002). This activation and interpretation is consistent with neuroimaging findings demonstrating that memory for the association between two types of visual information differentially activated the frontal pole (BA 10) relative to memory for the two types of information that were not linked (Wheeler, 2000). The activation of the motor attention network may result from small, additional hand movements in addition to the specified stereotyped movements for TOR, or it may be that TOR leads to the planning of intentional hand movements within an evolving context of exploration and hypothesis testing. Overall, the TOR activation patterns are consistent with a ventrolateral somatosensory pathway for TOR (Bonda et al., 1996; Caselli, 1991, 1993; Mishkin, 1979; Murray and

Mishkin, 1984; Reed and Caselli, 1994; Reed et al., 1996). The activation patterns replicate our previous fMRI study of TOR using real objects and naturalistic hand movements (Reed et al., 2004). TOR activated ventrolateral somatosensory cortex somatosensory association areas as well as a prefrontal motor attention network compared to movement alone. Not only are these areas postulated to be important for TOR and the integration of object features (Burton, 1984), but they are also implicated in appropriate response selection (Schumacher and D'Esposito, 2002).

In contrast, the direct comparison of LOC to TOR revealed bilateral superior parietal and precuneus activation consistent with spatial processing. These results are consistent with theories suggesting that superior parietal regions are used for converting sensory inputs into a common coordinate system to permit multimodal spatial processing (Creem and Proffitt, 2001; Goodale and Milner, 1992; Jones and Powell, 1970). At a macro level, much of the same neural machinery is used for tactile and visual object localization. Bilateral superior parietal (BA 7) and precuneus regions (BA 19) are activated by both modalities. This study produces similar activation patterns in dorsal regions (dorsal occipital cortex (BA 19) plus the inferior parietal lobule (BA 7)) during spatial localization, as have other positron emission tomography and fMRI visual localization studies (Clark et al., 1994; Goodale and Milner, 1992; Ungerleider and Haxby, 1994). Thus, activation of bilateral superior parietal lobes for tactile and visual localization suggests that common neural substrates may be used for tactile and visual spatial processing. This area may also be important for integrating representations of the hand and arm with visual space representations used for reaching and grasping (Colby and Duhamel, 1994). Further, it implies that information regarding spatial location information begins in modality-specific cortical areas and flows to modality-general processing regions.

Although our intent was to investigate what brain areas were recruited for tactile object recognition separately from those recruited for tactile object localization, there is also considerable overlap in neural activation for the two tasks. Both tasks activate portions of the ventrolateral and dorsal processing streams, in addition to the somatosensory cortex and inferior frontal gyrus. In particular, both activate right SII (BA 40), a part of inferior parietal cortex associated with higher level somatosensory processing, and left BA 7, a part of superior parietal cortex associated with spatial processing. This is consistent with the nature of the two tasks. When one recognizes an object by touch, one must localize it to grasp it. When one grasps an object in a location, it is difficult to avoid processing some object properties. The differences in these activations may stem in part from the attention devoted to task-relevant compared to task-irrelevant stimulus properties.

The role of task demands in determining the relative activation of neural substrates leads us to consider further how tactile object processing can provide insight into the multimodal functions of the dorsal pathway and whether it should be considered a “where” or a “how” pathway. After an extensive review of the behavioral and neuroscience literature, Creem and Proffitt (2001) have suggested that the posterior parietal cortex serves two kinds of functions for visual processing, which in turn are associated with distinct regions. The “how” system transforms spatial representations of location between reference frames (e.g., eye centered, arm centered) so as to support direct, perceptually guided action. The reference frames are hypothesized to be egocentric, and the representation is relatively short in duration. The “where” system

supports conscious representations that mediate complex spatial behavior and reported location. The operative reference frames in this case are more likely to be exocentric, and the representation is assumed to be more enduring in time. Creem and Proffitt have tentatively associated “how” and “where” with superior and inferior regions of posterior parietal cortex. In touch, however, the “how” and the “where” are intimately connected. Our LOC task (relative to the movement control) has two components—grasping the target and reporting its location in matrix (i.e., exocentric) coordinates. Thus, it invokes both the how and where systems. This suggests that the how and where system distinctions suggested for vision do not hold for touch.

In conclusion, the current study has implications for the functional organization of the brain. The dissociation of object and spatial processing streams appears to be a general feature of sensory systems that is reflected in functional and anatomical distinctions in the brain (Kaas and Hackett, 1999). In addition to the visual system, this “what–where” dissociation is found for the auditory system (e.g., Anourova et al., 2001; Kaas and Hackett, 1999; Maeder et al., 2001). Likewise, our results document a similar dissociation of labor in the human somatosensory system. Sensory systems appear to divide perception into two major subtasks: identifying objects in a ventral “what” pathway and locating objects in space in a dorsal “where” pathway. Sensory information is channeled into two parallel pathways that are proposed to originate from the same modality-specific cortical areas and to proceed to modality-general regions located dorsally in the posterior parietal cortex or ventrally in the temporal or inferior parietal lobes. Both streams of processing appear to terminate in the frontal lobes. This common organization scheme across sensory systems may provide the bases for integrating object information apprehended from various senses to create multimodal representations of objects in the environment.

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