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Object Familiarity Modulates the Relationship Between Visual Object Imagery and Haptic Shape Perception

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Abstract

Although visual cortical engagement in haptic shape perception is well established, its relationship with visual imagery remains controversial. We addressed this using functional magnetic resonance imaging during separate visual object imagery and haptic shape perception tasks. Two experiments were conducted. In the first experiment, the haptic shape task employed unfamiliar, meaningless objects, whereas familiar objects were used in the second experiment. The activations evoked by visual object imagery overlapped more extensively, and their magnitudes were more correlated, with those evoked during haptic shape perception of familiar, compared to unfamiliar, objects. In the companion paper (Deshpande et al., 2009), we used task-specific functional and effective connectivity analyses to provide convergent evidence: these analyses showed that the neural networks underlying visual imagery were similar to those underlying haptic shape perception of familiar, but not unfamiliar, objects. We conclude that visual object imagery is more closely linked to haptic shape perception when objects are familiar, compared to when they are unfamiliar.

Keywords

Multisensory; cross-modal; visual cortex; lateral occipital complex; somatosensory cortex; fMRI

Introduction

Visual cortical areas are routinely active during touch in normally sighted individuals (Sathian and Lacey, 2007). For example, the lateral occipital complex (LOC), an object-selective area in the ventral visual pathway (Malach et al., 1995), is also shape-selective during haptic perception (Amedi et al., 2001; James et al., 2002; Zhang et al., 2004; Stilla

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and Sathian, 2008) but the underlying reasons for this cross-modal recruitment remain uncertain. One possible explanation for LOC activation during haptic shape (HS) perception is that it is mediated by visual imagery (VI) (Sathian and Lacey, 2007). In support of this idea, the LOC is bilaterally active during VI (Amedi et al., 2001, 2005a), while the left LOC is active during imagery of either geometric or material object properties in response to visually presented word-cues (Newman et al., 2005) and also when generating mental images of shape cued by familiar sounds in both blind and sighted individuals (De Volder et al., 2001). More targeted evidence is that inter-individual variations in the magnitude of HS-selective activity in the right LOC (ipsilateral to the hand used for haptic perception) correlate with ratings of the vividness of VI (Zhang et al., 2004).

Others have argued that VI cannot explain haptically-evoked LOC activation because LOC activation magnitude is much less during VI than during haptic object identification (Amedi et al., 2001). Because none of these studies actually monitored performance on the imagery task, no firm conclusions can be drawn about the relationship between VI and HS perception. For instance, lower LOC activation magnitudes during VI might simply reflect the fact that participants were not required to maintain their images throughout the scan session. Another argument that has been advanced against a role for VI in HS perception is that congenitally blind people show similar activations (e.g., Pietrini et al., 2004). Although VI obviously cannot be involved in the congenitally blind, it is well known that visual deprivation is associated with extensive cross-modal reorganization (reviewed by Sathian and Stilla, 2009): this implies that different mechanisms could underlie recruitment of the same regions in blind compared to sighted individuals. An alternative to VI mediation is that LOC recruitment during HS perception reflects engagement of a multisensory representation of shape. We define a multisensory representation as one that can be both encoded and retrieved in more than one sensory modality (Sathian, 2004), as opposed to a visual image which can only be encoded in one modality although its retrieval might be triggered by cues in multiple modalities.

Here we tested the imagery hypothesis directly, using functional magnetic resonance imaging (fMRI) to examine activity during HS perception and, in separate sessions in the same subjects, activity during a VI task on which performance was monitored. This enabled us to directly relate activity during the two tasks. We conducted two experiments, the first using unfamiliar, and the second familiar, objects in the HS task to investigate the possible role of VI in mediating cross-modal recruitment of LOC activity during HS perception, and whether manipulating object familiarity would affect the role of VI. We hypothesized that, if the VI account were correct, then conjunction analyses should reveal common LOC activations during VI and HS perception and, further, that there would be an inter-task correlation in LOC activation magnitudes across subjects. Overlap and correlations between VI and HS might be expected not just in the LOC, but also in regions of frontoparietal cortex known to be involved in VI. We report the results of these overlap and correlational analyses in the present paper. In the companion paper (Deshpande et al., 2009), we report on task-specific functional and effective connectivity analyses that were used to provide converging evidence on the conclusions from the analyses reported in the present paper.

Materials and Methods

Participants

Eight neurologically normal participants (4 males, 4 females) took part in each experiment, after giving informed consent. One subject took part in both experiments. The age range was 18-30 years (mean 21.8) for Experiment 1 and 20-26 years (mean 23.2) for Experiment 2. All participants were right-handed, based on the validated subset of the Edinburgh handedness inventory (Raczkowski et al., 1974). We excluded participants with calluses on

their hands, and those for whom American English was a second/non-native language, because the VI task and its control task relied on verbal stimuli. The Institutional Review Board of Emory University approved all procedures.

Procedures

Imagery session

Stimuli and tasks: In the VI task (Figure 1a), participants heard pairs of high-imagery nouns, rated 5 or higher on a seven-point imageability scale (Paivio et al., 1968; Gilhooly and Logie, 1980). A set of 133 words was used to make 96 word-pairs; some words were repeated, but never within a trial block. Participants were instructed to generate mental visual images of the two objects that each word-pair represented, and then to determine whether the imaged objects were approximately the ‘same’ shape (for example, ‘snake-rope’) or ‘different’ shapes (for example, ‘pin-axe’). This task was adapted from one used in a previous neuropsychological study to show that a patient with visual agnosia had defective object imagery (Mehta et al., 1992). In the corresponding control task, designed on the basis of pilot studies, stimulus pairs comprised words or non-words (WnW task). Participants heard stimulus pairs that could be either two real, low-imagery words (rated 4 or lower on the seven-point imageability scale), two non-words (pronounceable nonsense syllables that did not form real English words (Gibbs and Van Orden, 1998; Pexman et al., 2001) and which are non-imageable by definition), or a real word and a non-word. Some non-words were altered to reduce their perceived resemblance to real English words. 96 real words and 96 non-words were used, none being repeated. Participants were instructed to determine whether the word-pairs fell into the ‘same’ category (both real words or both non-words) or ‘different’ categories (a real word paired with a non-word). In both VI and WnW tasks, stimuli were matched to contain the same number of syllables per stimulus in a given pair. The two tasks were also matched for the overall number of one-, two-, and three-syllable stimulus pairs.

