Separate Processing of Texture and Form in the Ventral Stream: Evidence from fMRI and Visual Agnosia

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Real-life visual object recognition requires the processing of more than just geometric (shape, size, and orientation) properties. Surface properties such as color and texture are equally important, particularly for providing information about the material properties of objects. Recent neuroimaging research suggests that geometric and surface properties are dealt with separately within the lateral occipital cortex (LOC) and the collateral sulcus (CoS), respectively. Here we compared objects that differed either in aspect ratio or in surface texture only, keeping all other visual properties constant. Results on brain-intact participants confirmed that surface texture activates an area in the posterior CoS, quite distinct from the area activated by shape within LOC. We also tested 2 patients with visual object agnosia, one of whom (DF) performed well on the texture task but at chance on the shape task, whereas the other (MS) showed the converse pattern. This behavioral double dissociation was matched by a parallel neuroimaging dissociation, with activation in CoS but not LOC in patient DF and activation in LOC but not CoS in patient MS. These data provide presumptive evidence that the areas respectively activated by shape and texture play a causally necessary role in the perceptual discrimination of these features.

Keywords: fMRI, humans, shape discrimination, texture discrimination, visual agnosia

Introduction

Until recently, investigators have assumed that geometric features play the key role in object recognition and have neglected surface features such as color and texture (Marr and Nishihara 1978; Biederman 1987). Yet, it is such surface features that allow the brain to infer the material or "stuff" of which an object is composed—a facility that is crucial for classifying objects in the natural world (Adelson 2001). Even though some theorists have recently begun to accept the importance of both geometric and surface features (Tarr et al. 1998; Tanaka et al. 2001), their attention has focused mainly on surface color and brightness. These cues can be highly diagnostic for object recognition (e.g., in natural vs. manufactured objects—Biederman and Ju 1988; Tanaka and Presnell 1999) when recognition takes place among objects belonging to the same structural category (Price and Humphreys 1989; Wurm et al. 1993) or when shape diagnosticity is reduced as a consequence of object occlusion (Tanaka and Presnell 1999), poor vision (Wurm et al. 1993), or visual agnosia (Humphrey et al. 1994; Mapelli and Behrmann 1997). Also, the rapid categorization of scenes (to capture their "gist") depends heavily on color and texture cues, independently of any identification of individual objects within the scene (Biederman et al. 1982; Moller and Hurlbert 1996; Oliva and Schyns 2000). Face recognition too has been found to depend heavily on surface pigmentation (Vuong et al. 2005).

Functional neuroimaging has revealed that the human brain devotes specific sectors of the visual cortex to extracting a range of visual features (for a review, see Grill-Spector and Malach 2004). It is now clear that shape recognition is linked with the lateral occipital cortex (LOC—Kourtzi and Kanwisher 2000a, 2000b; Grill-Spector et al. 2001; Hasson et al. 2001), color processing with areas visual area V4 (Lueck et al. 1989; McKeefry and Zeki 1997) and visual area V8 (Hadjikhani et al. 1998), and texture discrimination with the posterior collateral sulcus (CoS—Peuskens et al. 2004). Yet, of these different visual features, we know far more about the characteristics of LOC and its role in object recognition than about the brain areas that process surface-related properties.

Recent studies by Goodale and coworkers (Cant and Goodale 2007; Arnott et al. 2008; Cant et al. 2009) have taken a major step forward by proposing the existence of a general division of labor between LOC and medial occipital cortex for discriminating geometric versus material properties of objects, respectively. They showed that whereas attention to geometric properties of meaningless objects activated area LOC, attention to the material properties of the same objects (wood, tinfoil, marble, and other materials) activated more medial areas within the inferior occipital gyrus and the CoS. The authors proposed that medial occipital areas extract the surface information necessary to resolve fine differences between object materials. Their results fit nicely with those of Peuskens et al. (2004) who reported differential activations for shape discrimination in LOC and for surface pattern discrimination in the CoS when subjects were required to discriminate among moving 3D stimuli. It should be noted, however, that although these investigators varied the surface features of their stimulus objects to represent different kinds of material, they restricted themselves to "smooth" rather than indented surfaces throughout. In other words, the surface features that were varied did not include texture sensu strictu—that is, those surface properties that could be detected by touch as well as by vision (cf., Koenderink et al. 2007). In other words, the CoS region activated in these studies may have been responding to any of a cluster of cues including color, lightness, shading, and pattern, but probably not texture in this strict sense. It could be, for example, that the region activated includes within it a number of subareas, each quasi-independently responding to different surface features of the stimuli, though all signaling information that could be used by the brain to identify the material of which an object is composed. It therefore remains an open question whether visual texture per se might activate this same region, a specific subpart of it, or a quite different region.

The goal of the present paper is to explore this issue directly by examining the role played by medial and lateral occipital areas in processing shape versus texture cues presented in strict isolation. In Experiment 1, we tested neurologically intact participants using event-related functional magnetic resonance imaging (fMRI). In the paper of Cant and Goodale (2007), the distinction between geometric and surface features was approached in an intentionally global fashion. Accordingly, the stimuli differed in size as well as shape, whereas the "metallic" objects were brighter than the "marble" ones as well as having different surface patterning. In contrast, the stimuli we used in our geometric discrimination task differed only in the dimension of shape: the overall volume and texture was kept identical. Conversely, the stimuli used to study surface properties differed only in the dimension of texture (light reflectance, color, volume, and shape were kept identical). Having localized the brain areas selectively involved in shape and texture discrimination in Experiment 1, we asked in Experiment 2 whether damage to these areas would be associated with differential recognition deficits. To do this, we studied 2 patients with different forms of visual object agnosia, whose brain lesions, we hypothesized, might differentially implicate these 2 putative systems for shape and texture. We tested 1 well-studied patient with a selective deficit for discriminating geometric features of objects (DF: Milner et al. 1991) and a second well-studied patient with a deficit in discriminating colors (MS: Newcombe and Ratcliff 1975). We tested these 2 patients both behaviorally and in the magnetic resonance imaging (MRI) scanner using the same set of stimuli as used in Experiment 1.

