Are visual texture-selective areas recruited during haptic texture discrimination?

Samantha K. Podrebarac, Melvyn A. Goodale, Jacqueline C. Snow

A R T I C L E  I N F O

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Shape and texture provide cues to object identity, both when objects are explored using vision and via touch (haptics). Visual shape information is processed within the lateral occipital complex (LOC), while texture is processed in medial regions of the collateral sulcus (CoS). Evidence indicates that the LOC is recruited during both visual and haptic shape processing. Here we used functional magnetic resonance imaging (fMRI) to examine whether ‘visual’ texture-selective areas are similarly recruited when observers discriminate texture via touch. We used a blocked design in which participants discriminated either the texture or shape of unfamiliar 3-dimensional (3D) objects, via vision or touch. We observed significant haptic texture-selective fMRI responses in medial occipitotemporal cortex within areas adjacent to, but not overlapping, those recruited during visual texture discrimination. Although areas of ventromedial temporal cortex are recruited during visual and haptic texture perception, these areas appear to be spatially distinct and modality-specific.

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Introduction

Shape elements serve as important cues for object perception, but material properties also provide additional information that can facilitate recognition. For example, although an orange and a tennis ball have similar geometrical properties (such as shape, size, and curvature) they have different material properties (such as surface texture, roughness, stickiness, and compliance) that enable them to be accurately distinguished. Texture information can be extracted from the surface of objects using either vision or touch and provides a salient cue to object identity. Although the behavioral and neural correlates of multisensory shape perception have received detailed investigation, surprisingly little is known about whether surface texture is represented similarly in vision and touch (see Whitaker et al., 2008 for review).

The vast majority of human imaging studies on shape-based processing have focused on localizing regions of the brain that are involved in visual shape perception. One region that has consistently been implicated in visual shape processing is the lateral occipital cortex (LOC; for review see Grill-Spector and Malach, 2004). Although there have also been many imaging studies of color perception (for review, see Tanaka et al., 2001), the visual perception of surface texture has received comparatively less investigation. Recently, however, several imaging studies have reported a medial-to-lateral spatial division in human ventral temporal cortex, for the processing of visual surface texture versus shape cues, respectively. Specifically, Cant and Goodale (2007) found that areas within the collateral sulcus (CoS) and other more medial areas of the ventral stream are involved in the visual perception of texture, while more lateral regions, including LOC, are involved in visual shape processing (Cant and Goodale, 2007; Cant et al., 2009). These findings converge with similar earlier observations by Peuskens et al. (2004).

Behavioral and imaging studies with neuropsychological patients also provide convergent support for the involvement of ventro-medial regions of occipitotemporal cortex in visual texture perception and lateral occipitotemporal regions in visual shape perception. Cavina-Pratesi et al. (2010) examined texture and shape perception in two patients; D.F., who has bilateral lesions in the lateral occipital cortex but no damage to medial occipitotemporal regions, and patient M.S. who shows a complimentary lesion pattern to D.F. — intact LOC, but bilateral lesions in medial occipital areas. When attending to visual texture, D.F. showed fMRI activation in medial occipital areas, such as the CoS — the same region where M.S.’s lesion was located. Conversely, while attending to shape, M.S. showed activation in LOC, where D.F.’s lesion is located. Behavioral results converged nicely with the activation pattern: D.F. performed well on texture discrimination and at chance on the shape task, whereas M.S. showed the reverse pattern.

There is accumulating evidence from fMRI that laterally-located ‘visual’ shape-selective areas are also invoked during haptic shape processing (Allen and Humphreys, 2009; Amedi et al., 2001, 2002, 2005; Bonda et al., 1996; Delibert et al., 1999; Grefkes et al., 2002; James et al., 2002; Naumer et al., 2010; Peltier et al., 2007; Pietrini et al., 2004; Prather et al., 2004; Reed et al., 2004; Snow et al., in press; Stilla and Sathian, 2008; Stoesz et al., 2003; Tal and Amedi, 2009; Zhang et al., 2004). Most notably, Amedi et al. (2001, 2002)
demonstrated that a sub-region of the LOC, which they termed the ‘lateral occipital tactile–visual area’ (LOtv), was activated both when participants palpated objects with different shapes, and when they viewed the different objects. These findings have prompted the popular view that the lateral occipital area constitutes a region of multisensory cortex, facilitating visuo-haptic shape representation (Amedi et al., 2002, 2005; Lacey et al., 2009; Lucan et al., 2010; Sathian et al., 2011). Here, we asked an analogous question: whether medially-located areas implicated in visual perception of surface texture are also recruited during haptic perception of object surface texture. Although there have been a number of imaging studies that have examined haptic texture identification, these studies have focused largely on tactile routines (Simões-Franklin et al., 2011) and somatosensory neural correlates of unimodal tactile perception (Nelson et al., 2004; O’Sullivan et al., 1994; Servos et al., 2001; for review see Kaas and Collins, 2003). Other studies that have examined texture perception more directly across vision and touch, have presented the visual and haptic stimuli in different formats (i.e., images in vision, and real objects via touch) and in different spatial locations with respect to the head (i.e., visual stimuli are viewed via a mirror attached to the head coil, while haptic stimuli are palpated near the waist) (Eck et al., 2013).