Functional imaging: Participants lay supine in the scanner. They were blindfolded and instructed to keep their eyes closed. They held a fiberoptic response box in the right hand and used the second and third digits to press appropriate buttons indicating a ‘same’ or ‘different’ response. The stimuli were presented in a block design through headphones that attenuated external sounds by 20 dB to muffle scanner noise. Each 18s stimulation block comprised 6 stimulus pairs in a predetermined, pseudorandom order. Stimuli were presented over a 2s interval followed by a 1s inter-stimulus interval (ISI) during which participants responded. Rest blocks of 18s without stimulation separated active blocks, as well as beginning and ending each run. Four blocks of each task were pseudorandomly distributed through each of four runs for a total of 96 trials per task, with an equal number of ‘same’ and ‘different’ correct responses in each block. The sequence of run orders was counterbalanced across participants. The onset of each VI and WnW block was preceded by an auditory cue (‘shape’ or ‘words’) to instruct the participant as to which task was to be performed. Each rest block was preceded by the auditory cue ‘rest’. The stimuli were presented, and responses recorded, via Presentation software (Neurobehavioral Systems Inc., Albany, California).

Haptic session

Stimuli and tasks: In the HS task, participants were presented with a series of objects and performed a one-back ‘same/different’ shape discrimination. In Experiment 1, the shape stimuli were 42 three-dimensional, meaningless wooden blocks with smooth, painted surfaces, measuring approximately 5×5×2.5 cm, and varying in shape (Figure 1b). These abstract, meaningless objects were previously unfamiliar to participants who thus had no haptic or visual information about them stored in memory. In Experiment 2, the shape

stimuli were 42 three-dimensional familiar objects, for example, a rubber duck, a plastic spoon, a toy car, etc (Figure 1c). All the familiar objects were MRI-safe or had been rendered so by the removal of all metallic parts. The corresponding control task, a haptic texture (HT) task, was the same in both experiments. It comprised a one-back 'same/different' texture discrimination in which the 42 stimuli were 4×4×0.3 cm cardboard substrates onto which textured fabric or upholstery was glued (Figure 1b,c). The shape stimuli were all of the same texture in Experiment 1 and were grouped in blocks to minimize texture differences in Experiment 2. The texture stimuli were all of the same shape. Both shape and texture stimuli were consistently presented in a fixed orientation and participants were told not to rotate or re-orient stimuli during exploration.

Functional imaging: Participants lay supine in the scanner. They were blindfolded and had their eyes closed during haptic exploration. They were never allowed to see the haptic stimuli. A block design paradigm similar to that for the imagery session was used, except for the following details. Active blocks were of 30s duration. On each trial, an experimenter standing at the scanner aperture placed a stimulus directly into the participant's hand for 4s, immediately after which the object was removed. Participants explored each stimulus from the time it was placed in their hand until the time it was taken away. There was a 1s ISI during which responses were made using the other hand. The trial length was derived from pilot studies. Immediately preceding each active block, participants heard the cues 'shape' or 'texture' to instruct them which task would follow. Each type of active block was repeated six times, giving 36 shape and 36 texture trials in each run. Two runs were performed for each hand in Experiment 1, and two runs for the right hand only in Experiment 2. Thus, there were 72 shape and 72 texture trials in each 2-run sequence, with an approximately equal number of 'same' and 'different' correct responses in each run. The sequence and timing of object presentation and exploration were guided by preprogrammed instructions displayed to the experimenter on a computer screen using Presentation software.

MR scanning—MR scans were performed on a 3 Tesla Siemens Trio whole body scanner (Siemens Medical Solutions, Malvern, PA), using a standard quadrature headcoil. T2*-weighted functional images were acquired using a single-shot, gradient-recalled, echoplanar imaging (EPI) sequence for blood oxygenation level-dependent (BOLD) contrast. For the haptic scans, 21 axial slices of 5mm thickness were acquired. The imagery scans utilized acquisitions with 27 (4mm) axial slices. These slightly different acquisition parameters resulted in only a 3mm difference in coverage. Both functional sequences used the following parameters: repetition time (TR) 2000ms, echo time (TE) 30ms, field of view (FOV) 220mm, flip angle (FA) 90°, in-plane resolution 3.4×3.4mm, and in-plane matrix 64×64. High-resolution 3D anatomic images were acquired during both haptic and imagery sessions, using an MPRAGE sequence (TR 2300ms, TE 3.9ms, inversion time 1100ms, FA 8°) comprising 176 sagittal slices of 1mm thickness (FOV 256mm, in-plane resolution 1×1mm, in-plane matrix 256×256). Once magnetic stabilization was achieved in each run, the scanner triggered the computer running the Presentation software so that the sequence of experimental trials was synchronized with scan acquisition. The order of imagery and haptic sessions was counterbalanced across subjects and genders.

Image processing and analysis—Image processing and analysis was performed using BrainVoyager QX v1.6.3 and v 1.9.10 (Brain Innovation, Maastricht, Netherlands). Each subject's functional runs were real-time motion-corrected utilizing Siemens 3D-PACE (prospective acquisition motion correction). Functional images were preprocessed utilizing sinc interpolation for slice scan time correction, trilinear-sinc interpolation for intra-session alignment of functional volumes, and high-pass temporal filtering to 3 cycles per run to remove slow drifts in the data. Anatomic 3D images were processed, co-registered with the

functional data, and transformed into Talairach space (Talairach and Tournoux, 1988). Activations were localized with respect to 3D cortical anatomy with the help of an MRI atlas (Duvernoy, 1999).

For group analysis, the transformed data were spatially smoothed with an isotropic Gaussian kernel (full-width half-maximum 4mm). The 4mm filter is within the 3-6mm range recommended to reduce the possibility of blurring together activations that are in fact anatomically and/or functionally distinct (White et al., 2001). This is particularly important given our hypothesis of inter-task overlapping activations. This filter size is comparable to that used in other studies of the LOC (Amedi et al., 2005a (4mm); James et al., 2002 (6mm); Stilla and Sathian, 2008 (4mm)); and is substantially smaller than that used in many earlier studies (Amedi et al., 2003; Stoesz et al., 2003; Zhang et al., 2004 (all 8mm); De Volder et al., 2001 (15mm)). Runs were normalized based on percent signal change, to optimize preservation of individual effect sizes. Statistical analysis of group data used random-effects, general linear models (GLM) followed by pairwise contrasts (VI – WnW and HS – HT). Correction for multiple comparisons (corrected $p < 0.05$) was achieved by imposing a threshold for the volume of clusters comprising contiguous voxels that passed a voxel-wise threshold of $p < 0.05$, using a 3D extension (implemented in BrainVoyager QX) of the 2D Monte Carlo simulation procedure described by Forman et al. (1995). Corrections for the pairwise contrasts (VI – WnW and HS – HT) were performed within a mask comprising all voxels active in either task relative to baseline (thresholded at $p < .05$, uncorrected).