Patient DF, who developed visual form agnosia as a consequence of carbon monoxide poisoning, cannot use geometric shape to recognize objects, but her performance is much improved when allowed to use surface properties such as color and gray scale (Milner et al. 1991; Humphrey et al. 1994). In everyday life, DF is generally able to name the material from which an object is made (plastic, aluminum, wood, ceramic, and so on) and can often use such cues to help her identify the object. When tested using fMRI (James et al. 2003), DF not only showed a lack of brain activity when line drawings of objects were contrasted with scrambled versions of the same objects but also her lesion overlapped near perfectly with the activation within LOC found for the same comparison in neurologically intact participants. Furthermore, when pictures of real objects in color and gray scale were presented to DF, reliable activations were found only within medial occipital areas lying somewhat distant from her damaged LOC. Thus, no "shape"-related activity was present in DF's occipitotemporal "ventral stream," regardless of the richness of the stimuli; only surface features, when available, elicited activations. In a related study, the parahippocampal gyrus of DF (the so-called "place area") was found to be more responsive to appropriately colored pictures of scenes than to black/white ones (Steeves et al. 2004). That is, the presence of color and texture information (embedded in real pictures of houses and landscapes) not only enhanced DF's ability to recognize the stimuli but also led to increased activation levels within her medial occipitotemporal cortex. Together, these results suggest that when faced with objects and scenes, DF has to depend largely on their surface features and that this recognition is mediated by intact medial occipitotemporal cortices. Our question in the current study was whether DF would be able to discriminate visual textures in isolation and, in particular, whether there would be associated activity within her spared medial occipital cortex comparable with that seen in neurologically intact individuals.

Patient MS developed visual agnosia and cerebral achromatopsia after contracting suspected herpes encephalitis in 1971. His inability to experience or discriminate colors is well documented (for a recent review of achromatopsia following cortical damage, see, e.g., Heywood and Kentridge 2003), although he does retain the ability to use the boundaries between colors to segment objects from their backgrounds and to perceive motion (Heywood et al. 1998a, 1998b) and can discriminate between contrast borders differing in chromatic composition (Kentridge et al. 2004). Recent informal observations suggest that, in addition to his inability to perceive color, MS is also impaired in perceiving and discriminating other properties of object surfaces such as texture. In contrast to patient DF, therefore, MS can perceive and discriminate geometric structures when their edges are clearly defined by brightness or color, although he cannot use these edge contours to reconstruct the object's identity. When asked to perform an "oddity" discrimination task, MS scored well for shape but very poorly for color stimuli (Heywood et al. 1994). MS has large bilateral lesions involving the ventromedial occipitotemporal cortices. We therefore hypothesize that MS can perceive simple shapes by using the spared parts of his left occipital–temporal cortices and left striate cortex. In the current study, we asked whether MS's intact capability for discriminating geometric structure would be accompanied by brain activations similar to those localized in neurologically intact participants. Second, we asked whether MS would have a deficit in discriminating surface textures analogous to his achromatopsia, as a result of his extensive medial occipitotemporal lobe damage.

Materials and Methods

Subjects

Eleven young subjects (6 females; age range: 21–28 years) and 3 older males (age range: 50–58 years) participated in Experiment 1. They were all right handed as measured by the Edinburgh Handedness Inventory (Oldfield 1971). All had normal or corrected-to-normal vision and no history of neurological disorder. Two brain-damaged patients (DF and MS) participated in Experiment 2. DF is right handed and MS is left handed as measured by the Edinburgh Handedness Inventory (Oldfield 1971). All participants gave informed consent before beginning the experiment, which was approved by the Ethics Committees of Durham University and York Neuroimaging Centre (YNiC). All 14 subjects underwent repeated functional scans as well as 1 anatomical scan during the same session.

Patient DF has a profound visual form agnosia as a consequence of a hypoxic episode which damaged her bilateral ventral lateral-occipital cortex (Milner et al. 1991). Structural MRI shows that DF's most clearly defined lesions correspond bilaterally with the location of the LOC in the ventral stream of healthy subjects along with a small focus of damage in the left posterior parietal cortex (James et al. 2003). Along with her failure to recognize objects visually, she has particular difficulties in discriminating shape, lightness, orientation, and symmetry. Despite these deficits, she has preserved visual acuity, color vision, tactile recognition, and verbal intelligence.

Patient MS has a left homonymous hemianopia (with macular sparing), along with profound achromatopsia, prosopagnosia, and visual object agnosia, as a consequence of a presumed idiopathic herpes encephalitis infection that caused extensive damage to his bilateral ventromedial occipitotemporal cortices. Specifically, the left hemisphere damage includes the temporal pole, the parahippocampal and fourth temporal gyri of the temporal lobe, the CoS, and the mesial occipitotemporal junction (the latter damage presumably causes MS's achromatopsia: see Zeki 1990). The first, second, and third temporal gyri are intact, and the frontal and parietal lobes are preserved in their

entirety. Lesions within the right hemisphere encompass the same regions damaged in the left, with the addition of the second and third temporal gyri and the striate cortex (producing a left homonymous hemianopia). For a more extensive case description of MS, see Newcombe and Ratcliff (1975) and Heywood et al. (1994). Although MS is profoundly object agnosic, he does not have visual form agnosia: he can readily discriminate between different shapes.

