Haptic Shape Processing in Visual Cortex

Jacqueline C. Snow[1], Lars Strother[1], and Glyn W. Humphreys[2]

Abstract

■ Humans typically rely upon vision to identify object shape, but we can also recognize shape via touch (haptics). Our haptic shape recognition ability raises an intriguing question: To what extent do visual cortical shape recognition mechanisms support haptic object recognition? We addressed this question using a haptic fMRI repetition design, which allowed us to identify neuronal populations sensitive to the shape of objects that were touched but not seen. In addition to the expected shape-selective fMRI responses in dorsal frontoparietal areas, we observed widespread shape-selective responses in the ventral visual cortical pathway, including primary visual cortex. Our results indicate that shape processing via touch engages many of the same neural mechanisms as visual object recognition. The shape-specific repetition effects we observed in primary visual cortex show that visual sensory areas are engaged during the haptic exploration of object shape, even in the absence of concurrent shape-related visual input. Our results complement related findings in visually deprived individuals and highlight the fundamental role of the visual system in the processing of object shape. ■

INTRODUCTION

A critical question in cognitive neuroscience concerns whether or not sensory cortices are modality specific or are involved as part of a distributed system in the analysis of stimuli presented in other sensory modalities. In vision, primary visual cortex (V1) extracts and binds fundamental shape information (Field, Hayes, & Hess, 1993), which is combined into progressively more complex shape representations in higher ventral visual cortical areas (Kourtzi & Connor, 2011; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). Here we used fMRI to examine the potential involvement of primary visual cortex and other areas in ventral visual cortex during the haptic processing of objects that were touched but not seen.

Previous imaging studies of haptic shape encoding in the visual stream have predominantly focused on haptic shape sensitivity in higher-order areas such as the lateral occipital complex (LOC). Shape processing via touch has been shown to engage the LOC, and object-related activity in the LOC dissociates from the processing of felt textures (Kim & James, 2010; Naumer et al., 2010; Allen & Humphreys, 2009; Tal & Amedi, 2009; Stilla & Sathian, 2008; Peltier et al., 2007; Amedi, von Kriegstein, van Atteveldt, Beauchamp, & Naumer, 2005; Pietrini et al., 2004; Zhang, Weisser, Stilla, Prather, & Sathian, 2004; Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; Grefkes, Weiss, Zilles, & Fink, 2002; James et al., 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001). Activation of the LOC during object touch has been noted both in visually deprived individuals (Amedi et al., 2007; Burton, McLaren, & Sinclair, 2006;

Sadato et al., 1996), where it might reflect compensatory adaptation, and in healthy sighted observers, where this seems less likely (Amedi et al., 2001).

Evidence for somatosensory processing in primary visual cortex (V1), in contrast to the data on LOC, has largely come from individuals who have been blind from an early age. For example, the early blind (but not sighted controls) have shown activation of visual cortex during Braille reading and other tactile discrimination tasks using PET (Buchel, Price, Frackowiak, & Friston, 1998; Sadato et al., 1996, 1998). Using fMRI, tactile processing of embossed letters can elicit greater activation of early visual cortex in blind than sighted observers (Burton et al., 2006). Similarly, in blind individuals, TMS over visual cortex disrupts haptic letter recognition, demonstrating the necessary involvement of primary visual cortex in such individuals. The same is not the case for sighted controls (Cohen et al., 1997).

Attempts to evaluate whether V1 is involved in processing tactile shapes have predominantly assessed texture perception, involving (e.g.) dot-spacing or roughness discrimination tasks, so the involvement of this area in tactile shape perception is unknown (Merabet et al., 2007; Weisser, Stilla, Peltier, Hu, & Sathian, 2005). In contrast to the paucity of evidence for tactile shape processing in primary visual cortex, emerging data in studies of human audition and somatosensation have provided tantalizing evidence that primary sensory areas can process shape-related information arising from other sensory modalities. For example, visual displays of objects that strongly imply sound or touch can elicit content-specific activity patterns within primary auditory (Meyer et al., 2010) and somatosensory cortex (Meyer, Kaplan, Essex, Damasio, & Damasio, 2011), respectively.

[1]University of Nevada, [2]University of Oxford

Here we used fMRI in healthy sighted individuals to examine whether low-level (V1) and intermediate-level form-selective area (V4) are involved in processing object shape via touch. To confirm that our haptic repetition design and stimuli were sufficient to elicit repetition effects, we first examined shape-selective responses to palpated objects in the LOC—an area in which we might expect to observe shape-selective repetition effects based on the involvement of this area in previous studies of object touch, as outlined above. To enable a fine-grained analysis of visual cortex function, we used a haptic fMRI repetition design analogous to those previously used in vision (Grill-Spector & Malach, 2001; Grill-Spector et al., 1999) to identify neural populations sensitive to the shape of objects that are touched but not seen. Repetition designs have been applied successfully in the domain of somatosensation to examine brain regions involved in tactile pattern and frequency coding (Tamè et al., 2012; Li Hegner, Lee, Grodd, & Braun, 2010) and high-level shape processing (Tal & Amedi, 2009). In our study, all observers were normally sighted to rule out the involvement of adaptive changes linked to visual deprivation. The palpated objects in our study were not visible to participants and throughout the experiment observers maintained their gaze upon a central fixation point. We functionally isolated low-, intermediate-, and high-level visual shape processing areas using separate visual localizer tasks and determined the extent to which each of these areas were sensitive to haptic shape repetition. Brain areas that are sensitive to haptic shape cues should show a reduced fMRI response when object shape is repeated versus novel.

METHODS

Participants

Ten healthy right-handed observers (seven women, 22–38 years old), with normal or corrected-to-normal vision and normal somatosensation, each participated in three fMRI scans. Participants first completed a haptic fMRI repetition study and subsequently returned to complete two follow-up localizer tasks: one designed to isolate object-selective LOC and the second to isolate intermediate-level color/form processing area V4 and visual cortex. All participants were naïve with respect to the experimental design and hypotheses. Informed consent was obtained in accordance with procedures approved by the university ethics review board.

Stimuli

Stimuli for the haptic fMRI experiment comprised a set of 28 real-world objects and an additional set of six "nonobjects" for use on response trials (Figure 1). The "nonobjects" were 3-D shapes each constituted of parts of real objects. Pilot experiments, involving a different pool of individuals from the fMRI participants, confirmed

that the real objects could each be identified within 3 sec and that the "nonobjects" were not easily misidentified as real objects. For the LOC localizer, stimuli consisted of 300 × 300 pixel grayscale images and line drawings of
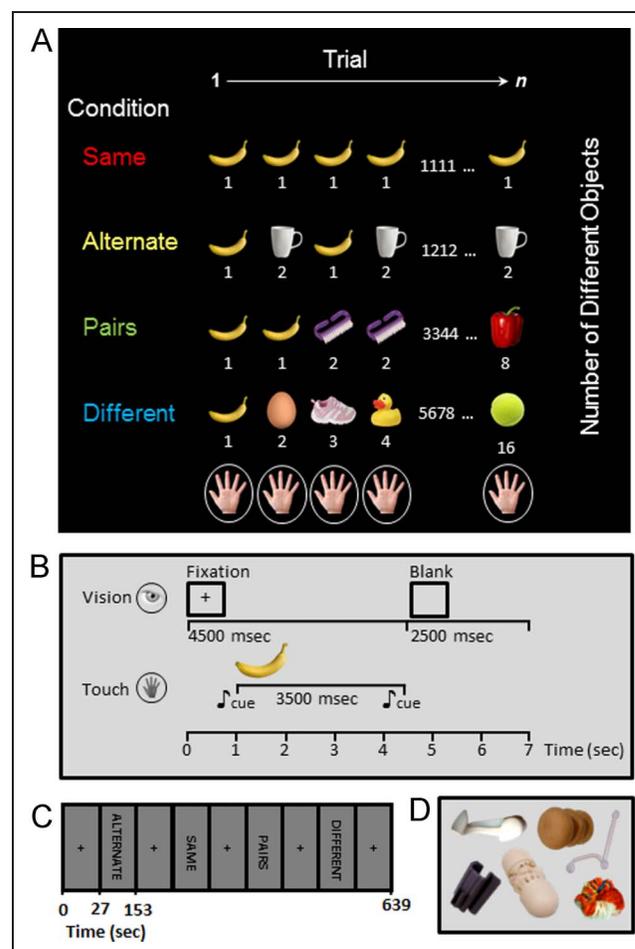