In order to test for the existence of significant inter-task overlaps in the VI and HS-evoked activations in each experiment, we carried out conjunction analyses to find voxels active on both the VI > WnW and the HS > HT contrast. This is a rigorous test of overlap, requiring the presence of significant activations in both VI and HS tasks. The nominal difference in axial resolution between the imagery and haptic runs was obviated by the (standard) re-sampling of the lower-resolution functional data into the higher-resolution anatomic space, and by spatial smoothing. In each experiment, correction of these conjunction analyses for multiple comparisons was performed by the cluster method, within a mask of voxels active in either the VI or the HS condition (relative to the respective control condition, thresholded at $p < .05$, uncorrected). To examine the relationships between activations evoked by the VI and HS tasks, we created regions of interest (ROIs) centered on the center of gravity of the overlap zones. The ROIs were constrained to be no larger than 125mm^3 ($5 \times 5 \times 5\text{mm}$ cube). Within these ROIs, the beta weights for the VI and HS conditions (relative to baseline) were determined for each participant. Taking these beta weights as indices of activation strengths, inter-task, across-subject correlations were run on them.

Results

Experiment 1

Psychophysics—In the VI task, mean ($\pm$ SEM) accuracy was $87.5 \pm 1.5\%$ with a mean reaction time (RT) of 2.41 ± 0.03 s. In the WnW task, mean accuracy was $79.8 \pm 4.9\%$ with a mean RT of 2.46 ± 0.04 s. Paired t-tests (two-tailed) showed no significant differences between these tasks on accuracy ($t_7 = 1.8$, $p = 0.12$) or RT ($t_7 = -1.7$, $p = 0.13$). Mean accuracy in the unfamiliar HS task was $91.1 \pm 2.3\%$ for the right hand and $93.1 \pm 1.4\%$ for the left hand. In the HT task, mean accuracy was $94.9 \pm 1.3\%$ for the right hand and $97.6 \pm 0.7\%$ for the left hand. Analysis of variance revealed that the slight accuracy difference favoring HT over HS was significant ($F_{1,7} = 9.1$, $p = 0.02$); but the effect of hand ($F_{1,7} = 3.3$, $p = 0.11$), and the interaction effect ($F_{1,7} = 0.03$, $p = 0.86$) were not significant. Accuracy on the VI and HS tasks was not significantly different ($t_7 = 1.2$, $p = .25$). Since the haptic trials involved exploration of objects handed to subjects by an experimenter, haptic RTs were not measured.

Imaging

Activations during VI: The VI task, relative to the WnW task, activated ventral visual cortex bilaterally, in the LOC, and the anterior and mid-fusiform gyrus (AF and MF respectively). The remaining activations were all in left hemisphere regions, including a number in frontal and cingulate cortex. Also notable were activations in the pulvinar nucleus of the thalamus (Pul), and the posterior-ventral intraparietal sulcus (pvIPS). Figure 2a illustrates the location of the VI activations, whose coordinates and peak *t* values are provided in Table 1.

Activations during unfamiliar HS: The HS – HT contrast for the right hand also activated bilateral LOC (the left LOC did not survive correction for multiple comparisons but was included because of our *a priori* hypothesis), along with extensive bilateral activation in the IPS with activation maxima in the superomedial and posterior IPS (smIPS and pIPS respectively). This contrast also showed a number of activations in fronto-cingulate cortex, the anterior insula (aIns) and the thalamus (ventral posterolateral (VPL) and lateral posterior (LP) nuclei). These activations are illustrated in Figure 2c and detailed in Table 2. The unfamiliar HS – HT contrast for the left hand revealed essentially similar, albeit slightly weaker, activations (Supplementary Figure 1 and Supplementary Table 1).

Overlap between VI- and unfamiliar HS-evoked activations: As Figure 3 and Table 3 (Experiment 1) show, the conjunction analysis of voxels active on both the VI – WnW and the HS – HT contrast (for the right hand) revealed inter-task overlap that was limited to the LOC bilaterally, left anterior IPS (aIPS) and left anterior-ventral IPS (avIPS). Note that the left LOC overlap zone was part of a region that did not survive correction for multiple comparisons on the HS – HT contrast, although it did on the VI – WnW contrast. Amedi et al. (2005b) report that the Talairach coordinates for the bisensory region of the LOC, termed LOTv, are remarkably consistent, the average *x*, *y*, and *z* coordinates being 51, -56, -7 for the right LOC and -47, -61, -5 for the left. Notably, the coordinates for the VI/HS overlap zone are consistent with these coordinates (Table 3, Experiment 1). These overlap zones were present in each individual subject, with the exception of the left aIPS overlap zone in one subject (Supplementary Table 2), as determined by application of a mask comprising cubes of 12mm side for each ROI, (cubes centered on the center of gravity of the group ROI). In the case of the left hand, the conjunction analysis revealed significant inter-task overlap in the LOC bilaterally for both hands (Supplementary Figure 2). The avIPS focus that was one of the right hand overlap zones also showed inter-task overlap for the left hand, but this did not survive correction for multiple comparisons on the conjunction analysis.

The time-courses of the blood oxygenation level-dependent (BOLD) signal in these overlap zones (Figure 4 for the right hand, Supplementary Figure 3 for the left) demonstrate engagement in both the VI and unfamiliar HS tasks, as well as task-specificity relative to the respective control tasks. In the left LOC and left avIPS, the magnitude of activation due to VI was comparable to that during HS perception for the right hand (Figure 4). For the right LOC in the case of either hand, for the left LOC (left hand), and for the left aIPS (right hand), HS-evoked activation was substantially stronger than VI-evoked activation (Figure 4, Supplementary Figure 3).

Inter-task-correlations: Within the overlap zones revealed by the conjunction analysis, we examined whether activation magnitudes in the VI and unfamiliar HS conditions were correlated across subjects. Of the four right-hand overlap zones, only the left avIPS showed a significant, positive inter-task correlation; only the right LOC showed such a correlation for the left hand (Table 3, Experiment 1). Within the LOC overlap zones, where inter-task correlations might have been expected if unfamiliar HS perception recruited activity through

VI, there was only a correlation for the right LOC, and this was only for contralateral (left) hand stimulation. Thus, these results offer at best, weak evidence for VI mediation of the unfamiliar HS-related activations, including those in the LOC.

It is important to note that the HS task used *unfamiliar*, meaningless objects, while the VI task necessarily involved retrieving representations of *familiar* objects from long-term memory. This raises the possibility that differences in object familiarity between the HS and VI tasks could account for the rather limited inter-task overlaps and correlations. Therefore, we conducted a second experiment in which we substituted a set of familiar objects in the HS task. We hypothesized that this would lead to greater overlap between activations in the VI and HS task, and also to a greater number of significant inter-task correlations.

Experiment 2

Here, the familiar HS task was presented to the right hand only, since the first experiment showed that differences between hands were minor. Apart from this, and the use of a familiar object set (Figure 1c), the experiment was identical to the first.