Apparatus, Stimuli, and Procedures

Subjects lay comfortably supine inside the bore of the scanner, with their head fixed in order to minimize movements. Stimuli were back projected (Dukane 8942 ImagePro 4500 lumens LCD projector in York, and SV-6011, Avotec, Inc., Stuart, FL, in Maastricht) onto a custom in-bore acrylic rear projection screen and were viewed through a mirror mounted on the head coil. Each trial lasted 14 s and consisted of a stimulation period (during which the experimental stimuli were presented for 4 s) and a baseline fixation period (during which a $0.54° \times 0.54°$ black fixation point was presented on a white background for 10 s).

The experimental stimuli were assembled using images of 3D meaningless objects synthesized using the POV-Ray ray-tracing package (Persistence of Vision Raytracer, version 3.6 http://www.povray.org/download/). The objects could vary in their geometric (shape) or surface (texture) features. Three different shapes (ellipsoids, cubes, and cylinders: see Fig. 1a-c) and 3 different types of texture (loosely approximating human skin, sandpaper, and a lunar surface: see Fig. 1d-f) were used. The textures were generated as 2D maps of surface distortion using bespoke C++ programs. These textures were then applied to model spheres as bump maps within POV-Ray. Each shape was produced using different aspect ratios between length and width while keeping the overall volume constant across aspect ratios and object types. Similarly, each texture type was produced at a different "roughness" by varying a parameter controlling the depth and sharpness of texture features. Object shape was always the same on the texture trials (aspect ratio = 1, i.e., spherical). Finally, each object could be rendered in 1 of 7 different spatial orientations (textured spheres displayed at different orientations are not identical as they present the observer with different samples of their quasi-random but nonuniform surface textures). The objects and the floor against which they were presented were made of a neutral gray, slightly glossy material and illuminated by fixed, neutrally colored lights. Perceptual discriminations of geometric and surface features were performed within each shape and texture type only (e.g., discrimination between different coarsenesses of sandpaper or between different ellipsoids).

On each trial, experimental stimuli were presented in triplets vertically aligned on the right side of the screen, centered at an eccentricity of $6.65°$ of visual angle. The stimuli measured 18×8 cm at a viewing distance of 60 cm. Lateralized presentation was chosen to facilitate object discrimination for patient MS (see Experiment 2) who has a left hemianopia. In each triplet, 2 of the stimuli were identical (except for their orientation) and 1 was different. The 2 identical stimuli were always adjacent, so that the odd one always appeared either on the top or on the bottom of the triplet (Fig. 1g,h). Each triplet was surrounded by a red single- or blue double-outline rectangle indicating to the subject the type of discrimination required on that trial (i.e., shape or texture). Whereas half of the subjects were instructed to discriminate shape in the presence of the red single-outline rectangle and texture with the blue double-outline rectangles, the others were given the converse instruction. These rectangle cues were chosen to accommodate both DF's and MS's visual deficits: DF was able to use the color cue, whereas conversely, MS could use the single/double-outline cue.

Participants were asked to press 1 of 2 buttons with the right hand to indicate whether the top or bottom of the 3 vertically aligned stimuli was the odd one with respect to either the shape or the texture of the objects. Participants were encouraged to respond as quickly and as accurately as possible before the offset of the stimulus (i.e., within 4 s). Participants were also instructed to look at the fixation point during the baseline period but to move their eyes freely if they so desired when the experimental stimuli were presented.

Stimuli and responses were controlled by Presentation software (version 9—Neurobehavioral System, Inc., Albany, NY). Manual responses were collected via keypads (Lumitouch pads—Photon Control, Inc., British Columbia, Canada) containing 2 keys, 1 for the index finger and 1 for the middle finger. To reduce cognitive demands caused by frequent task changes, a slow event-related design was used, with trials spaced every 14 s and organized in blocks of 3 trials each (e.g., TTTSSSTTTSSS). Each run was structured in a series of 10 blocks (5 blocks per task) with 3 trials per block, for a total of 30 trials (~7 min) per run. Each subject performed a minimum of 3 runs (for at least 45 trials per task) to a maximum of 5 runs (with a total number of 75 trials per task).

In Experiment 2, the apparatus, stimuli, and procedures were identical to those described above for Experiment 1 except for the following points. First, DF and MS practiced the tasks outside the scanner to familiarize themselves with the stimuli and the button press associations (MS 135 trials in total and DF 75 trials in total), whereas the young and age-matched controls saw the stimuli and practiced only
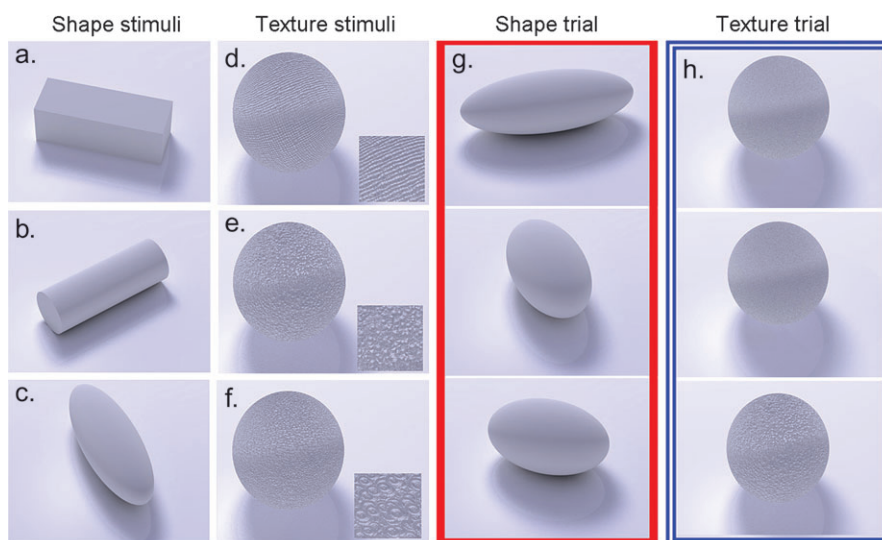