Figure 1. Experimental design. (A) Example of the four conditions used in the haptic experiment. Each row illustrates an example sequence from each condition. Using a parametric design, we manipulated the number of different objects palpated during each block. For brain regions involved in processing and/or representing object shape increases in object repetition should lead to a gradual fMRI response reduction, with the greatest differences expected between the Different and Same conditions. The identity of the repeated stimulus (e.g., the *banana*) was changed between runs to minimize carryover of repetition effects. (B) Example trial sequence. During the haptic experiment, participants lay supine within the scanner and palpated sequences of real-world objects with the left hand. Their task was to detect "nonobjects" that were presented occasionally during the sequence. Throughout each scan, observers were instructed to maintain their gaze upon a central fixation cross, which was viewed via a mirror attached to the top of the head coil. After a 1000-msec fixation period, participants received an auditory tone that signaled them to open their left hand ready to receive the object. Stimuli were palpated for 3500 msec before a second tone and simultaneous offset of the fixation cross signaled participants to release the stimulus. Intertrial interval (with blank screen) was 2500 msec. (C) The experiment had a block design in which sequences of somatosensory trials were alternated with blocks of fixation only. The duration of somatosensory blocks was 126 sec, and interleaved fixation blocks were 27 sec. (D) Examples of nonobject stimuli used on "catch trials" during each somatosensory sequence.

familiar and novel objects and scrambled versions of each set, each with overlapping grid lines as described in previous studies (Kourtzi, Erb, Grodd, & Bulthoff, 2003; Kourtzi & Kanwisher, 2000, 2001). Images were back-projected onto a screen, which was viewed via a mirror attached to the top of the head coil yielding a viewing distance of 65 cm. For the intermediate-level form (V4) and V1 localizer, stimuli consisted of 28,300 × 300 pixel high-resolution color photographs of the same set of objects presented during the haptic experiment, each photographed from a canonical perspective using a Sony (Tokyo) Alpha DSLR-A100 camera. The images were presented on a blank white background and overlaid with a central gray fixation cross (average image size = 120 × 150 pixels) and viewed via a mirror attached to the head coil, as described above.

Procedure and Design

In the haptic fMRI study, participants palpated sequences of real objects with the left hand. The experiment used a blocked design in which somatosensory sequences were interspersed with blocks of baseline fixation. Each stimulus block consisted of 18 consecutive somatosensory events: 16 events were object trials and the remaining two events were catch trials involving "nonobjects." Participants pressed a response button with the index finger of the right hand each time a catch trial was detected. Catch trials were employed to ensure that participants remained vigilant throughout the runs. Participants performed this task well, and incorrect identifications of nonobject trials were <1%. Importantly, the number of response (catch) trials was identical across all conditions. Participants were not exposed to the stimulus set before the testing session. The haptic experiment used a parametric design in which we modulated the repetition frequency of haptically presented objects. We tested four levels of haptic object repetition (Figure 1A). In the Same condition, a single object was repeatedly presented on all 16 object trials within a block. In the Different condition, a different object was presented on all 16 object trials. Repetition effects in-between the Same and Different conditions were examined using two intermediate conditions. In the Alternate condition, two different objects were presented in alternating order across each trial in a block. Finally, in the Pairs condition, eight different objects were presented within a block, each one twice in succession. Catch trials appeared randomly within each block of object trials (with the exception of the Pairs condition in which these trials arose before or after a pair, never in-between). The identity of the repeated stimulus (e.g., the *banana* in Figure 1) was substituted across runs (e.g., shaving brush/ball of string/toothbrush) to minimize long-term carryover repetition effects. Each run of the haptic experiment consisted of one block of trials from each of the four conditions, yielding four stimulus blocks within each run (Figure 1C). The order

of conditions was counterbalanced within participants using a balanced latin square design. Half of the participants completed conditions according to the order specified by a latin square, and the remaining participants completed conditions according to a mirror (reversed) square.

The stimulus sequence on each haptic trial is illustrated in Figure 1B. Trials began with a 1000-msec central visual fixation cross, followed by a 3500-msec haptic palpation period. The start of the palpation window was signaled by a 500-msec auditory tone, delivered to both the participant and the experimenter. At the onset of the tone, the experimenter placed a stimulus into the participant's open left hand. Participants were instructed to palpate the object for the duration of the trial and to make a button-press response where appropriate (i.e., catch trials). The end of the palpation period was indicated by a second 500 msec auditory tone (lower in pitch than the first) and the simultaneous offset of the visual fixation cross (2500 msec). Participants were instructed to release the object at the onset of the second auditory tone in preparation for the upcoming trial. Each trial had a total duration of 7 sec. With 18 trials per block, this yielded a total block duration of 126 sec. Fixation blocks (27 sec) were positioned at the start and end of the experiment, and in-between each stimulus block, yielding a total run length of 639 sec (with a repetition time [TR] = 3, yielding 213 functional volumes). Participants completed four runs of the haptic experiment.

All participants completed two further localizer tasks designed to identify V1 and intermediate-level color/form-selective area, most likely corresponding to area V4 (Gallant, Shoup, & Mazer, 2000), and high-level shape-selective regions within LOC. The LOC localizer had a blocked design with 16 stimulus blocks presented in a balanced order and interleaved fixation periods of 16 sec each. Twenty images were presented within each block. Images were presented for 250 msec with a blank interval of 550 msec between images. Participants were instructed to passively view the images while fixating. The low- and intermediate-level color/form area localizer used a block design in which participants viewed sequences of the same set of 18 different high-resolution color stimuli that had been palpated in the haptic experiment. Each trial began with a central black fixation cross (1000 msec), followed by the stimulus image (or nonobject) for 500 msec. Images were separated by a blank intertrial interval of 2500 msec. Total trial length was 4000 msec; with 18 images per block, the total block duration was 72 sec. Stimulus blocks in this task were interspersed with three other stimulus conditions, which were used for a separate experiment (not considered further here). Stimulus blocks were interleaved with 18-sec fixation blocks. A further 18 sec of fixation was added to the start and end of each run; the duration of the entire experiment was 378 sec. Block order was counterbalanced within and across participants in a similar fashion to the haptic experiment. Participants

completed four runs of the low-level visual/color area localizer and two runs of the LOC localizer. Stimulus presentation and timing were controlled using E-Prime software, except for the LOC localizer, which was controlled using Matlab.

MRI Acquisition

Scanning was carried out on a 3-T Philips (Andover, MA) MRI scanner with an eight-channel SENSE parallel head coil. Functional data for the haptic experiment and V1 localizer task were acquired using a single shot T2* weighted single-shot gradient-echo EPI sequence (echo time = 35 msec, TR = 3000 msec, field of view = 232 × 288 × 175 mm, voxel size = 2.5 × 2.5 × 2.5, 49 axial slices). Scan parameters for the LOC localizer task were as follows: TR = 200 msec, echo time = 30 msec, voxel size = 3.0 × 3.0 × 3.0, 32 axial slices. A total of 213 volumes were collected per run for the Haptic experiment, 126 volumes per run for the V4/primary visual cortex localizer task, and 168 volumes for each LOC localizer run. Functional data were aligned and reinterpolated to a high-resolution anatomical image for each participant obtained using an echo-planar 3-D T1-weighted image (1 × 1 × 1 mm slice thickness, 175 slices, field of view = 232 × 256 × 175).

Data Processing and ROI Analyses

Data were preprocessed and analyzed using Brain Voyager QX (Version 1.10.2, Brain Innovation, Maastricht, Netherlands). Functional data were initially preprocessed by motion correcting to the functional volume acquired closest in time to the anatomical scan and removing linear trends. No high-pass filter was applied to ensure that cycles of interest within each haptic run were not eliminated. 2-D functional images were aligned to the 3-D anatomical data and then transformed into Talairach space. Runs in which translational head motion spikes exceeded 2 mm of translation and/or 2° of rotation were excluded from the analyses (totaling only one run for one participant in the haptic experiment). Haptic data for one participant was excluded because of technical issues during the experiment (Runs 1–4) and above-threshold head motion in two subsequent scans (Runs 5–6).

Voxelwise Group Analyses

We first performed whole-volume voxelwise analyses on the group haptic data. fMRI signals for each participant were spatially smoothed (8 mm, FWHM Gaussian kernel). The data for the main experiment were smoothed to account for variability in the spatial location of functional regions across observers and improve signal-to-noise ratio. Data from each haptic run were analyzed using separate predictor functions for each experimental condition. The experiment had a block design, and all trials were included in the statistical analyses. Predictor functions were generated for the four conditions by convolving a rectangular wave function with a standard hemodynamic response function. Individual participant data were analyzed using a single-subject general linear model (GLM). Data for each participant were processed using a percent signal change (%SC) transformation and a correction for serial (temporal) correlations. Group data were then analyzed using a random effects GLM. Brain regions that showed significant haptic fMRI repetition effects at the whole-brain level were isolated using the contrast [+Different −Same] (Figure 2). The resultant group activation map was set to a statistical threshold of $p < .005$. A correction for cluster size was not applied to the group maps because small isolated clusters of activated voxels had already been removed (or greatly reduced in number) from the statistical maps by spatial smoothing; an additional cluster correction could therefore eliminate meaningful but spatially restricted activation in smaller areas such as primary visual and somatosensory cortex—areas in which isolated effects can be masked because of reduced signal overlap across observers.