Psychophysics—Mean VI accuracy was $85.6 \pm 1.7\%$ with a mean RT of 2.41 ± 0.16 s; mean WnW accuracy was $85.7 \pm 2.8\%$ with a mean RT of 2.48 ± 0.17 s. The slight RT difference between these tasks was significant on a paired (two-tailed) t test ($t_7 = -2.89$, $p = .02$), but accuracy did not differ significantly ($t_7 = 0.04$, $p = 0.97$). Mean HS accuracy was $94.3 \pm 0.9\%$; HT accuracy was $92.7 \pm 3.1\%$; these were not significantly different ($t_7 = 0.06$, $p = 0.57$). VI and HS accuracy were significantly different ($t_7 = 3.9$, $p = .005$).

Imaging

Activations during VI and familiar HS: The VI – WnW contrast revealed broadly similar activations to those in Experiment 1 (compare Figure 2a and 2b, and Tables 1 and 4). VI again recruited bilateral LOC and predominantly left hemispheric regions in frontal and cingulate cortex, thalamus (Pul), and the posterior IPS with maxima at pvIPS and avIPS/pIPS (Table 4). The familiar HS – HT contrast also activated bilateral LOC, extensive areas of frontoparietal, cingulate and temporal cortex, and subcortical regions including the Pul/LP nuclei of the thalamus (Figure 2d and Table 5).

Overlap between VI- and HS-evoked activations: In contrast to Experiment 1, the conjunction analysis for voxels active on both VI – WnW and HS – HT contrasts showed extensive inter-task overlap zones, as illustrated in Figure 5 and detailed in Table 3 (Experiment 2). These were located in the LOC bilaterally and, again, were consistent with the average Talairach coordinates reported for LOtv (Amedi et al., 2005b). Other overlap zones were exclusively in the left hemisphere: in the mid- and posterior fusiform gyrus (MF and PF respectively), pvIPS, dorsal premotor cortex (PMd), ventral premotor cortex (PMv), inferior frontal gyrus (IFG), orbitofrontal cortex (OFC), medial superior frontal gyrus (mSFG), and the Pul/LP thalamic region. Each of these overlap zones was confirmed in the majority of individual subjects (Supplementary Table 2). Figure 6 illustrates representative BOLD signal time-courses from these overlap zones, showing that both VI and familiar HS tasks evoked greater activation in these regions than their corresponding control tasks. The magnitude of activation was greater in the HS than the VI task in some regions (e.g., both LOCs) while the reverse was true for other regions (e.g., the left PMv and left IFG).

Inter-task-correlations: Importantly, despite variations in activation magnitude between tasks, 6 of the 11 overlap zones showed significant, positive inter-task correlations across subjects. These zones were in the LOCs bilaterally, and left pvIPS, PMv, IFG and the Pul/LP thalamic region (Table 3, Experiment 2). Thus, as we had hypothesized, substituting

familiar for unfamiliar objects in the HS task led to substantially more overlap between HS- and VI-evoked activity, and also to greater correlation between activation magnitudes in these tasks in multiple areas, including bilateral LOC and parts of left frontal cortex. These findings strongly implicate VI in mediating HS-evoked activations during perception of familiar, but not unfamiliar objects.

Comparison between experiments

Excluding the single subject common to both experiments (thus $n=7$ for each experiment), VI accuracy was $87.7 \pm 1.7\%$ in Experiment 1 and $85.2 \pm 2.1\%$ in Experiment 2; unfamiliar HS accuracy was $90.8 \pm 2.7\%$ and familiar HS was $94 \pm 1.1\%$. There were no significant differences in accuracy between experiments (VI: $t_{12} = .89$, $p = .4$; unfamiliar/familiar HS: $t_{12} = -1.08$, $p = .3$). Differences between task-specific activations in the two experiments were examined by computing random-effects task-by-experiment interactions, again omitting the single subject who was common to both experiments.

For the comparison of VI-specific activations between experiments, correction for multiple comparisons was performed by the cluster method, within a mask of voxels showing VI-selective activity in either experiment. Although there were some differences between VI-specific activations in the two experiments (Tables 1 and 4), the task-by-experiment interaction revealed only a few significant differences that, on further investigation, were attributable to slightly greater activations in the WnW task in Experiment 1 compared to Experiment 2 (data not shown). Further, inspection of the BOLD signal curves revealed that the majority of VI-specific activations in one experiment were also present in the other, suggesting that some of the differences were statistical in origin.

There were considerable differences in HS-specific activations between experiments. For familiar HS, the left LOC activation was larger than the right, while the reverse was true for unfamiliar HS. To test the hypothesis that greater HS-specific activity for familiar compared to unfamiliar objects was associated with VI, a mask was constructed comprising voxels with VI-specific activation in the combined subject set from both experiments ($n=14$, i.e. excluding the subject common to both experiments). Within this mask, a number of regions showed greater activity for familiar than unfamiliar objects. Most of these were in the VI-familiar HS overlap zones (Table 6a). In contrast, within the same VI mask, only two IPS foci, one posteriorly in avIPS/pIPS and the other superiorly in smIPS/supramarginal gyrus (SMG), showed greater activation for unfamiliar objects compared to familiar objects (Table 6b). These findings strengthen the link between VI and HS for familiar objects, while suggesting a specific role for the IPS foci in processing unfamiliar objects (see Discussion).

Within a mask comprising voxels active in either haptic condition in either experiment, HS-specific activations were stronger for unfamiliar than familiar objects in a range of frontoparietal, cingulate and thalamic regions, with a right-sided bias (Table 7). These differences may reflect aspects of HS processing that are more critical for unfamiliar objects, e.g. attention to the parts of the meaningless objects used in this experiment.

A within-subject contrast of familiar vs. unfamiliar HS (thresholded at $p < .05$, uncorrected) for the single participant common to both experiments showed that most of the differences between familiar and unfamiliar HS at the group level were also present in this single participant, suggesting that the differences were not merely attributable to different subject groups between experiments.

A number of HS-specific activations were common across subjects in both experiments (Table 8), as assessed with a random-effects analysis of the HS-HT contrast for the 14 subjects who each took part in only one of the experiments. These activations were corrected

for multiple comparisons by the false discovery rate (FDR) method (Genovese et al., 2002). The common activations included sites in frontoparieto-cingulate cortex and the LOC, similar to previous reports of HS-specific activity (Bodegard et al., 2001; Zhang et al., 2004; Stilla and Sathian, 2008).

Discussion

The present study clarifies the issue of whether LOC activation during HS perception reflects VI. Our conclusion is that HS perception of familiar objects is tightly linked to VI, whereas HS perception of unfamiliar, meaningless objects is, at best, weakly linked to VI. This conclusion is based on our finding of substantially greater overlap between VI- and HS-evoked activations for familiar compared to unfamiliar objects, together with that of many more significant correlations between VI and HS-evoked activation magnitudes for familiar than unfamiliar objects. These results are consistent with the notion that VI mediates many of the activations observed during HS perception of familiar objects, including the well-known cross-modal activation of the LOCs. However, VI mediation is probably absent or minimal in the case of activations in the LOCs and elsewhere during HS perception of unfamiliar objects. The companion paper (Deshpande et al., 2009) provides converging evidence for a differential role of VI during HS perception of familiar and unfamiliar objects, based on task-specific analyses of functional and effective connectivity. These analyses revealed that the neural network engaged during VI was remarkably similar to that active during familiar HS, but quite different from that recruited by unfamiliar HS. Further, the LOCs were dominated by bottom-up drive from somatosensory cortex in the case of unfamiliar HS, in keeping with engagement of a multisensory representation, whereas in the case of both familiar HS and VI, the LOCs were dominated by top-down inputs from prefrontal cortex, consistent with active visualization.