Figure 1. Experimental stimuli. Examples of the experimental stimuli (a–f) and arrays (g, h) used for the shape and texture discrimination tasks. Shape stimuli were images of 3D cuboids, cylinders, or ellipsoids, which could vary in their overall aspect ratio (ratio of width to length). Texture stimuli were images of 3D spheres that could vary in the grain of their surface indentations and that resembled human skin (d), sandpaper (e), or lunar surface (f). On each trial, stimuli were grouped into vertically aligned triplets (within each object category), and subjects were required to report which of the stimuli was the "odd one out" in terms of either shape (h) or texture (g) using a spatially compatible button press. Correct performance for the exemplars shown here would require the subjects to press the upper button for the shape trial (g) and the lower button for the texture trial (h).

a few trials of the task before entering the scanner. Second, the age-matched controls were asked to repeat the experiment outside the scanner to compare their behavioral performance with that of MS and DF. Third, the cues used to instruct MS about the discrimination task to perform (shape or texture) differed from the other subjects because he turned out to be more comfortable with written instructions than pictorial cues (i.e., single-line and double-line rectangles). MS's visual stimuli therefore included the words SHAPE or TEXTURE, presented in black capital letters to the right of the fixation point.

Imaging Parameters

All control participants and MS were tested at the YNiC (UK), and DF was tested at Maastricht Brain Imaging Center (The Netherlands).

Imaging performed at YNiC used a 3-T whole-body GE Excite MRI system. A high-density brain array 8 channels head coil was used in all experiments. Blood oxygenation level-dependent (BOLD)-based fMRI volumes were collected using optimized T_2^*-weighted segmented gradient echo planar imaging (26 cm field of view [FOV], with 64×64 matrix size for an in-plane resolution of 3 mm, repetition time [TR] = 2 s, time echo [TE] = 30 ms, flip angle [FA] = 90°). Each volume comprised 43 contiguous slices of 3 mm thickness, angled at approximately 30° from axial, to sample occipital, parietal, posterior temporal, and posterior/superior frontal cortices. During each experimental session, a T_1-weighted anatomic reference volume was acquired along the same orientation as the functional images using a 2D acquisition sequence (320×288 matrix size, 3.0 mm acquired slice thickness, time to inversion = 1050 ms, time repetition [TR] = 2975 ms, TE = 14 ms, FA = 90°).

Imaging performed at Maastricht Brain Imaging Center used a Siemens Allegra 3-T head scanner. BOLD-based fMRI volumes were collected using an optimized segmented T_2^*-weighted segmented gradient echo planar imaging (22.4 cm FOV with 64×64 matrix size for an in-plane resolution of 3.5 mm, RT = 2 s, TE = 50 ms, FA = 90°). Each volume comprised 30 contiguous slices of 3.5 mm thickness, angled at approximately 30° from axial, to sample occipital, parietal, posterior temporal, and posterior/superior frontal cortices. During each experimental session, a 3D T_1-weighted anatomic reference volume was acquired along the same orientation as the functional images using a "modified driven equilibrium Fourier transform" sequence (scan parameters: TR = 7.92 ms, TE = 2.4 ms, FA = 15°, matrix size = 256×256, FOV = 256×256 mm^2, 176 slices, slice thickness = 1 mm, no gap, total scan time = 13 min 43 s).

Data Analysis

Behavioral Data

For both experiments, reaction times (RTs) and accuracy were collected online. For Experiment 1, data were analyzed using analysis of variance (ANOVA) and t-test statistics merging data from young and age-matched controls. For Experiment 2, accuracy data in single subjects were analyzed using binomial and χ^2 tests.

Imaging Data

Data were analyzed using the BrainVoyager QX software package (version 1.9; Brain Innovation, Maastricht, The Netherlands). For each subject, functional data underwent 3D motion correction algorithms. No abrupt movements were detected in the animations, and no deviations larger than 1 mm (translations) or 1° (rotations) were observed in the motion correction output. Functional data were then preprocessed with linear trend removal and underwent high-pass temporal frequency filtering to remove frequencies below 3 cycles per run. Anatomical volumes were transformed into standard stereotaxic space (Talairach and Tournoux 1988). Functional volumes were then aligned to the transformed anatomical volumes, thereby transforming the functional data into a common stereotaxic space across subjects.