ROI Analyses

ROIs were isolated separately for each observer using independent functional localizer tasks. For each individual, ROIs were identified by selecting voxels within regions of ventral occipitotemporal cortex that were activated more strongly by intact images of objects than control stimuli. ROIs were isolated by first locating the peak voxel of functional activation within each anatomical area (described separately for each ROI below). Next, the statistical map for the localizer task for each individual was set to a minimum statistical threshold ($t > 3.0$, $p < .001$), and a VOI was selected around the peak voxel. LOC was identified by contrasting fMRI responses to grayscale intact objects versus their scrambled counterparts (Kourtzi & Kanwisher, 2000; Malach et al., 1995). As in previous studies in vision (Kourtzi, Erb, et al., 2003; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Grill-Spector et al., 1999), we isolated two subregions of the LOC complex: a region on the lateral surface near the lateral occipital sulcus (area LO) and a ventral occipitotemporal region extending into the posterior and mid-fusiform gyrus and occipitotemporal sulcus (pFus). Area LO was defined by locating the peak voxel of activation within the lateral convexity of occipitotemporal cortex, while pFus was defined by selecting the peak voxel more ventrally and anteriorly within the fusiform sulcus of inferior temporal cortex. Low- and intermediate-level visual form processing areas were defined by contrasting fMRI responses to colored objects versus fixation in the visual localizer task involving colored objects. Intermediate-level visual form area (V4) was identified by selecting the peak functional voxel within the temporo-occipital

Figure 2. Brain regions sensitive to the identity of haptically explored objects. Strong repetition effects were observed within the vicinity of the LOC bilaterally. Isolated repetition effects were also observed along the calcarine sulcus within V1 (see insets), within dorsal and anterior regions of the intraparietal sulcus (dIPS, aIPS), along the postcentral gyri and sulci (PoCG/PoCS), parietal operculum (OP), the precentral sulcus (PrCS), insular cortex (Ins), and the middle frontal gyrus (mFG). Haptic repetition effects were identified by contrasting group fMRI responses in the Different versus Same conditions using a whole-brain voxelwise contrast. Above-threshold ($p < .005$) activation is displayed on the inflated cortex of a representative participant, shown from lateral (top) and ventral (bottom) viewpoints. A detailed view of above-threshold group activation in the vicinity of the calcarine sulcus (dashed line) of primary visual cortex is shown in the lower insets, overlaid on sagittal slices on the high-resolution anatomical image of the same participant (LH = left hemisphere; RH = right hemisphere; A = anterior).
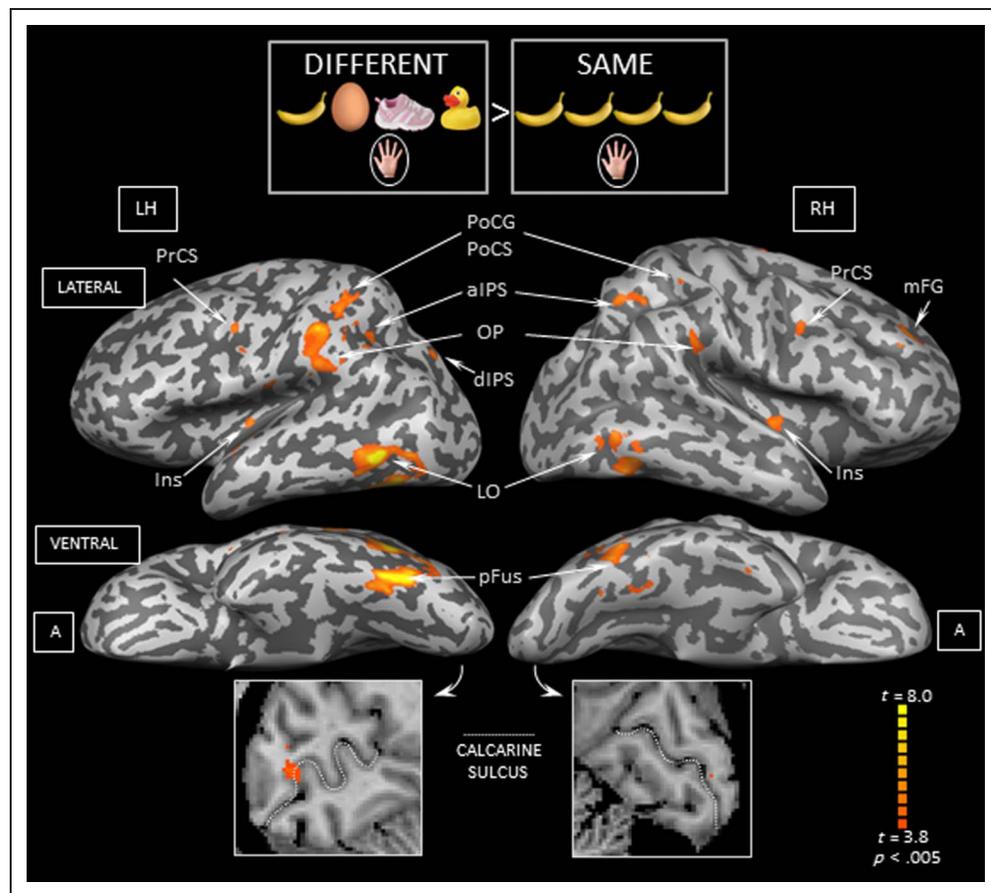
junction around the posterior branch of the collateral sulcus or on its lateral aspect within the fusiform gyrus (posterior to pFus; Gallant et al., 2000). Primary visual cortex ROIs were identified by selecting the voxel of peak functional activation on, or adjacent to, the calcarine sulcus. VOIs of up to 5 mm³ (i.e., 125 voxels) for V1 and V4 and 10 mm³ (i.e., 1000 voxels) for LO/pFus were selected around the peak voxel of activation in each region. ROI sizes for V1 and V4 were comparatively smaller than those within LOC to ensure that our analyses within these areas reflected fMRI responses within the defined areas of interest and did not include neighboring areas of occipital cortex (see Figures 4 and 5). ROI sizes for the LOC reflect functional responses within comparatively more spatially extended regions of lateral occipital and ventral temporal cortex (see Figure 3). One participant (denoted by the symbol (†) in Figure 4) showed attenuated activation in the visual localizer task, and consequently a threshold of $p < .05$ was applied to identify V1 in this instance.

Data from the haptic experiment were extracted from each ROI, and subsequent analyses were performed on unsmoothed data. Functional data were not smoothed

in the single-participant ROI analyses because there was no longer a problem of spatial mismatch between the functional regions of different observers and because smoothing could lead to the loss of otherwise meaningful fMRI signals in areas with a smaller spatial scale of activation or carryover activation arising from signals in nearby regions. fMRI signal intensities within each region were averaged, and the time courses were converted to %SC relative to the baseline fixation periods. The %SC fMRI data for each participant were then averaged across conditions and normalized for each time point within each hemisphere (L/R) and ROI, starting from the point of peak response, which occurred at a lag of 6 sec post-stimulus onset (Boynton, Engel, Glover, & Heeger, 1996) to the final volume of the block (volume 43). Data were normalized using the formula (X_t − Min/Max − Min), where X_t is the observed %SC at time point t within a block; Min and Max are the minimum and maximum fMRI responses across the four haptic conditions, respectively. The mean normalized signal changes for each haptic condition were averaged across participants to yield group data. The pattern of fMRI responses in each of the haptic repetition conditions was the same in the left and right hemispheres

for each ROI (i.e., fMRI responses were highest in the Different condition, followed by the Pairs and then Alternate conditions, and lowest in the Same condition), so the data were averaged across hemispheres. Repetition effects for each ROI in the haptic experiment were defined based on a main effect of Condition (number of different objects: 16, 8, 2, 1) using a one-way repeated-measures ANOVA ($p < .05$) and a significant difference between the Different and Same conditions in paired-samples t tests ($p < .05$; two-tailed).