Task-specific activations

VI—The VI task was adapted from a neuropsychological study which showed that a visually agnostic patient had deficits in VI (Mehta et al., 1992). Participants in the present study were instructed to generate visual images and reported doing so; several lines of evidence suggest that they did. Firstly, the mean RT of 2.41s in the VI task (in both experiments) is ample for generating visual images, as evidenced by the high accuracy rate of our participants and RTs ranging from 1.1-2.0s in various image generation studies (Kosslyn et al., 1988, 1995; Doricchi et al., 1995; Dean et al., 2005; Slotnick et al., 2005). Secondly, much work supports dual coding theory (Paivio, 2007), which argues that processing of concrete words involves sensorimotor, in addition to verbal, representations. The nouns chosen for the VI task were all highly imageable: according to dual coding theory, sensorimotor representations would be recruited for their processing and available for VI. Thirdly, if the VI task was solved solely by reference to semantic knowledge, activations would not have been expected in visual cortical areas such as the LOC and fusiform gyrus. Although it is theoretically possible that participants might have generated a haptic rather than visual image, vision is well known to be the preferred modality for shape processing, and shape is less salient than material object properties (such as texture) for haptic perception (Klatzky et al., 1987). For these reasons, we believe that participants did employ visual imagery in the VI task.

The contrast between the VI and WnW tasks yielded activations specific for VI of object shape, since common activity due to auditory, cognitive and motor processes was subtracted out. VI activated a widespread network of brain regions in occipitotemporal and frontoparietal cortex, including the LOC, consistent with previous studies (Ishai et al., 2000; Wise et al., 2000; De Volder et al., 2001; Amedi et al., 2001, 2005a; Newman et al., 2005).

LOC activity was more extensive on the left, possibly because imagery was triggered by verbal cues: this accords with left lateralization of LOC activity during visual object recognition when object naming is required (Large et al., 2007). We did not find the deactivations in auditory and somatosensory cortex previously reported by Amedi et al. (2005a) during VI; instead, these areas were non-selectively active during both the VI and WnW conditions. This is not surprising given our use of auditory stimuli and keypress responses, neither of which was used by Amedi et al. (2005a). A potential concern is that the VI and WnW tasks might require different levels of processing owing to greater semantic demands in the VI task. However, RTs were actually longer in the WnW task compared to the VI task, suggesting that the VI-specific activations were not due to greater difficulty of, or more prolonged processing in, the VI task.

HS perception—Both unfamiliar (James et al., 2002; Stilla and Sathian, 2008) and familiar (Amedi et al., 2001, 2002; Zhang et al., 2004) variants of the HS task have been employed in previous studies. As in these earlier studies, HS perception, relative to HT perception, recruited a network of areas including the LOC, regions of the IPS and frontocingulate cortex. Whereas there were only minimal differences between VI-evoked activations in the two experiments, the comparison between experiments revealed considerable differences in HS-specific activations even though the HS task in each experiment was nominally the same (the only difference being object familiarity). Differences favoring familiar objects were mainly in frontotemporal regions that were also active during VI. Greater HS-specific activation for familiar compared to unfamiliar objects was also found bilaterally in the parietal operculum in the field termed OP3 (Eickhoff et al., 2007). Since this is a texture-selective somatosensory region (Stilla and Sathian, 2008), this differential activation may reflect textural differences between objects, even though we had attempted to minimize these by grouping familiar objects of similar texture within blocks. Such differences in texture were absent in the unfamiliar object set. In contrast, differences favoring unfamiliar objects were mainly in frontoparietal regions.

While it is possible that these differences between HS perception of familiar and unfamiliar objects stemmed from differences in exploratory procedures (EPs) (Lederman and Klatzky, 1987), we consider this unlikely. Subjects used EPs relevant for shape information, initial enclosure and subsequent contour-following (Lederman and Klatzky 1987), during both HS tasks. We did not observe any systematic differences for familiar and unfamiliar objects, and there is no evidence that object familiarity alters the nature of EPs used for HS perception (Lederman and Klatzky, 1987, 1990), although we are not aware that a direct comparison has been made. It might be expected that unfamiliar HS would involve more finger movements than familiar HS, which could affect the signal-to-noise ratio and also result in greater activation in the superior parietal lobule (SPL) for unfamiliar HS, relating to increased kinesthetic attention and tactile working memory load (Stoeckel et al., 2004). However, we did not observe HS-specific activity in the SPL that differed for unfamiliar and familiar HS. Moreover, inspection of Figures 4 and 6 suggest that the magnitudes of both the HS-selective signal and of the standard errors (noise) were comparable in the unfamiliar and familiar HS tasks. Also, there was no significant difference in HS accuracy between experiments, although the non-significantly greater accuracy for familiar HS is consistent with findings that haptic identification of familiar objects is both fast (Klatzky & Lederman, 1995) and accurate (Klatzky et al., 1985). Although VI accuracy was significantly lower than HS (familiar) accuracy, this is not of major consequence since we did not directly contrast activity in these two tasks. Each task was compared with its own control, and behavioral measures did not differ significantly between tasks in the experimental-control task pairs, the exception being the slightly greater accuracy for HT compared to unfamiliar HS – this small difference seems unlikely to have been very important. The unfamiliar objects used here were abstract and meaningless, unlike a previous study (Lacey &

Campbell, 2006) that used items and components of caving and climbing equipment that showed obvious signs of meaningful, purposive design, but were unfamiliar to the participants. Thus, further work is necessary to establish whether the differences between experiments depend on the unfamiliar objects being meaningless.