In an fMRI study of visuo-haptic processing of surface shape and texture, Stillia and Sathian (2008) found bilateral haptic-only texture-selectivity in the parietal operculum and posterior insula, in addition to overlapping haptic and visual texture-activation in the right medial occipital cortex (MOC). This group argued that an absence of correlation between fMRI responses during visual vs. haptic texture perception in the MOC reflected the existence of unimodal neurons in this area, rather than multisensory cortex. In a later examination of visual and haptic perception of location and texture, Sathian et al. (2011) found bilateral haptic texture-selectivity in parietal operculum and posterior visual cortex. They also reported bimodal activity in some regions of posterior visual cortex, left inferior frontal cortex, and the MOC. Interestingly, this study did not report any visual or haptic response to texture in the collateral sulcus, as was found in previous studies (Cant and Goodale, 2007; Cant et al., 2009; Eck et al., 2013; Peuskens et al., 2004; Puce et al., 1996). The reason for the apparent discrepancy in involvement of CoS in texture-based processing is unclear. Notably, however, Stillia and Sathian (2008) explored haptic and visual perception of texture and shape using two different sets of object stimuli; one consisted of objects of the same shape that differed in their textural features, and the other was comprised of objects that differed in their shape, but not their surface texture (rather than objects that varied in both shape and texture, as is typically the case when exploring objects in the natural environment). Similarly, Stillia and Sathian (2008) used 3-dimensional (3D) stimuli for the haptic condition, but 2-dimensional (2D) images for the visual condition. This may be problematic because activation patterns in occipitotemporal cortex may be influenced by the ‘graspability’ of an object (Gallivan et al., 2013). Ideally, therefore, an optimal design for examining the possible co-recruitment of texture-selective regions in ventro-medial temporal cortex during vision versus touch would be to use stimuli that have a similar 3-dimensional structure in both the visual and haptic conditions.

In the current study, we used fMRI to examine the brain regions involved in visual and haptic recognition of surface texture and shape. Importantly, participants explored physically identical stimuli in both the haptic and the visual conditions. Also, we used a unique head tile configuration so that the spatial location of the stimuli, with respect to the head, remained constant across vision and touch blocks. We were primarily interested in whether or not medial ventral-stream structures implicated in the visual perception of surface texture were also engaged when participants explored the same textures via touch. To do this, we used a block-design fMRI study in which participants attended to either the “shape” or “texture” of objects in a given block. fMRI responses to shape and texture were examined using vision or touch in separate epochs. For trials in each sensory modality, we contrasted fMRI activation during texture blocks with that observed in shape blocks, to reveal areas of the brain that were involved in the perception of object texture in vision, and via touch. We also examined brain regions that were involved in visual versus haptic processing of object shape. We found that although a similar cortical region of medial occipitotemporal cortex was activated during both haptic and visual texture judgments, the areas of activation were not overlapping. Anterior and middle regions of the collateral sulcus (mCoS, pCoS) were activated bilaterally during visual-texture judgments (replicating previous studies), whereas during haptic-texture judgments, we observed activation contralateral to the palpating hand in the left hemisphere (LH) in an area adjacent to, but slightly posteriorly to the analogous region of pCoS activated during visual texture discrimination.

Methods

Participants

Participants were 15 right-handed individuals aged 19 to 32 (M = 27 SE = 1; 6 female) with normal or corrected-to-normal vision. Informed consent was collected in accordance with the guidelines approved by the University of Western Ontario Health Sciences Research Ethics Board and in accordance with the standards outlined in the 1964 Declaration of Helsinki. Participants were compensated $25 for each hour of their time.

Stimuli

The stimuli were 3D shapes made of hard white plastic casting resin (Fig. 1a). Two different texture patterns were combined with two different 3D shapes to create four distinguishable object stimuli; one shape was a 3D pyramid and the other was a 3D quadrilateral. One texture consisted of rows of indented dots positioned at equal spacing along all surfaces of the object. The second texture comprised of rows of indented lines, also present at equal spacing along each face of the object.