The fMRI data were analyzed using a general linear model—GLM (a random-effect GLM was used for the group average analysis). The model included 2 experimental predictors (shape and texture) and 6 motion correction predictors (x, y, z for translation and for rotation). The period of fixation (10 s) was used as a baseline. The experimental predictors were modeled as a transient (4 s or 2 volumes) epoch where the square-wave function for each phase was convolved with the

default BrainVoyager QX "2-gamma" function designed to estimate hemodynamic response properties. Prior to analysis, the data were z normalized; thus, beta weights extracted from the active clusters represent an estimate of the magnitude of activation for each condition (constrained by the shape of the expected hemodynamic response function) in units of z scores.

In the averaged voxelwise group analysis, statistical activation maps were set to reliable threshold levels and cluster volumes ($P < 0.0001$, minimum cluster size = 373 mm^3) using Monte Carlo simulations (performed using BrainVoyager QX) to verify that our regions of interest were unlikely to have arisen due to chance as a consequence of multiple comparisons.

After having identified the areas that were activated by a comparison of interest, we performed post hoc analyses on the beta weights. Beta weights were extracted for each subject and each condition separately and were analyzed using 2-tailed t-test statistics with subject-related variability as error estimates.

In Experiment 2, the imaging data were preprocessed and analyzed as described in Experiment 1. For single-subject analysis, regions were defined in each individual by contrasting conditions (using separate study predictors in order to weight for the contribution of each run) at a threshold of $P < 0.001$, uncorrected.

Results

Experiment 1

Behavioral Results

Accuracy was analyzed by 1-way ANOVA comparing the number of correct responses for shape and texture trials. We found that accuracy was significantly higher ($F_{1,27} = 96.55$, $P < 0.0001$) for shape (89%) than for texture (62%) trials. Importantly, for our purposes, however, accuracy was significantly ($P < 0.0001$) above chance for both types of trials as measured by one-sample t-test. RTs were analyzed by a 2-way repeated-measures ANOVA using trial type (correct vs. error) and stimuli (shape vs. texture) as within-subjects factors. Both main effects (trial type and stimuli) and their interaction reached significance. In particular, we found that RTs for shape discriminations (mean 2163 ms) were significantly ($F_{1,13} = 29.6$, $P < 0.0001$) faster than those for texture (mean 3165 ms). Moreover, RTs were significantly faster ($F_{1,13} = 48.2$, $P < 0.0001$) on correct (mean 2546 ms) than on error (mean 2783 ms) trials, though as suggested by the interaction ($F_{1,13} = 8.87$, $P < 0.011$), this was so only for shape trials (mean correct 1941 ms, mean error 2385 ms). As shown in Figure 2, both the young participants and age-matched controls showed a similar pattern of performance on RTs and accuracy. These results show that, although texture stimuli were more difficult to discriminate, our healthy subjects were able to perform both discrimination tasks above chance. They also show that the poorer performance on texture trials was not due to a lack of diligence, given that responses were equally fast on correct and incorrect trials.

Imaging Results: Shape Processing

In order to localize the brain areas active during the processing of object geometry, we contrasted shape discrimination versus texture discrimination trials in our group average. We found bilateral foci of activations along the lateral occipitotemporal cortex and one focus of activation in the left dorsal extrastriate visual cortex (stereotaxic coordinates for the activated areas are shown in Table 1). As shown in Figure 3a, the bilateral activations along the lateral occipitotemporal cortex were congruent with the location of LOC in previous literature (e.g., Malach et al. 2002). The more dorsal activation was distributed
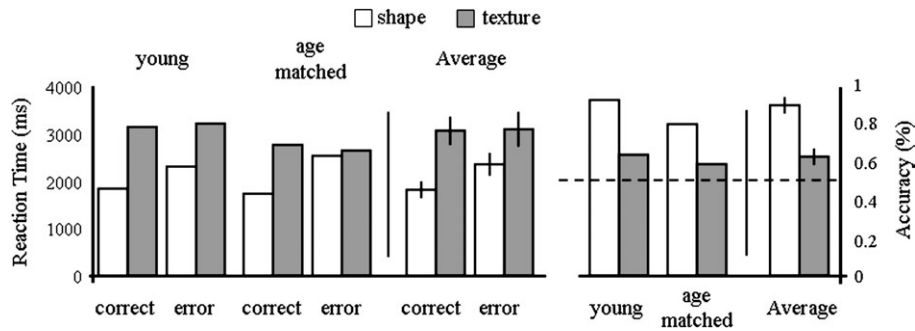
Figure 2. Behavioral results for Experiment 1. Reaction time (left panel) and percent correct responses (right panel) for shape (white) and texture (gray) trials plotted separately for participants (11 young controls, 3 age-matched controls, and their average) and trial type (correct and error). Bars represent 95% confidence interval. Horizontal dotted line represents chance level.

Table 1

Brain areas active in the 2 contrasts of interest

Brain areas	Hemisphere	Talairach coordinates			t
		x	y	z	
Shape versus texture discrimination					
LOC	Left	−45	−62	−2	3.08
LOC	Right	46	−67	−3	3.08
V3A	Left	−9	−89	15	4.0
Texture versus shape discrimination					
pCoS	Left	−18	−87	−19	3.2
	Right	21	−83	−19	3.2
LOG	Left	−17	−90	−8	4.0
Anterior insula	Left	−35	16	9	4.0
	Right	36	10	10	4.0
cIPS	Left	−28	−59	−40	4.2
	Right	24	−64	37	4.5
mFG	Left	47	17	38	4.0
SMA	Left	−6	5	53	4.3
	Right	2	9	53	4.3

Note: LOC, lateral occipital cortex; pCoS, posterior collateral sulcus.