Relationship between VI and HS perception

The most specific relationships between VI and HS are those revealed by significant inter-task correlations of activation magnitude in the overlap zones, many of which were more active during familiar than unfamiliar HS. Overall, these correlated overlap zones which were in the LOC bilaterally, and in the left PMv, Pul/LP thalamic region, IFG and pvIPS, were in regions implicated in various aspects of VI and/or visuo-haptic processing, and were probably the loci of processing that was highly similar between VI and HS (familiar). In the LOCs, the common process is likely to have been VI of object shape (Amedi et al., 2001, 2005a; De Volder et al., 2001; Newman et al., 2005). The IFG zone was probably involved in top-down generation and control of imagery processes (Kosslyn et al., 1993; Ishai et al., 2000; Mechelli et al., 2004) and the Pul/LP thalamic zone could reflect processes of attention-shifting within a visual buffer that maintains visual images (Kosslyn et al., 1993; Kosslyn, 1994). The pvIPS zone was located near a superior parietal focus involved in content-independent interactions with visual cortical areas during VI (Mechelli et al., 2004), and close to a region implicated in visuo-haptic shape matching (Saito et al., 2003). Further, activation magnitudes in this region show significant inter-task correlations during haptic and visual shape perception (Stilla and Sathian, 2008). The function of the PMv zone is not clear, although it is the locus of a number of interesting multisensory interactions (Graziano et al., 1997; Ehrsson et al., 2004; Rizzolatti and Craighero, 2004). Less specific relationships between VI and HS are suggested by the overlap zones in which activation magnitudes were not significantly correlated between tasks. For example, the OFC may be involved in rapidly collecting gist input to evaluate hypotheses about object identity by generating analogies with existing representations (Bar et al., 2006; Bar, 2007).

Except for the right LOC, all overlap zones in both experiments were in the left hemisphere. Several factors may have contributed to this left hemisphere preference. Firstly, image generation appears to depend more on the left hemisphere when based on categorical spatial relations, and on the right hemisphere when based on coordinate spatial relations (Kosslyn et al., 1995). Because of the sequential nature of haptic processing, associated mental image generation may be easier using categorical rather than coordinate relations (Findlay et al., 1994). Secondly, verbal factors were probably important, since we used verbal cues for VI and the left LOC is preferentially recruited in object naming whereas visual object matching engages the right LOC (Large et al., 2007). While the overlap zone was much larger in the left than the right LOC for familiar objects, the reverse was true for unfamiliar objects. Together with the correlation between the magnitudes of visually- and haptically-evoked activity during perception of unfamiliar shapes in the right but not the left LOC (Stilla and Sathian, 2008), this suggests that the right LOC may house a modality-independent representation that is more important for unfamiliar than familiar objects.

The only overlap zones showing correlated activity during VI and HS (unfamiliar) were in the left avIPS (for the right hand) and the right LOC (for the left hand): these may reflect transient imagery of basic elements of the unfamiliar object shapes. For 2D familiar basic geometric shapes (e.g., square, circle, triangle), inter-individual variations in the magnitude of HS-selective activity in the right LOC, ipsilateral to the stimulated hand, were correlated with ratings of the vividness of VI (Zhang et al., 2004). The IPS is involved in visuo-haptic processing of both object shape and location (Stilla & Sathian, 2008; Gibson et al., 2008), the main difference being concomitant LOC activity during shape processing but concomitant FEF activity during location processing. Several IPS activations (aIPS, smIPS,

avIPS and pIPS) were stronger during unfamiliar than familiar HS, suggesting a specific role for the IPS in unfamiliar shape perception. The aIPS focus is close to a site processing visual discrimination of surface orientation in a delayed-matching task and may be the human homolog of the macaque anterior intraparietal area, AIP (Shikata et al., 2008), an area that facilitates visuo-haptic cross-modal interactions with objects (Grefkes and Fink, 2005). The smIPS focus is near a region involved in transforming visual coordinate information into motor programs for reaching (Grefkes et al., 2004): this has been proposed as the human homolog of the macaque medial intraparietal area, MIP (Grefkes and Fink, 2005). The avIPS focus is close to a retinotopically identified region designated IPS1 (Swisher et al., 2007), while the pIPS focus is in the vicinity of a neighboring retinotopic area designated IPS2 (Swisher et al., 2007) and also of an area involved in processing visual surface orientation, and referred to as the human homolog of the macaque caudal intraparietal area, CIP (Shikata et al., 2008). Interestingly, within the IPS1/IPS2 complex there are interleaved tactile areas responsive during roughness judgments (Swisher et al., 2007). The pIPS and aIPS foci are close to sites active in haptic exploration of 3-D objects, bimanual construction of 3-D objects, and imagery of object construction (Jancke et al., 2001).

Recent work suggests two types of VI: object imagery, referring to pictorial representations of objects, and spatial imagery, involving schematic representations of the spatial relations between object parts (Kozhevnikov et al., 2005; Blajenkova et al., 2006). Object imagery may suit familiar shapes and objects, as encountered during both familiar HS and VI, whereas spatial imagery might be more relevant for unfamiliar, meaningless objects. In support of this, spatial, but not object, imagery scores correlate with cross-modal visuo-haptic recognition accuracy for unfamiliar objects (Lacey et al., 2007b). Participants in both experiments completed the Object-Spatial Imagery Questionnaire (OSIQ) (Blajenkova et al., 2006): participants who preferred spatial imagery tended to be more accurate at unfamiliar HS than those who preferred object imagery while the reverse was true for familiar HS. This is consistent with our suggestion that different types of VI might support HS perception depending on object familiarity (Lacey et al., 2009) but requires further investigation as the OSIQ does not test object or spatial imagery directly, and the relationships observed here were relatively weak. Based on the involvement of IPS areas in both location and shape processing during haptic perception (Stilla & Sathian, 2008; Gibson et al., 2008), together with these various prior findings, we proposed that the role of the IPS in haptic perception of unfamiliar shape may be in the assembly of object shape representations from component parts, with the aid of spatial imagery (Lacey et al., 2009). Further work will be necessary to investigate this proposal. Regardless of the possible role of spatial imagery in the unfamiliar HS task, it is clear that the role of object imagery, which is the subject of the present paper, is limited at best for unfamiliar objects, in contrast to the major role of object imagery in the familiar HS task.

We previously suggested that vision and touch may share a representation of shape, flexibly accessible via both top-down and bottom-up pathways (Lacey et al., 2007a). The LOC is a strong candidate for the site of this representation, given its modality-independent engagement during shape perception (Amedi et al., 2001, 2002, 2007; James et al., 2002; Zhang et al., 2004; Stilla and Sathian, 2008). The connectivity analyses presented in the companion paper (Deshpande et al., 2009) lend strong support to the idea of a flexibly accessible multisensory shape representation: depending on the task, modality-independent representations of object shape in the LOC may be accessed either top-down, to support VI, as in the VI and familiar HS tasks, or bottom-up, directly from somatosensory input, as in the unfamiliar HS task.