RESULTS

In the domain of vision, selectivity to object shape in the ventral visual system has been measured based on the

Figure 3. Visually defined areas within the LOC are highly sensitive to the shape of objects that are touched but not seen. (A) In line with similar studies in vision, we isolated two visual subregions within LOC: a posterior lateral sub-region (area LO) and a more ventral anterior subregion (pFus). Shape-selective regions were identified in individual observers by contrasting fMRI responses to images of objects with images of textures, using a separate localizer task. ROIs for each participant (see color code bar) are overlaid on axial (left) and saggital (middle, right) slices of the averaged anatomical image. The average position of LO and pFus ROIs in the z (vertical) and x (horizontal) planes is indicated in Talairach coordinates below each anatomical image. Anatomical images are displayed in neurological convention (left hemisphere on left side of image). (B) Observers showed a highly consistent effect of haptic repetition in LO and pFus: fMRI responses were stronger for Different versus Repeated objects. Histograms display the mean (*SE*) normalized fMRI responses for each participant in LO (left) and pFus (right) in the Different (blue) and Same (red) conditions of the haptic experiment, averaged across hemispheres. (C) Averaged fMRI responses across the group revealed a strong main effect of haptic condition, and response magnitude gradually decreased with parametric increases in stimulus repetition. Histogram displays group mean (*SE*) fMRI responses in each of the four haptic conditions, within visual LO (left) and pFus (right). *Significant differences between the Different and Same conditions ($p < .001$).
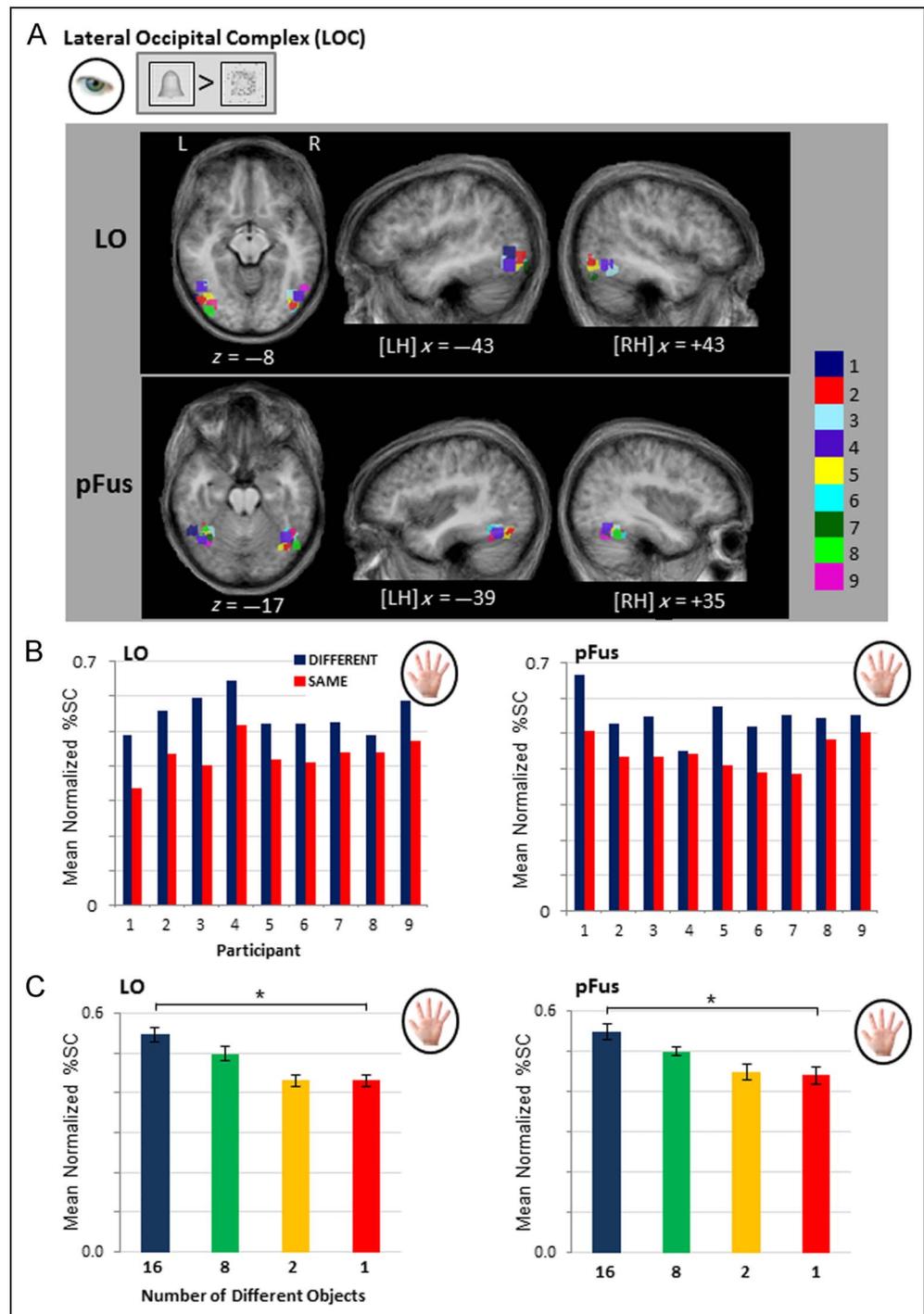
Figure 4. Shape-selective fMRI responses to haptically explored objects within intermediate-level visual processing area V4. (A) Visual responses to colored objects and ROIs within V4 are shown for each participant. V4 was isolated by contrasting fMRI responses to colored objects versus fixation in a separate task. Above-threshold visual activation ($p < .001$) within ventral occipitotemporal cortex is illustrated in yellow. V4 ROIs (shown in purple) were centered upon the peak voxel of visual activation within the posterior branch of the collateral sulcus or on its lateral aspect within the fusiform gyrus in each hemisphere. (B) The effect of haptic object repetition was again consistent across observers; fMRI signals in V4 were greater when participants touched different objects compared with when they touched the same object repeatedly. Histograms display mean (SE) normalized fMRI responses for each participant in V4 in the Different (blue) and Same (red) conditions of the haptic experiment, averaged across hemispheres. (C) fMRI responses in the four haptic conditions showed a significant effect of touched object identity in V4. The histogram displays group mean (SE) fMRI responses in each condition, averaged across hemispheres ($*p < .005$).
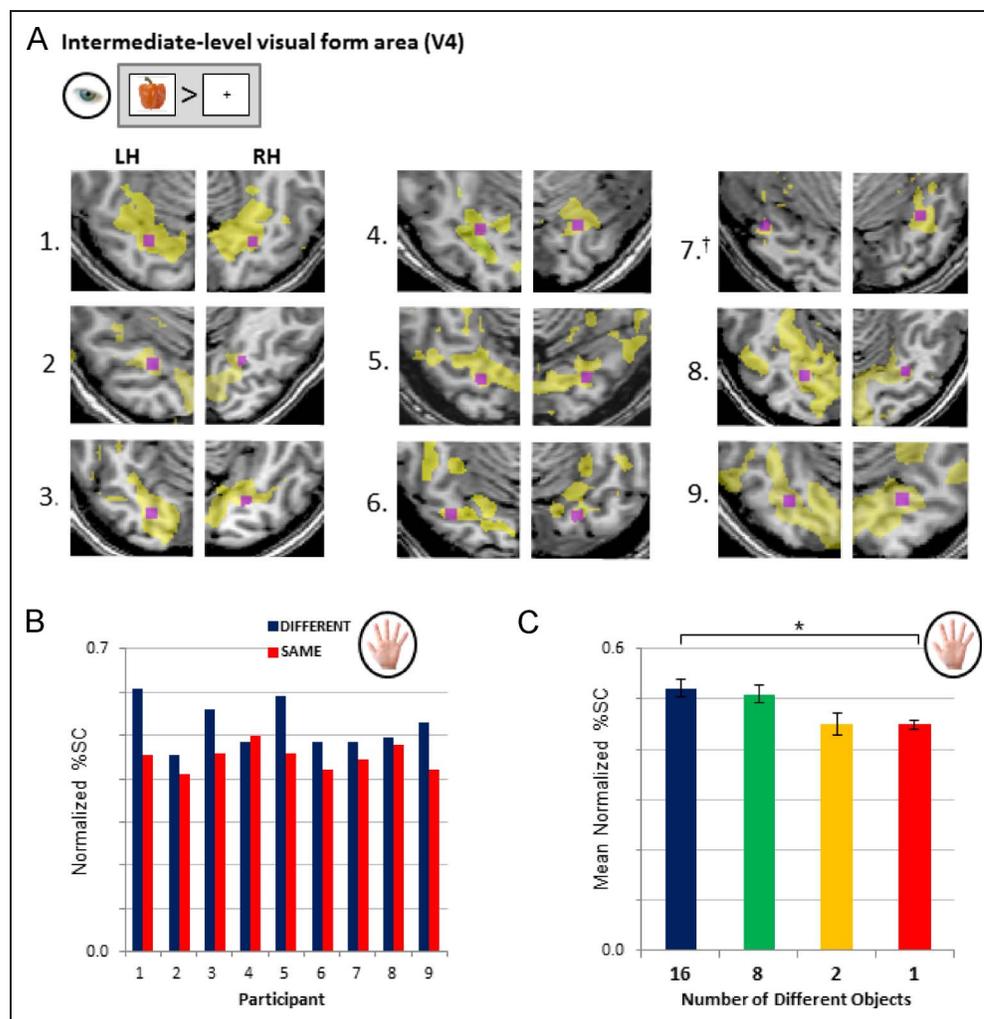
strength of fMRI responses to parametric manipulations of object repetition frequency (Grill-Spector & Malach, 2001; Grill-Spector et al., 1999). Here we used an analogous design in the domain of haptics, in which we manipulated the repetition frequency of touched object shape to examine brain regions that are involved in processing and/or representing haptically derived shape cues. We first identified regions across the whole brain that showed sensitivity to haptic shape repetition. Next, we functionally isolated ventral visual areas LOC, V4, and V1, based on their responses to visual stimulation in separate tasks, and examined the sensitivity of each region to haptic shape. We were primarily interested in haptic repetition effects in primary visual cortex; we began our ROI analyses in the LOC to validate the sensitivity of our procedure and design, before examining haptic repetition effects in areas progressively more posterior within the occipital cortex.