Experimental procedure and design

During the experiment, the participants lay supine within the scanner bore, with the head secured within the lower half (6 elements) of a 12-channel head coil. A flex coil was positioned over the front of the head to increase signal:noise in frontal areas. Critically, the head coil was tilted forward by 30° to enable direct viewing of the stimuli. The stimulus objects were presented upon a platform mounted above the participants’ waist. The height of the platform was set such that participants could view the stimuli comfortably, without requiring eye strain or head motion (Fig. 1b). The stimulus workspace was illuminated by an LED fixed to the head-coil, and by a built-in light within the bore of the scanner. All stimuli were presented within reach of the right hand. The orientation of the objects on each trial was varied randomly across five different orientations along the z-axis so that each shape was presented an equal number of times in each orientation across experimental epochs.

The same block-design was employed in the vision and haptic epochs. In vision epochs, participants examined the three-dimensional objects visually; in haptic epochs, participants palpated the stimulus objects. In shape blocks, participants were explicitly instructed to attend to the shape of the objects; during texture blocks, participants were instructed to attend to the texture of the objects. Each epoch started with an auditory cue instructing participants to either “look” at or “touch” the objects for the duration of the epoch. Another auditory cue was delivered at the onset of each block indicating to the participant whether they were to attend to the “texture” or to the “shape” of the objects. In each block, five consecutive pairs of objects were presented. After each pair, participants received an auditory cue, which served as a signal for them to make a button-press response. The participants’ task was to indicate whether the preceding pair of objects were the
same or different with respect to their texture, or shape (as per the block instructions). Responses were made using the left and right keys on an fMRI-compatible response-box using the index finger of the left hand. On each trial, the stimuli were presented for 2 s each, followed by a 2 s inter-trial rest interval (Figs. 2a, b). In texture blocks, the objects varied in their texture, while their shape remained constant. The reverse was the case for shape blocks; stimuli varied in their shape but surface texture remained constant. Six blocks were included in each epoch. The duration of each block in both the vision and haptic epochs was 50 s, and blocks were separated by 16 s of baseline (rest). During baseline

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**Fig. 1.** (a) Stimuli used in the experiment. Two textures (rows of indented lines and rows of indented dots) were combined with two shape exemplars (pyramid and asymmetrical quadrilateral) to create the 3D object stimuli used in the experiment. (b) Experimental setup. Participants lay supine in the scanner with the head firmly secured within the head coil. Critically, the head coil was tilted forward at an angle of ~30° to enable direct viewing of the objects. Stimuli were presented on a black platform fixed above the participants’ waist. LCD PLATO goggles (modified for use within the fMRI environment) were used to control stimulus visibility and trial duration. During vision epochs (left panel) the PLATO lenses became transparent (open) for the duration of the trial, before returning to their opaque (closed) state. While the lenses were open, participants were instructed to maintain fixation upon an LED positioned above the stimulus. During haptic epochs (right panel) the PLATO goggles remained closed throughout all trials and participants palpated the stimuli positioned on the table with their dominant right hand. Participants were trained to palpate stimuli using a subtle rotation of the forearm, which minimized head motion. In both the vision and haptic epochs, participants received an auditory cue to indicate the start and end of each trial.

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**Fig. 2.** Stimulus sequence and experimental design. (a) An example of six blocks in a vision epoch. In half of the blocks participants were instructed to attend to object shape, and in the remaining blocks participants attended to object texture. (b) Example trial sequence within a “shape” block. Each block started with an auditory cue indicating the block condition (attend shape/texture). Participants were then presented with sequential pairs of objects (2 s each), and each stimulus pair varied either in their texture, or shape. Participants made a button-press same/different response using the left hand. Illustrated in (b) are two sample trials within a block. In the experiment, each block consisted of five trials. Stimulus timing parameters were identical for shape and texture blocks, in the haptic and visual epochs.
periods, the PLATO goggles remained closed and participants were instructed to keep their eyes closed.

The same paradigm was used for both vision and haptic epochs. An auditory “go” cue (beep) signaled trial onset, and a second auditory “stop” cue signaled the end of the trial. An identical auditory cue was presented during both vision and haptic epochs. In vision epochs, stimulus viewing time was controlled using modified crystal LCD PLATO goggles (Translucent Technologies: www.translucent.ca/plato). During haptic epochs, the goggles remained closed throughout the entire scan. When exploring objects in the haptic condition, participants were encouraged to keep their eyes closed, to use a natural palpating motion, and to refrain from moving or lifting the objects. In the vision condition, participants were instructed to fixate on a small red LED light located just above the object on the table during each trial. Epoch order was counter-balanced within and between observers using a balanced Latin square design (Bradley, 1958) and response button mapping was counterbalanced across participants. On average, each participant completed five haptic epochs and five vision epochs and the total experimental scan time was 1 h and 36 min (plus approximately 1 h of setup time).