Figure 3. Group activation maps and beta weights for shape versus texture discrimination. (*a*) Brain areas activated by contrasting shape versus texture discrimination: left and right LOC and left V3A. The group activation map is based on the Talairach-averaged group results, shown for clarity on a single subject's anatomical scan (which is not representative of the sulcal patterns for all subjects). (*b*) Averaged beta weights measured in each brain area for shape and texture trials, split between correct and error trials (shape_c = shape-correct, shape_e = shape-error, texture_c = texture-correct, and texture_e = texture-error). Bars represent 95% interval confidence. Talairach coordinates for the activated areas are shown in Table 1. L, left; R, right; A, anterior; P, posterior.

lateral to the left parietooccipital sulcus, and it may be identifiable with visual area V3A (Tootell et al. 1997).

Imaging Results: Texture Processing

In order to localize brain areas active during the processing of surface texture, we contrasted texture discrimination versus shape discrimination trials in our group average. We found 3 foci of activation in the ventral posterior portion of the occipital cortex, 2 foci of activation in the frontal cortex, 2 foci of activation in the parietal cortex, and 2 foci of activation in the anterior insular cortex (stereotaxic coordinates for the activated areas are given in Table 1). Figure 4*a* shows the location of the activated areas superimposed on axial slices. The occipital activations were located more medially and posteriorly than those recorded during the shape discrimination task. Two bilateral foci lay in the very posterior and ventral end of the lateral occipital gyrus (LOG; Damasio 2005), caudally to the CoS (henceforth referred to as pCoS). The third occipital focus was also located at the posterior end of the LOG but more dorsally than the previous ones and only in the right hemisphere. The parietal activations were located bilaterally within the posterior end of the intraparietal sulcus (IPS) (perhaps coincident with the caudal IPS [cIPS], which has been associated with surface orientation discrimination in previous work: Shikata et al. 2001). The frontal activations lay in the supplementary motor area (SMA), bilaterally in the anterior insular cortex, and in the right middle frontal gyrus (mFG).
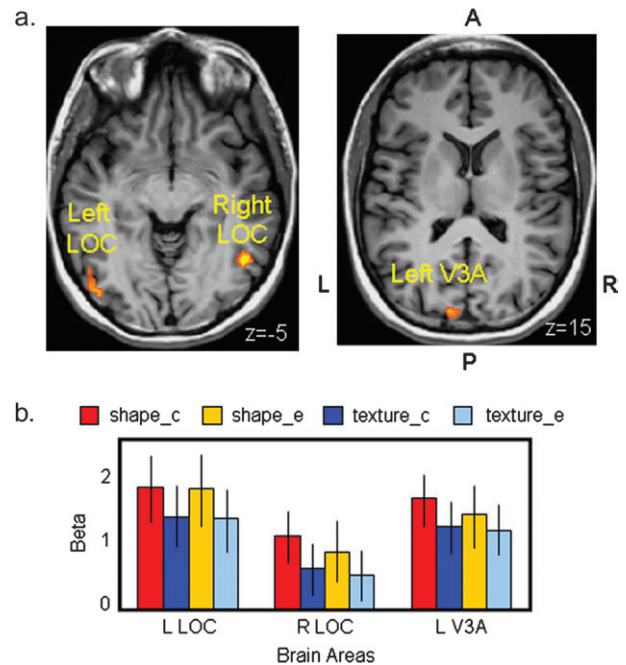
Imaging Results: Shape and Texture Processing