Whole-brain Voxelwise Analyses

The design of the haptic experiment is illustrated in Figure 1. Shape-selective responses were examined using a parametric fMRI repetition design in which areas sensitive to object identity were expected to show greater fMRI adaptation (i.e., an attenuated fMRI response) with corresponding increases in repetition frequency (Grill-Spector, Henson, & Martin, 2006). We started by using whole-brain voxelwise contrasts to identify regions that were most sensitive to haptic repetition using the contrast [+Different − Same] (Figure 2). We observed robust bilateral haptic fMRI adaptation effects within lateral and ventromedial regions of occipitotemporal cortex, in the vicinity of the LOC (left hemisphere: 8297 voxels, maximum t value = 18.32; right hemisphere: 1990 voxels, maximum t value = 7.34). Bilateral effects of haptic shape repetition were also observed within

dorsal and anterior intraparietal sulcus, the insula, and in the precentral sulcus in the vicinity of ventral premotor area (Chouinard & Paus, 2006). Haptic shape repetition effects were also observed bilaterally in somatosensory cortex, extending along the post-central gyri and sulci and ventrally into the parietal operculum, corresponding to the expected location of secondary somatosensory cortex as described in previous studies (Burton, Sinclair, Wingert, & Dierker, 2008; Eickhoff, Grefkes, Zilles, & Fink, 2007; Eickhoff, Amunts, Mohlberg, & Zilles, 2006; Eickhoff, Schleicher, Zilles, & Amunts, 2006). Shape-selective fMRI responses were observed too within middle frontal gyrus in the right hemisphere. We also found isolated but above-threshold haptic repetition-related clusters in the vicinity of the calcarine sulcus in primary visual cortex (Figure 2, bottom insets), most notably in the left hemisphere. Note that the calcarine structure varies considerably from one individual to the next, and in the context of a random-effects voxelwise GLM, isolated effects can be masked because of reduced signal overlap across observers. Our result was observed despite this constraint.

Interestingly, the haptic fMRI adaptation effects within many of the activated areas (e.g., within somatosensory areas, LOC, and V1), although bilateral, appeared to have a greater spatial extent in the left than the right hemisphere.

ROI Analyses

Next, we measured haptic shape repetition effects within visually defined ROIs along occipitotemporal cortex. Visual areas for our ROI analyses were defined separately for each participant based on visual fMRI tasks conducted separately from the main haptic experiment (see Methods). Haptic repetition effects in each ROI were defined on the basis of two criteria: a main effect of haptic Condition (number of different objects: 16, 8, 2, 1) as defined using a one-way repeated-measures ANOVA, and a significant response difference (Δ) between the Different ($_D$) and Same ($_S$) conditions ($\Delta_{D,S}$ two-tailed; Konen & Kastner, 2008). To the extent that a visual area is sensitive to object shape, repetition effects should be maximal in the Same condition (i.e., lowest fMRI response), followed by the

Figure 5. fMRI responses in primary visual cortex (V1) were strongly modulated by the identity of touched objects. (A) V1 was localized by contrasting fMRI response to objects with fixation in a separate task. Above-threshold visual responses for each participant in each hemisphere is shown in yellow ($p < .001$). ROIs (shown in red) were centered upon the voxel of peak visual activation on or just above the calcarine sulcus (dashed line) in each participant. (B) Surprisingly, observers showed robust and consistent repetition effects within V1, although the objects were touched rather than seen. Histograms display the mean (*SE*) normalized fMRI responses for each participant in V1 in the Different (blue) and Same (red) conditions, averaged across hemispheres. (C) Group fMRI responses in V1 showed a strong main effect of repetition, and signal strength reflected parametric changes in repetition frequency. The histogram shows group mean (*SE*) fMRI responses in each haptic condition (*$p < .005$).
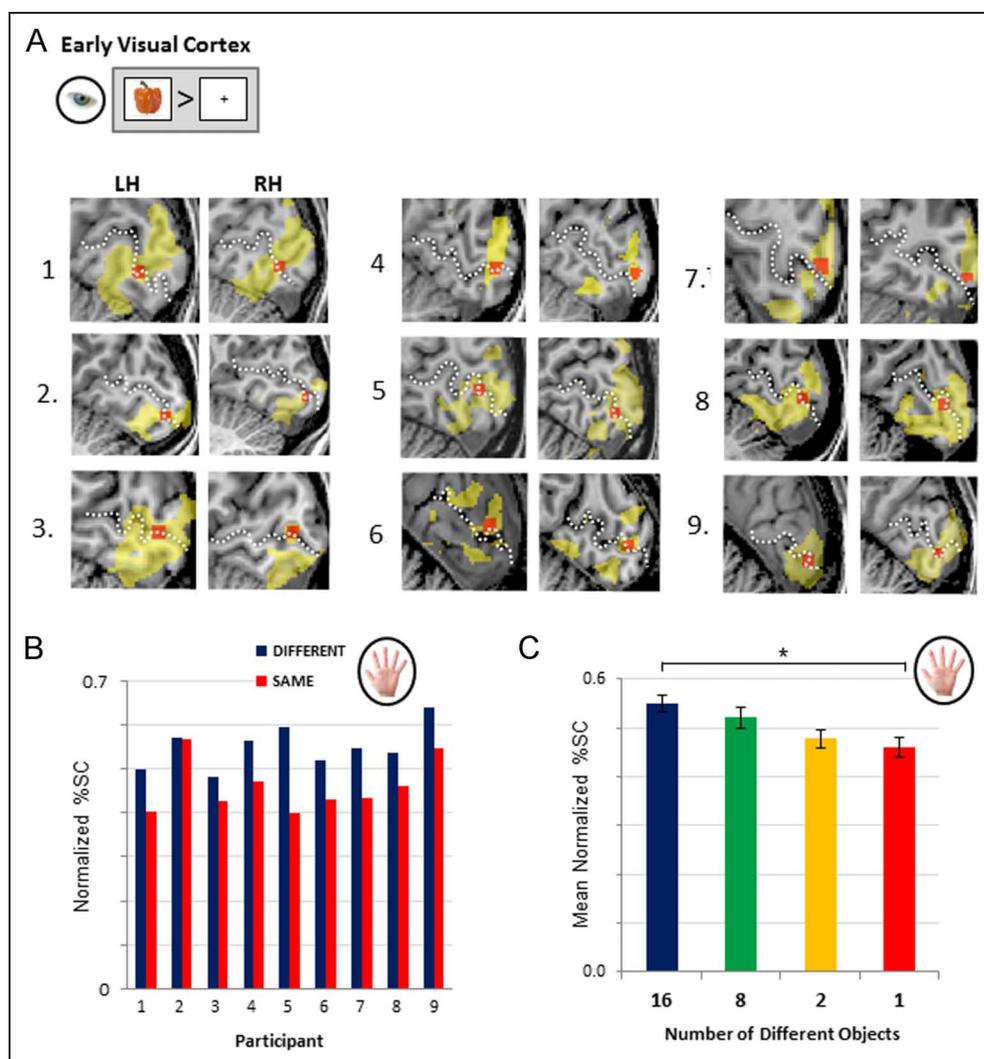
Pairs and Alternate conditions, and lowest in the Different condition (i.e., highest fMRI response). Regions that are not sensitive to repetition are expected to show a constant fMRI response across the four conditions.