**MRI acquisition**

The experiment was carried out on a 3-Tesla Siemens Magnetom Tim Trio imaging system at the Robarts Research Institute at Western University (London, Ontario, Canada). The functional data was acquired with a T2*-weighted single-shot gradient-echo echo-planar imaging sequence with interleaved slice acquisition. Foam padding was used to

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**Fig. 3.** (a) Significant visual texture-selective activation was observed in the cingulate gyrus (CG) and insula (INS) of the right hemisphere, and bilaterally along middle and posterior regions of the collateral sulcus (mCoS and pCoS). Visual texture-selective areas were isolated using the contrast [visual texture > visual shape] (p < 0.005, corrected). The level of each in-plane slice in the z (vertical) plane is demarcated here (and in all subsequent figures) on the sagittal anatomical image, with in-plane slices shown from dorsal (left) to ventral (right). (b) Significant fMRI responses to haptically explored textures (vs. shapes) were observed in the right middle frontal gyrus (MFG), left insula (INS), and in the posterior region of the left collateral sulcus (pCoS), contralateral to the palpating hand. (c) Texture-selective fMRI responses during visual and haptic exploration lay adjacent, but did not overlap, within ventral temporal cortex, even at a relaxed statistical threshold (p < 0.01, uncorrected). Texture-selective fMRI activation for haptic (shown in blue) and visual (shown in yellow) epochs. Visual texture-selective responses were observed bilaterally along mCoS and pCoS. Conversely, while haptic texture-selective responses were observed in the left hemisphere contralateral to the palpating hand, this activation was limited to mCoS.
minimize head motion in the tilted head-coil and a strap was used to minimize upper arm motion. The parameters for obtaining functional data were: field of view (FOV) = 210 mm × 210 mm; in-plane resolution = 3.0 mm × 3.0 mm, slice thickness = 3.5 (zero gap); 36 axial slices; echo time (TE) = 30; repetition time (TR) = 2000 ms; flip angle (FA) = 78°. Functional data were aligned to high-resolution anatomical images obtained using a 3D T1-weighted MP RAGE sequence (TE = 2.98 ms TR = 2300 ms; TI (inversion time) = 900 ms; FA = 9°; 192 contiguous slices of 1 mm thickness; FOV = 240 mm × 256 mm).

Data pre-processing and analysis

The data were pre-processed and analyzed using Brain Voyager QX (Version 1.10.2, Brain Innovation, Maastricht, Netherlands). Following slice scan-time correction, functional data were assessed for head motion and/or magnet artifacts by viewing cine-loop animation and examining motion detection parameter plots following 3D motion correction algorithms on the untransformed two-dimensional data. All functional data were aligned to the volume acquired closest in time to the anatomical scan. Data from one participant was excluded due to excessive head motion in the haptic epochs (greater than 3 cm within an epoch), and data from one additional participant was excluded due to the presence of severe scanner artifacts in the data. Functional data were pre-processed with high-pass temporal filtering to remove frequencies below 3 cycles/epoch. Functional volumes were then superimposed on anatomical brain images transformed into Talairach space (Talairach and Tournoux, 1988).

Voxel-wise random-effects general linear model (GLM) analyses were performed on the averaged data of 13 participants, separately for the haptic and visual epochs. A 6-mm Gaussian kernel was used in the spatial smoothing of the functional images in the epochs, and separate predictor functions were generated for each experimental condition. Predictor functions were generated by convolving a rectangular wave function with a standard haemodynamic response function. Data were processed using a percent signal change (%SC) transformation. We performed a series of statistical contrasts on the group data, each designed to localize visual and haptic regions selective for shape and for texture. For each contrast, group activation maps were set to a minimum statistical threshold (p < 0.005). Cluster-size corrections were applied using Brain Voyager's cluster threshold estimation plug-in (p < 0.05).

Based on the results of the whole-brain voxelwise analyses, we performed follow-up region-of-interest (ROI) analyses to investigate the extent to which visual texture-selective areas showed sensitivity to haptic texture (versus shape), and vice versa for haptic texture-selective areas. ROIs consisted of the texture-selective areas identified in the group-based RFX voxelwise contrasts in the vision, and the haptic epochs. Sensitivity to visual or haptic texture in each ROI was examined using an RFX GLM to contrast texture versus shape responses. Data for the contrast were the smoothed %SC data from independent epochs from the alternate sensory modality (i.e., haptic, or visual, epochs respectively).