Conclusions

Visual object imagery is functionally related to haptic perception of familiar, but not unfamiliar, meaningless objects, since imagery-evoked activations overlap much more and display more correlated activation magnitudes with haptically-evoked activations in the case of familiar, compared to unfamiliar, objects. Moreover, as shown in the companion paper, the neural networks underlying visual object imagery are similar to those involved in haptic perception of familiar, but not unfamiliar objects. Thus, object familiarity modulates the relationship between visual object imagery and haptic shape perception.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Appendix: Anatomical abbreviations used

AC	anterior cingulate
AF	anterior fusiform
aIns	anterior insula
aIPS	anterior intraparietal sulcus
avIPS	anterior-ventral intraparietal sulcus
FEF	frontal eye field
IFG	inferior frontal gyrus
IPS	intraparietal sulcus
LOC	lateral occipital complex
LP	lateral posterior thalamic nucleus
MC	mid-cingulate
MF	mid-fusiform
MFG	middle frontal gyrus
mSFG	medial superior frontal gyrus
OFC	orbitofrontal cortex
OP	parietal operculum
PC	posterior cingulate
PCS	postcentral sulcus
PF	posterior fusiform
pIPS	posterior intraparietal sulcus
PMd	dorsal premotor cortex
PMv	ventral premotor cortex

Prec	precuneus
pSMA	pre-supplementary motor area
Pul	pulvinar thalamic nucleus
pvIPS	posterior-ventral intraparietal sulcus
SFG	superior frontal gyrus
SMA	supplementary motor area
smIPS	superomedial intraparietal sulcus
VPL	ventral posterolateral thalamic nucleus.

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Figure 2.

Activations during VI (from VI-WnW contrast) in (a) Experiment 1 and (b) Experiment 2, and during HS perception (from HS-HT contrast) for (c) unfamiliar shapes in Experiment 1 and (d) familiar shapes in Experiment 2. Cluster-corrected for multiple comparisons, voxel-wise threshold $p < .05$. Talairach plane is given below each slice; radiologic convention used (right hemisphere on left). Color scale: t-scale for the contrasts.

Figure 3. Conjunction analysis of activations during VI and unfamiliar HS (right hand only) for Experiment 1. Details as in Figure 2.

Figure 4.
Time-courses of activation in VI/unfamiliar HS conjunction zones (HS right hand only) for Experiment 1. Error bars: SEM.

Figure 5. Conjunction analysis of activations during VI and familiar HS for Experiment 2. Details as in Figure 2.

Figure 6.
Time-courses of activation in selected VI/familiar HS conjunction zones for Experiment 2.
Error bars: SEM.

Table 1

Activations during VI (from VI – WnW contrast) in Experiment 1. x,y,z: Talairach coordinates for the center of gravity of the activation; tmax: peak t value.

Region	x	y	z	tmax
L LOC	-46	-51	-11	7.6
R LOC	42	-50	-8	5
L MF	-30	-25	-12	6.4
R MF	32	-28	-12	7.9
L AF	-31	1	-23	6
R AF	34	-14	-17	8.5
L pvIPS	-28	-69	34	7.9
L OP3	-38	-6	4	4.4
L SFG	-10	16	52	9.3
L FEF	-30	4	52	4
L PMd	-35	0	42	6.6
L PMv	-43	5	27	6.3
L inferior frontal sulcus	-48	29	23	12.8
L OFC	-37	38	4	7.1
L PC	-6	-36	38	4.1
L AC	-5	30	31	4.9
L Pul	-17	-31	2	6.8

Table 2

Activations during HS (unfamiliar), for right hand stimulation only, from HS – HT contrast in Experiment 1 (the L LOC focus is uncorrected for multiple comparisons, see main text). x,y,z: Talairach coordinates for the center of gravity of the activation; tmax: peak t value.

Region	x	y	z	tmax
L LOC	-49	-59	-5	4.5
R LOC	45	-56	-9	6.2
L collateral sulcus	-43	-33	-16	3.9
L pIPS	-18	-58	45	7.2
R pIPS	17	-59	49	10.5
L smIPS	-30	-42	45	8.1
R smIPS	29	-47	44	10.2
L PCS	-49	-25	37	7.5
R PCS	42	-30	39	10.2
L postcentral gyrus	-32	-25	53	7.1
SMA (contralateral to hand)	-2	-7	51	8.1
L FEF	-27	-10	49	9.5
R FEF	22	-10	52	8.3
L PMv	-46	0	34	3.9
R PMv	47	5	28	17.8
R MFG	29	34	29	3.8
L IFG	-41	18	7	6.6
R inferior temporal gyrus	60	-31	-11	5.2
L aIns (2 foci)	-30	14	3	6.7
	-30	19	10	6.6
R aIns (2 foci)	31	18	1	10.7
MC	0	-3	36	5.1
AC	0	26	33	4.9
R PC (2 foci)	11	-32	35	4.1
	4	-31	25	7.4
L thalamus (LP)	-14	-20	12	9.4
L thalamus (VPL)	-11	-19	-1	8.3
R thalamus (LP)	10	-14	14	8.1
R thalamus (VPL)	11	-15	1	7

Table 3

Conjunction analysis of activations during VI and HS perception (right hand only). x, y, z: mean Talairach coordinates for the center of gravity of the activation; n_vox: number of activated voxels in conjunction zone; r, p: correlation coefficients and p values for correlations between beta weights of VI- and HS-evoked activations relative to baseline (significant correlations in bold type).

Region	Unfamiliar objects (Experiment 1)						Familiar objects (Experiment 2)					
	x	y	z	n_vox	r	p	x	y	z	n_vox	r	p
L LOC *	-51.0	-58.0	-6.0	343	.64	.09	-46.0	-59.0	-5.5	2795	.82	.01
R LOC *	45.0	-52.0	-8.4	1268	.3	.5	44.0	-54.0	-7.3	624	.75	.03
L avIPS	-21.0	-64.0	39.0	607	.82	.01						
L alPS	-36.0	-37.0	33.0	888	.57	.1						
L MF							-33.0	-25.0	-14.0	627	.3	.46
L PF							-37.0	-45.0	-14.0	1089	.22	.6
L pvIPS							-26.0	-72.0	32.0	2792	.74	.03
L PMd							-35.0	3.1	44.0	864	.48	.23
L PMv							-40.0	9.8	28.0	1190	.86	.007
L IFG							-42.0	41.0	-0.2	818	.89	.003
L OFC							-35.0	30.0	-5.8	1522	.6	.12
L mSFG							-9.2	33.0	44.0	2590	.04	.93
L thalamus (Pul/LP)							-11.0	-29.0	5.3	1048	.94	.001

* These regions also showed an inter-task overlap for left hand stimulation in Experiment 1 (R LOC: $r = .77$, $p = .03$; L LOC: $r = -.24$, $p = .57$).

Table 4

Activations during VI (from VI–WnW contrast) in Experiment 2. x,y,z: Talairach coordinates for the center of gravity of the activation; tmax: peak t value.