Haptic Shape Sensitivity in LOC

To validate our procedure and design, parametric effects of haptic repetition were measured first within the LOC—an area that shows strong sensitivity to visual shape repetition (Grill-Spector et al., 1999). Following from analogous studies in vision, repetition effects were examined within two visual subregions of the LOC: area LO, located on the lateral bank of occipitotemporal cortex, and posterior fusiform sulcus (pFus), positioned comparatively more anteriorly on the ventromedial surface of the temporal lobe. Each subregion was localized by contrasting fMRI responses to grayscale images of intact objects with images of their scrambled counterparts (see Methods). Figure 3A illustrates visual ROIs selected within LO (top) and pFus (bottom) for each participant, overlaid on the average high-resolution anatomical image. The effect of haptic shape repetition in the anterior and posterior subregions of the LOC was highly consistent across participants within areas LO and pFus, with qualitatively higher mean fMRI signals in the Different versus Same haptic conditions (Figure 3B). Mean signal changes evoked by the four haptic conditions averaged across participants are displayed in Figure 3C. As expected, repetition effects were highly significant in both subregions (LO: main effect of repetition, $F = 40.02$, $p < .001$ [$\Delta_{D,S}\ t = 8.60$, $p < .001$]; pFus: main effect of repetition, $F = 16.84$, $p < .001$ [$\Delta_{D,S}\ t = 5.61$, $p = .001$]; repetition effects were significant within both left and right hemispheres), and both subregions showed a parametric effect of repetition, with a gradual fMRI response reduction with increasing repetition frequency.

Haptic Shape Sensitivity within Low- and Intermediate-level Visual Form Processing Areas

Next, we examine shape-specific responses within the posterior branch of the collateral sulcus, in an area most likely to correspond with V4 (Gallant et al., 2000). Axial anatomical slices in Figure 4A illustrate visual fMRI responses for each participant within ventral temporal cortex that showed stronger fMRI responses to colored images of objects versus fixation ($p < .001$; activation shown in yellow). ROIs were centered upon the peak voxel of activation around the posterior branch of the collateral sulcus (shown in purple; see Methods). The effect of haptic shape repetition was highly consistent across participants, with qualitatively higher fMRI signals in the Different versus Same conditions in eight of nine observers (Figure 4B). Analysis of mean fMRI signal changes evoked during the four repetition conditions revealed a significant haptic repetition effect (main effect of haptic repetition: $F = 7.10$, $p = .001$; $\Delta_{16,1}$, $t = 4.03$,

$p = .004$), and there was a reduction in fMRI response with increases in repetition frequency (Figure 4C).

Finally, we examined sensitivity to haptic shape repetition within primary visual cortex. Saggital anatomical slices in Figure 5A illustrate fMRI responses for each observer along the calcarine sulcus in each hemisphere that showed stronger fMRI responses to images of objects versus fixation ($p < .001$; activation shown in yellow). ROIs in V1 were centered upon the voxel of peak activation on or immediately adjacent to the calcarine sulcus (shown in red; see Methods). As expected, the region of peak activation in the calcarine sulcus elicited by our colored object stimuli was almost identical to that elicited by the grayscale object stimuli used in the LOC localizer. Functional data for the haptic experiment were extracted from each ROI and averaged across hemispheres. The effect of haptic shape repetition within primary visual cortex was strikingly consistent across observers, with qualitatively greater fMRI responses in the Different versus Same conditions in all participants (Figure 5B). Analysis of mean signal changes evoked during the four haptic repetition conditions showed a significant effect of repetition (main effect of repetition: $F = 7.10$, $p = .001$; $\Delta_{D,S}\ t = 4.03$, $p = .004$; repetition effects were significant within both left and right hemispheres; Figure 5C).

DISCUSSION

Using a haptic fMRI repetition paradigm, we found that visually defined areas in occipital and temporal cortex were involved in analyzing the shape of objects that were touched, but not seen. Although numerous dorsal fronto-parietal regions were sensitive to the repetition frequency of haptically explored objects, strong shape-selective responses were observed ventrally in LOC (Figure 2). ROI analyses confirmed that fMRI responses in both area LO and pFus subregions of the LOC were sensitive to haptic shape (Figure 3). In addition to this, primary visual cortex and medial-temporal visual form processing areas also showed a significant reduction in fMRI response with increases in haptic shape repetition (Figures 4 and 5). The pattern of haptic repetition effects we have observed in regions of occipital and ventral temporal cortex is strikingly similar to those reported in analogous fMRI repetition studies in the domain of vision (Grill-Spector et al., 1999). Taken together, our data suggest that low-level visual areas are functionally involved in processing the shape of objects explored with the hand.

We used whole-brain analyses of fMRI repetition effects to isolate regions involved in processing the shape of objects explored via touch. Shape-selective fMRI responses were observed within dorsal frontoparietal areas, including the IPS, primary somatosensory areas along the post-central gyri and sulci and parietal operculum (corresponding to area SII), the precentral sulcus (corresponding to ventral premotor area), anterior insula, and middle frontal gyrus. In addition, bilateral shape-selective fMRI responses

were observed within occipital cortex and on the lateral and ventral surface of the temporal lobe within the vicinity of the LOC. The brain regions in parietal, frontal, and temporal cortex that showed fMRI adaptation effects in our group analysis are consistent with areas reported in previous fMRI studies of haptic shape recognition and in current models of haptic object recognition (Lacey & Sathian, 2011; James & Kim, 2010; Lucan, Foxe, Gomez-Ramirez, Sathian, & Molholm, 2010; Lacey, Tal, Amedi, & Sathian, 2009; James, Kim, & Fisher, 2007; Amedi et al., 2002, 2005; James, James, Humphrey, & Goodale, 2005). Interestingly, in our study, many of these fMRI responses were moderately left-lateralized (a greater number of contiguously significant voxels in the left hemisphere as compared with the right). Left lateralization of fMRI responses, particularly in visual object-processing areas along occipitotemporal cortex, has recently been explained as being due to left-lateralized high spatial frequency channels (Woodhead, Wise, Sereno, & Leech, 2011). It is possible that the pattern of our haptic results are related to this, but future experiments would be necessary to address this possibility more directly. The sensitivity to haptic shape we observed within LOC is compatible with a growing list of imaging (James et al., 2002; Amedi et al., 2001), neuropsychological (Allen & Humphreys, 2009), and TMS (Mancini, Bolognini, Bricolo, & Vallar, 2011) studies that have implicated this region in haptic shape recognition (for comprehensive reviews, see Kim & James, 2011; Lacey & Sathian, 2011; James et al., 2005). In contrast to previous reports (Tal & Amedi, 2009; Amedi et al., 2001, 2002), however, we found shape-selective responses to touched objects were not limited to subregions of the LOC but were evident across the complex within both posterodorsal (LO) and anteroventral (pFus) subregions, perhaps reflecting the increased sensitivity of the fMRI repetition procedure.

Haptic Shape Processing in Low- and Intermediate-level Visual Areas

Objects examined via touch alone also elicited shape-specific fMRI responses within low- and intermediate-level and visual form processing areas. In our ROI analyses, fMRI responses in primary visual cortex and V4 were highly consistent across observers and there was a gradual reduction in fMRI response with systematic increases in haptic shape repetition. These data suggest that haptic shape processing engages much of the ventral visual system. Our data provide important new evidence in the domain of vision in humans (Vasconcelos et al., 2011) that a primary sensory area that has not been stimulated directly (with relevant sensory input) can represent information about object shape when this information has been acquired from a different sensory modality (Meyer et al., 2010, 2011).

The observed calcarine response to tactile form in our study concurs with previous reports of calcarine activa-tion in tasks requiring the discrimination of tactile surfaces (Merabet et al., 2007; Burton et al., 2006; Weisser et al., 2005). Here we extend these findings in several important respects. First, previous studies have found a nonspecific response of primary visual cortex to tactile stimulation (i.e., letter [Weisser et al., 2005] or texture [Merabet et al., 2007; Burton et al., 2006] vs. baseline), whereas we used a sensitive repetition design to reveal a stimulus-specific response to tactile form in primary visual cortex—one that was modulated parametrically by changes in object shape. In addition, whereas previous studies have reported primary visual cortex activation in early blind individuals (Burton et al., 2006; Buchel et al., 1998; Sadato et al., 1996, 1998) or in healthy observers following visual deprivation (i.e., 2 hr of blindfolding; Weisser et al., 2005), we observed shape-specific responses in primary visual cortex in healthy observers who were not deprived of visual input, either before or during the haptic task.

These data raise questions about the potential contribution of primary visual cortex to haptic shape recognition. A primary sensory area remote from the site of initial stimulation might be recruited for stimulus processing if it is well suited to the analysis of the relevant sensory input and if doing so confers a perceptual advantage—for example, by improving sensitivity, optimizing processing speed, or reducing computational demand. The integration of pattern information across multiple fingers is understood to be relatively poor, thereby making the "effective field of view" of an object significantly smaller than in vision (Loomis, Klatzky, & Lederman, 1991). Neurons in primary visual cortex have small receptive fields that provide high-resolution information about local changes in contrast, orientation, and spatial frequency. As a preliminary processor of basic units of shape (DeValois & DeValois, 1988), primary visual cortex could provide high-resolution details about haptically explored edges, their spatial frequency, and curvature. Indeed, TMS of visual cortex has been shown to interfere with fine-grained tactile discrimination (Merabet et al., 2004; Zangaladze, Epstein, Grafton, & Sathian, 1999). Similarly, exploring objects via touch is not holistic (as in vision) but involves a characteristically serial feature-by-feature analysis, and the object's position on the receptor surface (the hand) changes during the course of exploration. Primary visual cortex might therefore assist in assembling temporally piecemeal shape cues derived from touch to form a more stable representation of shape.