Results

Whole brain random effects analysis

Texture versus shape

As expected, participants made no errors on the shape or texture discrimination tasks, either in vision or touch. First, to isolate visual texture-selective brain areas, we compared fMRI responses on visual texture versus shape trials using the contrast [visual texture > visual shape]. Significant fMRI activation was observed in the right cingulate gyrus (CG) and the insular cortex (INS) of the right hemisphere. Consistent with previous studies in vision, we also observed texture-selective responses bilaterally within the CoS (Fig. 3a). It should be noted that the CoS is a lengthy structure that spans almost the entire surface of ventrotemporal cortex. CoS extends from its caudal end in the occipital lobe, between the lingual and fusiform gyri, anteriorly to form the division between parahippocampal and tempo-occipital gyri (Ono et al., 1990). The activation we observed for visual textures (versus shape) lies caudally within the sulcus, within the middle (mCoS) and posterior (pCoS) regions of the sulcus, posterior to the pons (Fig. 3a; Table 1).

Next, haptic texture-selective brain regions were isolated by contrasting fMRI responses on haptic texture versus shape trials [haptic texture > haptic shape]. This contrast revealed significant activation in the right middle frontal gyrus (MFG), left insula, and in pCoS, dorsal to the activation we found for visual textures (Fig. 3b; Table 1). Importantly, the clusters identified in the visual-texture contrast did not overlap with those of the haptic-texture contrast. Subsequent examination of the visual vs. haptic texture-selective activation at a relaxed statistical threshold (p < 0.01, uncorrected) confirmed the same result; although haptic and visual texture-selective responses were revealed along mCoS and pCoS, these areas of activation lay adjacent to one another and did not overlap (Fig. 3c).

Shape versus texture

We next examined brain regions that showed sensitivity to the shape of our real-object stimuli during exploration in vision, and in touch (Fig. 4). Shape-selective areas were isolated using the contrast [visual shape > visual texture] in vision epochs, and the contrast [haptic shape > haptic texture] in haptic epochs. Significant visual shape-selective fMRI responses were observed bilaterally in the LOC and the left middle and superior temporal gyri (MTG, STG) (see Table 2). Visual shape-selective responses were also observed within the parietal operculum (PO) in the vicinity of secondary somatosensory cortex (SII), and within early visual areas (Fig. 4a). Haptic shape-selective fMRI responses were limited to the intraparietal sulcus (IPS) in the RH (Fig. 4b). Overall activation in the haptic shape > texture contrast was less extensive than the comparable contrast in vision, and we did not observe significantly greater shape (vs. texture) responses in the LOC during haptic shape exploration.

Texture versus baseline rest

Given that our texture stimuli were regular geometric patterns, it is possible that observers identified these stimuli as being ‘shape-like’ (possibly explaining the lack of LOC activation in haptic shape vs. texture epochs). To examine fMRI responses during our texture task more broadly, we contrasted activation during visual texture blocks with baseline rest, and during haptic texture blocks with baseline rest (RFX, p < 0.005, corrected). As expected, the contrast of texture versus rest in vision blocks produced robust activation throughout the ventral visual stream (including LOC). Haptic texture perception versus rest elicited above-threshold fMRI responses within dorsal somatosensory and motor networks. The contrast of haptic texture versus rest also

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revealed activation within the LOC, indicating that this area was activated both during visual and haptic texture perception. Interestingly, an analogous contrast of shape and of texture blocks in vision versus rest showed a similar involvement of LOC in both tasks. Activation for haptically-explored textures (but not texture perception in vision) was observed in the cerebellum, immediately adjacent and medial to the visual texture responses in ventral temporal cortex — probably reflecting motor-based planning. Strong overlap in visual and haptic fMRI responses to texture vs. rest were observed bilaterally within parietal and frontal cortex, the LOC, and in early visual cortex near the calcarine sulcus (Fig. 5). Importantly, however, we again found no overlap between fMRI responses to surface texture in vision and touch in ventromedial temporal cortex (including the collateral sulcus, the fusiform, or lingual gyrus).

ROI analyses

We next used a region-of-interest approach to determine whether or not brain areas involved in the analysis of visual surface texture also showed selectivity to textures explored via touch. The regions of interest for this analysis were brain areas that showed above-threshold activation to visual texture vs. shape in the (independent) vision epochs of the whole-brain voxel-wise group-based RFX analysis (i.e., CG, INS, mCoS, pCoS) described above. Within each ROI, we ran the contrast [haptic texture > haptic shape] using data from the haptic epochs. Consistent with the findings of the whole-brain voxel-wise analyses in which we found adjacent, but not overlapping, texture-selective responses in vision versus touch, we did not observe texture-selective fMRI responses in any of the visual texture-selective ROIs (right CG (t = 1.90, p = 0.08); right INS (t = 0.98, p = 0.35); left CoS (t = 0.63, p = 0.54; t = 0.65, p = 0.53), and right CoS (t = 1.14, p = 0.28; t = −0.80, p = 0.44).