Given that geometric and surface discriminations were performed using separate sets of stimuli, it was considered necessary to check whether they activated similar brain areas overall. Even though, as shown above, attention to texture or shape preferentially modulates activity within dedicated areas, we would still expect both stimulus types to activate common brain areas when compared with baseline. Although the shape stimuli did not differ in texture, they did have a value on the texture dimension (smooth), and similarly although the texture stimuli did not differ in shape, they all had a particular shape (spherical). Moreover, in both discrimination tasks, subjects performed a key-press response using the same finger. Figure 5 shows brain activity for
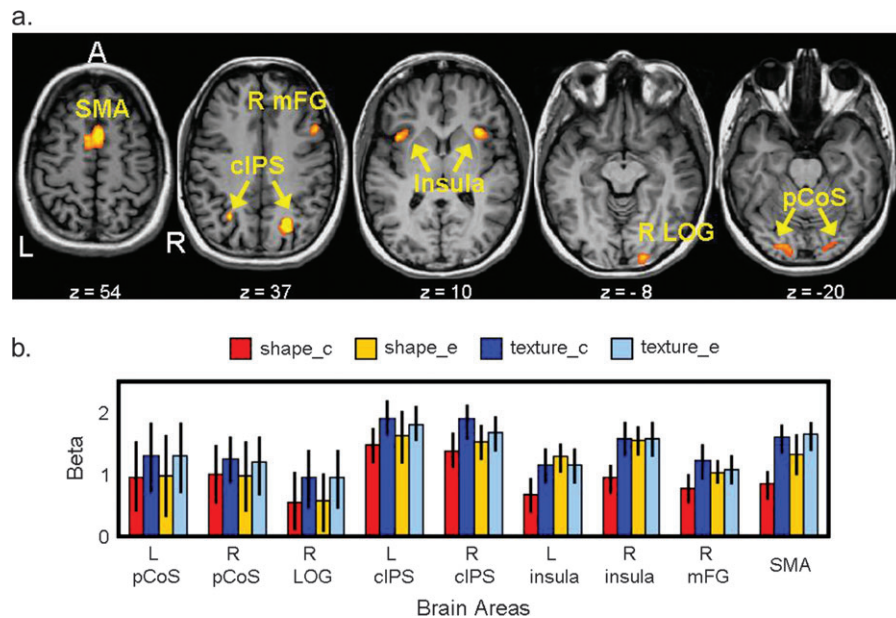
Figure 4. Group activation maps and beta weights for texture versus shape discrimination. (*a*) Brain areas activated by contrasting texture versus shape discrimination: left and right posterior collateral sulcus (pCoS), right LOG, cIPS, SMA, anterior insular cortex (insula), and right mFG. The group activation map is based on the Talairach-averaged group results, shown on a single subject's anatomical scan. (*b*) Averaged beta weights measured in each brain area for shape and texture trials split between correct and error trials (shape_c = shape-correct, shape_e = shape-error, texture_c = texture-correct, and texture_e = texture-error). Bars represent 95% confidence interval. Talairach coordinates for the activated areas are shown in Table 1. L, left; R, right; A, anterior; P, posterior.
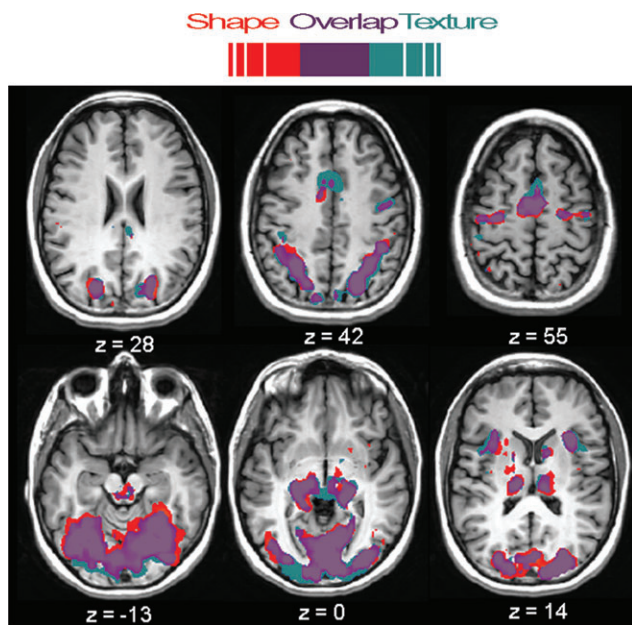

Figure 5. Overlaid activation maps for brain activations recorded for shape and texture discriminations. Brain areas activated for the comparison of shape discrimination versus baseline (depicted in red), texture discrimination versus baseline (depicted in green), and their overlap (depicted in purple) in control participants. Overlapping activity was distributed bilaterally in striate and extrastriate visual areas, occipitotemporal and occipitoparietal cortices, IPS, lateral and medial motor areas, cerebellum, and thalamus.

shape versus baseline (in red), for texture versus baseline (in green), and their overlap (in purple) in our control participants. As is clearly apparent, when compared with baseline, our texture and shape discriminations activated very similar brain pathways. Overlapping activity was distributed bilaterally across brain areas

from visual stimulation through to motor response striate and extrastriate visual areas, occipitotemporal and occipitoparietal cortices, IPS, lateral and medial motor areas, and subcortical structures such as cerebellum and thalamus.

Imaging Results: Correct and Incorrect Trials

The lower accuracy and slower RTs on texture than on shape trials suggests differential task difficulty and/or differential deployment of attentional resources between the 2 tasks. It is possible that such nonspecific factors were the cause of the activations in occipital, parietal, insular, and frontal cortices that were seen in our contrast of texture discrimination versus shape discrimination. In order to isolate those brain areas sensitive to texture discrimination only, we partitioned our shape and texture data between correct and incorrect trials (shape-correct, shape-error, texture-correct, and texture-error) by adding "error" and "correct" predictors into the GLM. This way we could check whether the activity within areas more active for texture than shape was modulated by accuracy. This analysis was based on the assumption that errors would have occurred mainly on more difficult trials, which would themselves be those requiring more attentional resources. We would expect that whereas brain areas sensitive to task difficulty should respond more on incorrect than correct trials for both shape and texture stimuli, brain areas involved in texture discrimination specifically should not be modulated by performance on shape stimuli.

The results are plotted in Figure 4*b*. Beta weights for each condition were analyzed with a 3-way repeated-measures ANOVA using brain areas (left pCoS, right pCoS, right LOG, left cIPS, right cIPS, right insula, left insula, mFG, and SMA), stimuli (shape and texture), and accuracy (correct and error) as within-subject factors. The interaction between brain areas × accuracy × stimuli reached significance ($F_{8,96} = 3.60$, $P < 0.001$),

showing that the brain areas active for texture versus shape showed a different pattern of activation as a function of stimulus type and accuracy. Planned post hoc t-tests showed that whereas none of the brain areas were sensitive to differences between texture-error and texture-correct trials (for all comparisons, $P > 0.3$), bilateral SMA, bilateral insula, and right mFG showed higher beta values on shape-error than on shape-correct trials (for all comparisons, $P < 0.005$). These higher beta weights for shape-error than shape-correct trials suggest that the bilateral SMA, bilateral insula, and right frontal area activations relate to task difficulty and/or attention deployment. Conversely, the lack of correct/error modulation for shape trials within the bilateral pCoS, right LOG, and bilateral cIPS suggests that their role lies in texture discrimination per se. The lack of any differential activations between texture-error and texture-correct trials can be readily attributed to the difficulty level of the texture stimuli on all trials. This pattern of results matches the interaction between trial type and stimuli found in the RT data. Indeed, higher brain activity for shape-error versus shape-correct only maps well onto the slower mean RT recorded on incorrect than correct trials during the shape condition.