Multisensory Shape Processing in the Visual System

The neural processes and networks that support multisensory activation of primary sensory areas in humans remain largely undetermined (Schroeder & Foxe, 2005). However, evidence suggests that somatosensory

responses in visual areas are mediated by the combined activity of at least two separate mechanisms: a top–down signal arising from multimodal association areas and direct feed-forward signal from long-range cortico-cortical pathways in primary somatosensory cortex (Merabet et al., 2007). Presumably, top–down signals from high-level areas preserve the spatial organization of haptically acquired features via multisensory coordinate transformations (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005).

The shape-selective responses we observed within LOC are consistent with previous "multimodal" accounts that posit that information from vision and touch converges within LOC (or the "tactile-visual" area LO$_{TV}$)—an area that forms a critical locus for cross-modal visuo-haptic shape representation (Lacey & Sathian, 2011; James & Kim, 2010; Lucan et al., 2010; Lacey et al., 2009; Tal & Amedi, 2009; James et al., 2005, 2007; Peltier et al., 2007; Amedi et al., 2001, 2002, 2005; Beauchamp, 2005). This "convergence zone" is argued to be multi-modal or even "amodal" (Kim & Zatorre, 2011; Amedi et al., 2007), in the sense that shape information is represented in abstract form, irrespective of the origin of sensory input. However, we also observed shape-specific responses in low- and intermediate-level visual processing areas and attributing repetition effects in different areas to different underlying selectivity profiles can be problematic. Our data therefore raise the question of whether cross-modal response properties should also be extended to neural populations within primary visual cortex. Alternatively, although LOC is recruited during visual and haptic shape recognition, this could reflect the activity of interdigitated subpopulations of unimodal cells (Banati, Goerres, Tjoa, Aggleton, & Grasby, 2000).

The shape-selective responses we observed in ventral occipital areas could also reflect processes related to visual imagery (Stokes, Thompson, Cusack, & Duncan, 2009; Pietrini et al., 2004; Kosslyn et al., 1999; Kosslyn, Thompson, Kim, & Alpert, 1995). However, Amedi et al. (2001) found that haptic shape-based responses in LOC could not be accounted for by visual imagery, and evidence from patients with visual object agnosia (Allen & Humphreys, 2009) and early blind individuals (Amedi et al., 2007; Sadato et al., 1996) suggests that visual experience and/or imagery are not necessary for LOC activation. Shape-selective responses in visual cortex could also reflect preparatory attention (Stokes, Thompson, Nobre, & Duncan, 2009), the maintenance of object-specific information within visual working memory (Harrison & Tong, 2009), or the retrieval of form-based information from memory (Ferber, Humphrey, & Vilis, 2003). Indeed, retrieving information from visual or verbal memory has been shown to elicit modality-specific fMRI activation within brain regions involved in the initial sensory processing of the same stimuli (Wheeler, Petersen, & Buckner, 2000). It is possible, therefore, that the shape-selective fMRI responses we observed throughout the visual system during object touch reflects a retrieval-based "reactivation" process that propagates to early sensory areas (Buckner & Wheeler, 2001). Our findings raise the intriguing possibility that such shape-based reactivation processes could extend to primary modality-specific areas as well as across sensory modalities. Top–down effects of expectation or prediction have also been argued to provide a plausible explanation for fMR repetition phenomena (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008).

We used an oddball identification task to ensure continuity of vigilance during the blocks. Our logic was that, to consistently detect the oddball, observers would have to attend to the shape properties of an object presented within a block. It is worth noting that the same number of oddball occurrences was implemented within each type of block. This means that, before the presentation of a stimulus within a block, there is equivalent uncertainty as to whether or not the upcoming stimulus will be an oddball. Equating for uncertainty of oddball occurrence between block types should result in identical levels of vigilance between the different conditions. If, instead, vigilance is determined by the variability of object shape within a block—irrespective of the occurrence of the oddball—then one might expect greater fMRI responses in the Different versus Same blocks. However, this criticism applies to all fMRI adaptation studies that have employed block designs (Summerfield et al., 2008). Furthermore, if the fMRI responses we observed were predominantly because of attentional effects, one might expect strong fMRI responses in fronto-parietal circuits classically involved in attentional control and distractor filtering (Yantis & Serences, 2003; Corbetta & Shulman, 2002). In our whole-brain random effects analysis, however, we observed robust and spatially extensive responses in early and midlevel visual and somatosensory cortices but comparatively reduced responses in frontal and parietal cortex. Nevertheless, it will be informative in future studies to examine directly the extent to which brain regions recruited during visual attentional control match those invoked during haptic shape recognition tasks. Furthermore, future investigations could examine fMRI responses to haptically presented objects that vary parametrically in their shape features (Bodegård, Geyer, Grefkes, Zilles, & Roland, 2001; Hadjikhani & Roland, 1998; Klatzky, Lederman, & Reed, 1989).

Finally, our results do not imply that the visual system is necessary for haptic object recognition, which needs to be tested using intervention approaches. However, we speculate that the visual system is recruited during the recognition of objects via touch because the visual object recognition system is rapid and efficient, and shape cues processed within visual circuits may be relayed back to somatosensory and motor areas to guide ongoing motoric exploration. Whatever the case, our results demonstrate that the visual system is routinely recruited to process the shape of objects explored via touch in normal sighted observers.

REFERENCES

Allen, H. A., & Humphreys, G. W. (2009). Direct tactile stimulation of dorsal occipitotemporal cortex in a visual agnosic. *Current Biology, 19,* 1044–1049.

Amedi, A., Jacobson, G., Hendler, T., Malach, R., & Zohary, E. (2002). Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cerebral Cortex, 12,* 1202–1212.

Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience, 4,* 324–330.

Amedi, A., Stern, W. M., Camprodon, J. A., Bermpohl, F., Merabet, L., Rotman, S., et al. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. *Nature Neuroscience, 10,* 687–689.

Amedi, A., von Kriegstein, K., van Atteveldt, N. M., Beauchamp, M. S., & Naumer, M. J. (2005). Functional imaging of human crossmodal identification and object recognition. *Experimental Brain Research, 166,* 559–571.

Avillac, M., Deneve, S., Olivier, E., Pouget, A., & Duhamel, J. R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience, 8,* 941–949.

Banati, R. B., Goerres, G. W., Tjoa, C., Aggleton, J. P., & Grasby, P. (2000). The functional anatomy of visual-tactile integration in man: A study using positron emission tomography. *Neuropsychologia, 38,* 115–124.

Beauchamp, M. S. (2005). See me, hear me, touch me: Multisensory integration in lateral occipital-temporal cortex. *Current Opinion in Neurobiology, 15,* 145–153.

Bodegård, A., Geyer, S., Grefkes, C., Zilles, K., & Roland, P. E. (2001). Hierarchical processing of tactile shape in the human brain. *Neuron, 31,* 317–328.

Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience, 16,* 4207–4221.

Buchel, C., Price, C., Frackowiak, R. S., & Friston, K. (1998). Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain, 121,* 409–419.

Buckner, R. L., & Wheeler, M. E. (2001). The cognitive neuroscience of remembering. *Nature Reviews Neuroscience, 2,* 624–634.

Burton, H., McLaren, D. G., & Sinclair, R. J. (2006). Reading embossed capital letters: An fMRI study in blind and sighted individuals. *Human Brain Mapping, 27,* 325–339.

Burton, H., Sinclair, R., Wingert, J., & Dierker, D. (2008). Multiple parietal operculum subdivisions in humans: Tactile activation maps. *Somatosensory and Motor Research, 25,* 149–162.

Chouinard, P. A., & Paus, T. (2006). The primary motor and premotor areas of the human cerebral cortex. *Neuroscientist, 12,* 143–152.

Cohen, L. G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., et al. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature, 389,* 180–183.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201–215.

DeValois, R. L., & DeValois, K. K. (1988). *Spatial vision.* New York: Oxford University Press.

Eickhoff, S. B., Amunts, K., Mohlberg, H., & Zilles, K. (2006). The human parietal operculum. II. Stereotaxic maps and correlation with functional imaging results. *Cerebral Cortex, 16,* 268–279.

Eickhoff, S. B., Grefkes, C., Zilles, K., & Fink, G. R. (2007). The somatotopic organization of cytoarchitectonic areas on the human parietal operculum. *Cerebral Cortex, 17,* 1800–1811.