Finally, we ran a complimentary region-of-interest analysis to determine whether areas showing above-threshold haptic texture-selective activation in the whole-brain voxel-wise analysis also showed selectivity for visual textures (i.e., MFG, INS, pCoS). A contrast of [texture > shape] using data from the (independent) visual epochs revealed no significant differences in any haptic ROIs (right MFG (t = −1.0, p = 0.33), the left INS (t = 1.75, p = 0.12) or in the left pCoS (t = 0.24, p = 0.81)).

In summary, during visual analysis of surface texture, we found greater activation for texture versus shape within medial regions of the collateral sulcus, as expected based on prior literature (Cant and Goodale, 2007; Cant et al., 2009; Cavina-Pratesi et al., 2010). Surprisingly, however, fMRI responses to haptically-explored textures (vs. haptic shape) did not overlap with regions identified during visual texture (vs. visual shape) perception. Although left pCoS was activated when participants perceived texture (vs. shape) via touch, this region lay adjacent to, but did not overlap with, texture-selective areas in vision. Analyses of visual and haptic texture perception versus baseline (rest) also revealed no regions of co-activation within medial ventrottemporal cortex. Taken together, our results suggest that although medial ventrottemporal cortex is recruited in the analysis of surface texture in both vision and touch, there is nevertheless a degree of spatial specificity between neural populations that are sensitive to visual versus haptic inputs. Multivariate fMRI techniques may reveal inter-digitation between different sensory representations of surface texture that were not revealed using a univariate approach, although this would require more trials than we were able to acquire in the current study using manual presentation of real objects.

We observed discrete, non-overlapping regions of activation for haptic and visual texture within the CoS. One reason that haptic and visual representations of surface texture may be spatially distinct in ventromedial temporal cortex is that each modality is capable of coding

**Table 2**

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**Discussion**

We used fMRI to investigate whether medial occipitotemporal regions of visual cortex that are known to be involved in the perception of visual surface-texture, are also involved in the perception of surface-texture via touch. We observed bilateral visual texture-selective responses in the middle and posterior regions of the collateral sulcus consistent previous imaging studies in vision (Cant and Goodale, 2007; Cant et al., 2009; Cavina-Pratesi et al., 2010). Surprisingly, however, fMRI responses to haptically-explored textures (vs. haptic shape) did not overlap with regions identified during visual texture (vs. visual shape) perception. Although left pCoS was activated when participants perceived texture (vs. shape) via touch, this region lay adjacent to, but did not overlap with, texture-selective areas in vision. Analyses of visual and haptic texture perception versus baseline (rest) also revealed no regions of co-activation within medial ventrottemporal cortex. Taken together, our results suggest that although medial ventrottemporal cortex is recruited in the analysis of surface texture in both vision and touch, there is nevertheless a degree of spatial specificity between neural populations that are sensitive to visual versus haptic inputs. Multivariate fMRI techniques may reveal inter-digitation between different sensory representations of surface texture that were not revealed using a univariate approach, although this would require more trials than we were able to acquire in the current study using manual presentation of real objects.

We observed discrete, non-overlapping regions of activation for haptic and visual texture within the CoS. One reason that haptic and visual representations of surface texture may be spatially distinct in ventromedial temporal cortex is that each modality is capable of coding
different types of object surface properties. For example, using vision, one can determine that a surface is shiny without perceiving it as being sticky; the percept of “stickiness” occurs only when one manually feels the surface. Additionally, behavioral research suggests that at least for perceiving surface texture, bimodal processing is no better than unimodal (Bjorkman, 1967; Guest and Spence, 2003; Heller, 1982; Lederman and Abbott, 1981; Picard, 2007). Further, the difference in spatial scale between shape and texture representations may differ between vision and touch because the spatial resolution of the two modalities also differs. Visual and haptic texture (vs. shape) perception also resulted in activation of non-overlapping regions of frontal cortex and insula. Sathian et al. (2011) also found texture-selective fMRI responses in the insula, in line with previous studies in monkeys (Robinson and Burton, 1980), although they acknowledged that further research was required to determine the nature of insular involvement in texture perception. The cingulate gyrus involvement in haptic texture perception could reflect task-related components such as error detection, or the online monitoring of task performance (Carter et al, 1998).