Region	x	y	z	tmax
L LOC	-45	-44	-5	10.7
R LOC	51	-58	-8	7.3
L MF	-24	-33	-14	6.6
R calcarine	8	-81	8	6.1
R superior occipital gyrus	6	-82	18	4
L inferior occipital sulcus	-24	-65	19	7.6
L pvIPS	-27	-68	26	5.4
L avIPS/pIPS	-27	-67	40	9.4
L central sulcus	-15	-22	62	5.9
L mSFG	-12	35	38	5.8
L PMd (2 foci)	-32	5	45	4.7
	-29	4	37	5.3
L PMv	-46	5	31	8.9
L IFG	-40	45	4	6.2
L inferior frontal sulcus	-36	34	16	4.3
L OFC	-36	32	-8	7.9
R OFC	31	35	-3	4.2
L AC	-6	33	31	7
L MC	-12	-4	34	6.8
R MC	9	-7	38	9.1
L Pul	-11	-33	5	4.1
R medial cerebellum	13	-68	-27	7.4
R lateral cerebellum	28	-65	-30	4.6
R posterolateral cerebellum	32	-77	-30	5.4

Table 5

Activations during HS (familiar), from HS – HT contrast in Experiment 2. x,y,z: Talairach coordinates for the center of gravity of the activation; tmax: peak t value.

Region	x	y	z	tmax
L LOC	-49	-64	-8	7.7
R LOC	46	-54	-5	4.9
L MF	-34	-22	-14	4.2
L PF	-35	-38	-13	3.8
L inferior temporal sulcus	-55	-45	4	3.7
R inferior temporal sulcus	50	-34	-5	4
R middle temporal gyrus	48	-47	8	5.1
R superior temporal sulcus	46	-38	15	4.1
R superior temporal gyrus	45	-38	24	4.1
L pVIPS	-30	-76	22	7.7
R avIPS/pIPS	25	-60	44	5.8
L pIPS	-24	-67	47	3.1
R pIPS	23	-53	51	10.6
L smIPS	-34	-42	55	9.3
R smIPS	40	-31	47	6.8
L aIPS	-39	-32	38	8
R aIPS	31	-33	37	6.2
R lateral superior parietal gyrus	33	-46	56	7.6
R medial superior parietal gyrus	15	-52	58	11
L OP1	-51	-28	25	3.2
R OP1	51	-28	27	5.7
L OP3	-40	-28	26	4.5
L Prec (2 foci)	-9	-53	56	5.9
	-6	-49	45	4.8
L SFG	-12	8	50	6.9
L anterior SFG	-4	29	51	6.3
L superior frontal sulcus (2 foci)	-13	30	37	6.5
	-24	33	40	12.3
L pre-SMA	-4	8	53	6.2
R pre-SMA (2 foci)	7	3	60	10.6
	6	14	48	7.3
R SMA	7	-7	54	6.9
L FEF	-29	-13	53	5.5
R FEF	27	-15	53	6
L PMv	-49	13	16	6.7
R PMv	34	3	27	5
L MFG (2 foci)	-24	22	41	6.8
	-37	15	31	4.6
L inferior frontal sulcus	-45	20	16	6.9

Region	x	y	z	tmax
L IFG	-51	9	8	6.3
R AC	4	15	24	3.7
L MC	-4	-22	39	6.2
L amygdala	-14	-7	-8	12.6
R basal forebrain	20	2	-7	3.8
L putamen	-20	15	2	2.9
R putamen	15	10	8	3.8
L globus pallidus	-10	-1	4	5.4
R globus pallidus	10	-2	10	5.6
L thalamus (Pul/LP)	-18	-27	8	8.6
L thalamus (Pul)	-6	-25	6	6.6
L thalamus (mediodorsal nucleus)	-10	-15	13	7.9
R thalamus (Pul/LP)	14	-23	7	4.3
R thalamus (Pul)	4	-19	13	4.5
L superomedial cerebellum	-18	-42	-20	4.9
L superior cerebellum	-28	-52	-23	7
L lateral cerebellum	-40	-51	-27	4.1
Inferior vermis	0	-70	-26	5.7
R posteromedial cerebellum	21	-80	-22	5.1
R posterior cerebellum	29	-75	-26	4.9
R lateral cerebellum	41	-61	-28	4.3

Table 6

(a) HS-specific activations stronger for familiar than unfamiliar objects (*VI-HS overlap zones) within VI-WnW mask; (b) HS-specific activations stronger for unfamiliar than familiar objects within VI-WnW mask. x,y,z: Talairach coordinates for the center of gravity of the activation.

	Region	x	y	z
(a)	L MF	-22	-27	-12
	L PF (close to LOC) *	-38	-46	-12
	L inferior temporal gyrus	-54	-42	-2
	L anterior calcarine	-7	-50	10
	L Prec	-6	-51	11
	L OP3	-32	-21	22
	R OP3	38	-19	21
	L PMd *	-37	3	49
	L PMv *	-44	10	24
	L IFG *	-44	38	0
	L inferior frontal sulcus	-40	31	13
	L OFC *	-36	35	-5
	L amygdala	-20	-3	-13
	L thalamus (Pul) *	-14	-35	3
(b)	L avIPS/pIPS	-20	-65	45
	L smIPS/SMG	-32	-43	45

Table 7

HS-specific activations stronger for unfamiliar than familiar objects within a mask comprising voxels active in either haptic condition in either experiment. x,y,z: Talairach coordinates for the center of gravity of the activation.

Region	x	y	z
L pIPS	-18	-58	45
R pIPS	16	-60	46
L smIPS	-31	-43	45
R smIPS	31	-46	44
L SMG	-45	-36	51
R SMG (2 foci)	40	-39	48
	48	-37	46
R aIPS	36	-43	41
L Prec	-12	-60	45
R Prec	9	-67	43
L postcentral gyrus	-26	-27	52
L FEF	-20	-15	52
R FEF	20	-10	46
R inferior frontal sulcus	30	46	15
R IFG	46	22	11
R aIns	32	17	1
R AC	5	27	28
R PC	3	-35	22
L thalamus (VPL)	-13	-17	10
R thalamus (mediodorsal, LP, Pul)	12	-17	13

Table 8

HS-specific activations common to both familiar and unfamiliar objects. x,y,z: Talairach coordinates for the center of gravity of the activation.

Region	x	y	z
L LOC	-48	-61	-4
R LOC	46	-52	-6
L pIPS	-22	-64	49
R pIPS	23	-59	48
L smIPS	-30	-46	52
R smIPS	29	-47	49
L PCS	-48	-25	37
R PCS	48	-24	36
L OP3	-41	-23	18
L central sulcus	-29	-23	54
SMA	3	-2	51
L FEF	-27	-12	50
R FEF	29	-10	51
L PMv	-41	-1	34
R PMv	47	5	31
L superior frontal sulcus	-26	38	28
R superior frontal sulcus	26	34	28
L aIns	-31	20	2
L AC	-6	23	29
R AC	9	19	29
MC	1	-3	35
L thalamus (Pul)	-16	-23	10
L thalamus (mediodorsal nucleus)	-10	-18	11
R thalamus (Pul)	14	-22	6
R thalamus (anterior nucleus)	10	-3	12