Eickhoff, S. B., Schleicher, A., Zilles, K., & Amunts, K. (2006). The human parietal operculum. I. Cytoarchitectonic mapping of subdivisions. *Cerebral Cortex, 16,* 254–267.

Ferber, S., Humphrey, G. K., & Vilis, T. (2003). The lateral occipital complex subserves the perceptual persistence of motion-defined groupings. *Cerebral Cortex, 13,* 716–721.

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local "association field." *Vision Research, 33,* 173–193.

Gallant, J. L., Shoup, R. E., & Mazer, J. A. (2000). A human extrastriate area functionally homologous to macaque V4. *Neuron, 27,* 227–235.

Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: An fMRI study implies equivalencies between humans and monkeys. *Neuron, 35,* 173–184.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10,* 14–23.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24,* 187–203.

Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience, 3,* 837–843.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica, 107,* 293–321.

Hadjikhani, N., & Roland, P. E. (1998). Cross-modal transfer of information between the tactile and the visual representations in the human brain: A positron emission tomographic study. *Journal of Neuroscience, 18,* 1072–1084.

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature, 458,* 632–635.

James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S., & Goodale, M. A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia, 40,* 1706–1714.

James, T. W., James, K. H., Humphrey, G. K., & Goodale, M. A. (2005). *Do visual and tactile object representations share the same neural substrate?* Mahwah, NJ: Erlbaum.

James, T. W., & Kim, S. (2010). Dorsal and ventral cortical pathways for visuo-haptic shape integration revealed using fMRI. In M. J. Naumer & J. J. Kaiser (Eds.), *Multisensory object perception in the primate brain* (pp. 231–250). New York: Springer.

James, T. W., Kim, S., & Fisher, J. S. (2007). The neural basis of haptic object processing. *Canadian Journal of Experimental Psychology, 61,* 219–229.

Kim, J. K., & Zatorre, R. J. (2011). Tactile-auditory shape learning engages the lateral occipital complex. *Journal of Neuroscience, 31,* 7848–7856.

Kim, S., & James, T. W. (2010). Enhanced effectiveness in visuo-haptic object-selective brain regions with increasing stimulus salience. *Human Brain Mapping, 31,* 678–693.

Kim, S., & James, T. W. (2011). Hierarchical neural pathways of haptic object processing. In M. J. Hertenstein & S. J. Weiss (Eds.), *The handbook of touch: Neuroscience, behavioral, and health perspectives* (pp. 143–160). New York: Springer.

Klatzky, R. L., Lederman, S., & Reed, C. (1989). Haptic integration of object properties: Textures, hardness, and planar contour. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 45–57.

Konen, C. S., & Kastner, S. (2008). Two hierarchically organized neural systems for object information in human visual cortex. *Nature Neuroscience, 11,* 224–231.

Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., et al. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science, 284,* 167–170.

Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature, 378,* 496–498.

Kourtzi, Z., & Connor, C. E. (2011). Neural representations for object perception: Structure, category, and adaptive coding. *Annual Review of Neuroscience, 34,* 45–67.

Kourtzi, Z., Erb, M., Grodd, W., & Bulthoff, H. H. (2003). Representation of the perceived 3-D object shape in the human lateral occipital complex. *Cerebral Cortex, 13,* 911–920.

Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience, 20,* 3310–3318.

Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science, 293,* 1506–1509.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: Monkey and human fMRI studies. *Neuron, 37,* 333–346.

Lacey, S., & Sathian, K. (2011). Multisensory object representation: Insights from studies of vision and touch. *Progress in Brain Research, 191,* 165–176.

Lacey, S., Tal, N., Amedi, A., & Sathian, K. (2009). A putative model of multisensory object representation. *Brain Topography, 21,* 269–274.

Li Hegner, Y., Lee, Y., Grodd, W., & Braun, C. (2010). Comparing tactile pattern and vibrotactile frequency discrimination: A human fMRI study. *Journal of Neurophysiology, 103,* 3115–3122.

Loomis, J. M., Klatzky, R. L., & Lederman, S. J. (1991). Similarity of tactual and visual picture recognition with limited field of view. *Perception, 20,* 167–177.

Lucan, J. N., Foxe, J. J., Gomez-Ramirez, M., Sathian, K., & Molholm, S. (2010). Tactile shape discrimination recruits human lateral occipital complex during early perceptual processing. *Human Brain Mapping, 31,* 1813–1821.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A., 92,* 8135–8139.

Mancini, F., Bolognini, N., Bricolo, E., & Vallar, G. (2011). Cross-modal processing in the occipitotemporal cortex:

A TMS study of the Muller–Lyer illusion. *Journal of Cognitive Neuroscience, 23,* 1987–1997.

Merabet, L. B., Swisher, J. D., McMains, S. A., Halko, M. A., Amedi, A., Pascual-Leone, A., et al. (2007). Combined activation and deactivation of visual cortex during tactile sensory processing. *Journal of Neurophysiology, 97,* 1633–1641.

Merabet, L., Thut, G., Murray, B., Andrews, J., Hsiao, S., & Pascual-Leone, A. (2004). Feeling by sight or seeing by touch? *Neuron, 42,* 173–179.

Meyer, K., Kaplan, J. T., Essex, R., Damasio, H., & Damasio, A. (2011). Seeing touch is correlated with content-specific activity in primary somatosensory cortex. *Cerebral Cortex, 21,* 2113–2121.

Meyer, K., Kaplan, J. T., Essex, R., Webber, C., Damasio, H., & Damasio, A. (2010). Predicting visual stimuli on the basis of activity in auditory cortices. *Nature Neuroscience, 13,* 667–668.

Naumer, M. J., Ratz, L., Yalachkov, Y., Polony, A., Doehrmann, O., van de Ven, V., et al. (2010). Visuohaptic convergence in a corticocerebellar network. *European Journal of Neuroscience, 31,* 1730–1736.

Peltier, S., Stilla, R., Mariola, E., LaConte, S., Hu, X., & Sathian, K. (2007). Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. *Neuropsychologia, 45,* 476–483.

Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., et al. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences, U.S.A., 101,* 5658–5663.

Sadato, N., Pascual-Leone, A., Grafman, J., Deiber, M. P., Ibanez, V., & Hallett, M. (1998). Neural networks for Braille reading by the blind. *Brain, 121,* 1213–1229.

Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Deiber, M. P., Dold, G., et al. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature, 380,* 526–528.

Schroeder, C. E., & Foxe, J. (2005). Multisensory contributions to low-level, "unisensory" processing. *Current Opinion in Neurobiology, 15,* 454–458.

Stilla, R., & Sathian, K. (2008). Selective visuo-haptic processing of shape and texture. *Human Brain Mapping, 29,* 1123–1138.

Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top–down activation of shape-specific population codes in visual cortex during mental imagery. *Journal of Neuroscience, 29,* 1565–1572.

Stokes, M., Thompson, R., Nobre, A. C., & Duncan, J. (2009). Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proceedings of the National Academy of Sciences, U.S.A., 106,* 19569–19574.

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience, 11,* 1004–1006.

Tal, N., & Amedi, A. (2009). Multisensory visual-tactile object related network in humans: Insights gained using a novel crossmodal adaptation approach. *Experimental Brain Research, 198,* 165–182.

Tamè, L., Braun, C., Lingnau, A., Schwarzbach, J., Demarchi, G., Li Hegner, Y., et al. (2012). The contribution of primary and secondary somatosensory cortices to the representation of body parts and body sides: An fMRI adaptation study. *Journal of Cognitive Neuroscience, 24,* 2306–2320.

Vasconcelos, N., Pantoja, J., Belchior, H., Caixeta, F. V., Faber, J., Freire, M. A., et al. (2011). Cross-modal responses in the primary visual cortex encode complex objects and correlate with tactile discrimination. *Proceedings of the National Academy of Sciences, U.S.A., 108,* 15408–15413.

Weisser, V., Stilla, R., Peltier, S., Hu, X., & Sathian, K. (2005). Short-term visual deprivation alters neural processing

of tactile form. *Experimental Brain Research, 166,* 572–582.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences, U.S.A., 97,* 11125–11129.

Woodhead, Z. V., Wise, R. J., Sereno, M., & Leech, R. (2011). Dissociation of sensitivity to spatial frequency in word and face preferential areas of the fusiform gyrus. *Cerebral Cortex, 21,* 2307–2312.

Yantis, S., & Serences, J. T. (2003). Cortical mechanisms of space-based and object-based attentional control. *Current Opinion in Neurobiology, 13,* 187–193.

Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature, 401,* 587–590.

Zhang, M., Weisser, V. D., Stilla, R., Prather, S. C., & Sathian, K. (2004). Multisensory cortical processing of object shape and its relation to mental imagery. *Cognitive, Affective and Behavioral Neuroscience, 4,* 251–259.