The proximity of haptic and visual responses to surface texture in medial ventral temporal cortex suggests, however, that these processes may be closely linked (Eck et al., 2013). For example, perceiving a surface property in vision may invoke previous haptic experiences with the same surface (Cant and Goodale, 2007). Indeed, in real-world contexts we rarely perceive texture using vision or touch alone. More often, percepts arising from touch are accompanied, if not motivated, by initial visual perception (Eck et al., 2013; Schifferstein and Cleiren, 2005; Whitaker et al., 2008). Lacey et al. (2010) argue that multisensory representations of surface properties such as texture are likely to include information derived from modality-independent representations. It is possible that the haptic activation we observed in the ‘visual processing stream’ reflects a process of cognitive association between the visual appearance of objects and their material properties that facilitates recognition. A similar argument has been made for the close spatial relationship between neural responses to acoustic and somatosensory surface properties in ventral temporal cortex. Using fMRI, Arnott et al. (2008) reported that a region within right anterior parahippocampal cortex was activated when observers listened to sounds associated with the handling of different materials (such as paper and tinfoil) but a more posterior region was activated when observers perceived material properties using vision. Taken together, the available evidence suggests that different unimodal areas of occipitotemporal cortex are specialized for processing and/or representing the material properties of objects, based on the sensory modality (vision, touch, audition) with which information is perceived or invoked via learned associations. Further, the fact that we observed non-overlapping fMRI response to visual and haptic textures in ventral temporal cortex argues against the possibility that observers relied upon visual imagery to discriminate the haptic textures (Amedi et al., 2001; Merabet et al., 2007; Sathian et al., 1997). Haptic texture perception elicited significant activation only in the left hemisphere (contralateral to the palpating hand) rather than bilaterally, as might be predicted using an imagery account.

Eck et al. (2013) compared cortical activation for matching versus non-matching surface textures similar to those used here and found that analogous cortical networks were activated during both visual and haptic texture perception, including the collateral sulcus, posterior fusiform and lingual gyri. Simultaneous bimodal exploration of textures in vision and touch in their study yielded parametric texture-selective responses in early occipital cortex. The authors argued that their results supported strong cross-modal interactions between visual and haptic texture processing. In our study, textures were presented either in vision, or touch, but not in both modalities simultaneously. Temporal synchronicity could therefore be an important factor in driving texture-selective responses in ventral temporal cortex. What is unclear however is why Eck et al. (2013) found overlap of unimodal fMRI responses to visual and haptic textures in collateral sulcus and other ventral temporal regions, but we did not — even in the contrasts of texture perception versus rest in each modality. Notably, Eck et al. (2013) used 2D images of textures viewed via a mirror, whereas we used real visual textures that were identical to the palpated stimuli, and there was a direct spatial correspondence between the visual and haptic workspace (owing to our head tilt setup). It is possible that the act of perceiving 2D textures in a different spatial reference frame in touch versus vision elicits visual imagery in the haptic task (perhaps due to differences in task difficulty or updating of co-ordinate transformations between the modalities) thereby producing ‘co-activation’ in texture-processing regions of ventral temporal cortex.

In the current study we used simple textures that consisted of embedded patterns of dots or lines. Surface texture can range from simplified monochrome patterns, such as those employed here (Eck et al., 2013), to more complex textures (Cavina-Pratesi et al., 2010) and realistic colored surfaces (such as wood-grain or marble, Cant and Goodale, 2007; Cant et al., 2009). Simple textures provide a degree of control over stimulus properties and task difficulty across sensory modalities (see also Cavina-Pratesi et al., 2010). More naturalistic textures convey information about fine-scale and sometimes irregular changes in surface structure, and might therefore be processed differently from artificial exemplars. A previous haptic study by Sathian et al. (2011) employed naturalistic textures (i.e., real materials) and reported
multisensory visuo-haptic texture responses within the left lingual gyrus of inferior temporal cortex, but not in the collateral sulcus as was observed here and in previous studies of texture perception in vision (Cant and Goodale, 2007; Cant et al., 2009; Peuskens et al., 2004; Puce et al., 1996). Future studies might begin to resolve some of these issues by using a greater range of stimuli and more naturalistic surface textures.

Importantly, given that our stimuli conveyed texture by dots or lines of 2–4 mm in regular geometric patterns, the textures may have been identified as ‘shapes’ at a local spatial scale. The shape vs. texture contrasts could therefore reflect activation associated with shifting attention between shape cues at global vs. local spatial scales, respectively. This could explain the lack of haptic shape (vs. texture) fMRI responses in LOC, if both the shape and texture tasks involved shape-related processes (Kassuba et al., 2011). This may also explain the shape (vs. texture) activity we observed in visual cortex, as striate and extrastriate areas are known to be important for integrating local shape details into global contours (Field et al., 1993), and show selectivity for object shape via touch (Snow et al., in press). Similarly, we observed IPS activity in the RH during haptic shape vs. texture perception, and the IPS has been associated with shifts in attention between global vs. local form (Weissman and Woldorff, 2005). On the contrary, however, we did observe bilateral LOC activation in our visual shape vs. texture contrast (Kourtzi and Kanwisher, 2001). The above formulation therefore requires an explanation as to why global (shape)/local (texture) attention shifts should be greater when observers touch objects than when they are viewed. Further, several studies that have reported robust activation in the LOC during object touch have used common objects (Amedi et al., 2002; Kassuba et al., 2011), rather than novel shapes. James et al. (2002) found that haptic LOC activation is modulated by the participants’ level of familiarity with an object. Therefore the weaker response of LOC during shape exploration in our study may be related to object novelty/ unfamiliarity. An alternative explanation for these data is that the LOC could be involved in processing or integrating information about the surface structure of objects, in addition to shape. In fact, this does not seem unreasonable, given that textual cues in both the visual and haptic modalities can provide important information about object shape. The global/local attention argument also predicts a strong overall reduction in texture-related fMRI responses, since both tasks putatively involved shape perception. On the contrary, however, we observed texture-related fMRI responses in expected areas of ventral temporal cortex. The IPS activation we observed during haptic shape (vs. texture) perception is also consistent with the findings of a number of fMRI studies demonstrating shape-related IPS responses during object touch (Amedi et al., 2001, 2002; Deibert et al., 1999; Greffkes et al., 2002; Miquee et al., 2007; O’Sullivan et al., 1994; Pettier et al., 2007; Reed et al., 2004; Snow et al., in press; Stoesz et al., 2003) and neurophysiological evidence in nonhuman primates (Murata et al., 2000). Notably, two of the fMRI studies of haptic shape encoding in humans reported robust IPS activation when eye movements were controlled using a visual fixation point during the haptic events (Greffkes et al., 2002; Snow et al., in press).

Finally, we cannot rule out the possibility that the haptic IPS activity is attributable to eye movements (since the eyes were closed during haptic blocks), although this seems unlikely because we did not observe activation in areas such as the frontal eye fields (Petit and Hanby, 1999).

Although linguistic descriptors such as ‘texture’, ‘pattern’, ‘form’, and ‘shape’, are commonly used to describe surface-based and geometric properties of objects, these terms are often loosely defined and the extent to which they map onto processes that underlie haptic and visual information processing, is a complex problem. Moreover, the way in which a stimulus is perceived, for example as a shape or a texture, may differ between sensory modalities due to differences in their spatial resolution. For example, the integration of pattern information across multiple fingers is relatively poor, thereby making the effective field of view significantly smaller in touch than in vision (Loomis et al., 1991). Similarly, temporal differences in the way in which information is acquired between vision and touch may also influence how a stimulus is perceived. Unlike in vision, exploring objects via touch 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. Future behavioral psychophysics, multivariate fMRI designs, and analysis techniques such as multidimensional scaling (e.g., Hollins et al., 1993) will no doubt help to bring us closer to unpacking the underlying cognitive and neural processes that enable us to recognize objects and their characteristic features in vision and touch.

Finally, our design was modeled, in part, on that of Cant and Goodale (2007) who used an fMRI adaptation procedure to examine texture-selectivity in vision. Using this approach, the task-relevant property (either texture or shape) was varied, while the other was held constant. Our study draws on a similar approach; we used a block design to maximize statistical power, while at the same time the task-irrelevant stimulus dimension (shape/texture) was held constant across all trials. Because our analyses focused on overall activation differences between shape and texture blocks, and adaptation effects are maximal (i.e., greatest signal reduction) when stimuli are repeated, one should observe maximal signal differences between the attended and unattended dimensions. For similar reasons to those outlined above, a potential drawback of this study is the number of stimulus exemplars used (n = 4). The repetition of our exemplars across blocks could elicit carry-over adaptation effects during the course of each epoch, which would reduce overall fMRI signals in both the attended and unattended stimulus dimensions. Nevertheless, one of the strengths of our study is that we used real object stimuli in a common workspace between vision and touch. An obvious challenge with this approach is that control over stimulus presentation and timing rapidly becomes complicated with large numbers of stimuli that require manual presentation. We are currently developing new techniques for rapidly presenting larger numbers of real objects in the confines of the fMRI scanner.

Conclusion

Using fMRI, we found that the perception of surface texture via touch activates brain areas within medial ventral temporal cortex that are strikingly similar to those that have been identified during surface texture perception in vision. Surprisingly, however, regions of the collateral sulcus sensitive to haptic texture lay immediately adjacent to, but not overlapping, with areas responsive to visual textures. Visual and haptic texture inputs appear to be processed in spatially distinct and functionally specialized regions of medial ventrotemporal cortex.

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