We also performed a similar 3-way repeated-measures ANOVA using brain areas (left LOC, right LOC, and left V3A), stimuli (shape vs. texture), and accuracy (correct vs. error) for those brain areas more active during shape discrimination than texture discrimination. Only the main effects of brain areas ($F_{2,24} = 5.3$, $P < 0.013$) and stimuli ($F_{1,12} = 26.3$, $P < 0.0001$) reached significance, showing that activation within right LOC was significantly lower ($P = 0.005$) than in left LOC or V3A (which did not differ from each other: $P = 0.1$) and that shape stimuli elicited a significantly higher ($P = 0.0001$) response than the texture stimuli. More importantly, as shown in Figure 3b, activations in neither bilateral LOC nor the right V3A were modulated by discrimination accuracy. Thus, activation maps for texture versus shape and for shape versus texture, using correct trials only, revealed a pattern of results very similar to those found for all trials aggregated together (Fig. 1, Supplementary material).

To address this question in a different way, we also computed correlations between beta weight differences (beta weight for texture minus beta weight for shape in brain areas more active in texture discrimination, and the converse for the brain areas more active for shape discrimination) and discrimination accuracy. We found no significant correlation between beta weight differences and accuracy (left pCoS: $r^2 = 0.105$, $P =$ 0.258; right pCoS: $r^2 = 0.156$, $P = 0.162$; right LOG: $r^2 = 0.013$, $P = 0.716$; left cIPS: $r^2 = 0.206$, $P = 0.119$; right cIPS: $r^2 = 0.018$, $P = 0.665$; left LOC: $r^2 = 0.051$, $P = 0.460$; right LOC: $r^2 = 0.150$, $P = 0.191$; right V3A: $r^2 = 0.008$, $P = 0.773$). This provides further evidence that the differences in brain activity reported for shape and texture discrimination were not due to differences in difficulty.

In summary, these analyses indicate that behavioral difficulty was not a factor in the activation patterns observed in these higher level areas within the ventral stream. This inference is consistent with previous research reporting no differential activity in LOC when subjects were asked to perform tasks at different levels of difficulty or attentional demand (simple detection vs. object identification, Grill-Spector 2003).

Experiment 2

Behavioral Data
Individual accuracy scores for DF, MS, and 3 age-matched controls are shown in Figure 6. When tested outside the scanner, all age-matched controls showed a higher accuracy for shape than for texture discrimination, as expected from Experiment 1, but again performance for both types of stimuli was significantly above chance ($P < 0.01$). DF and MS showed an opposite pattern of results from one another. As shown in Table 2, DF's performance rose above chance only for the texture discrimination (66% correct), which was significantly more accurate ($\chi_1^2 = 5.32$, $P = 0.021$) than her shape discrimination (46% correct). Conversely, patient MS performed above chance only for shape discrimination (72% correct), which was significantly more accurate ($\chi_1^2 = 13.15$, $P = 0.0001$) than his texture discrimination (45% correct). When DF and MS were compared with each other, we found that shape discrimination was significantly better in MS ($\chi_1^2 = 12.86$, $P = 0.0001$), whereas texture discrimination was significantly better in DF ($\chi_1^2 = 4.56$, $P = 0.033$).

Behavioral data collected in the scanner showed similar trends, though they were less clear than those collected outside (see Table 2). Whereas DF's accuracy was higher for texture discrimination (57% correct) than for shape discrimination (40% correct), MS showed a higher accuracy for shape (72% correct) than for texture (50% correct). When DF and MS were compared with each other, we found that shape discrimination was significantly better in MS ($\chi_1^2 = 14.313$, $P = 0.0001$), though the converse difference in performance for
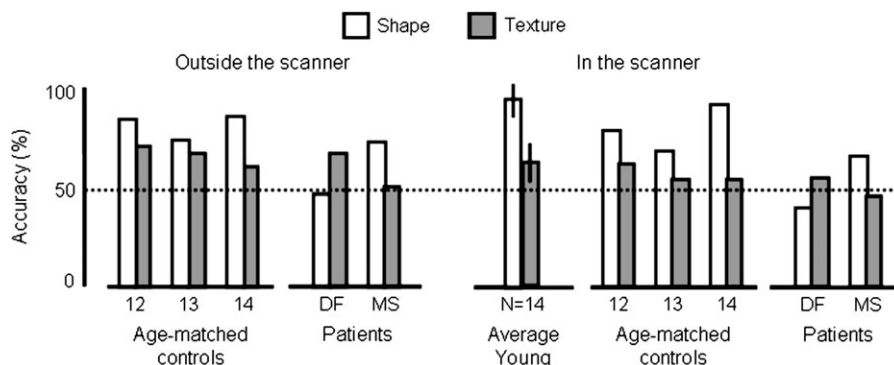

Figure 6. Behavioral data. Percent correct responses for shape (white) and texture (gray) trials plotted for 3 age-matched controls, for patient DF and patient MS outside (left panel) and inside (right panel) the scanner. Average data for young participants inside the scanner are reported as reference; bars represent 95% confidence interval. Dotted line represents chance level.

Table 2

Behavioral results for DF, MS, and age-matched controls

| Subject and age | Performance and one-tailed binomial significance | | | | Chi squared | |
| | Shape | | Texture | | Shape versus texture | |
	Score	P	Score	P	χ^2	P
Outside the scanner						
DF 52	35/75	0.68	50/75	0.002	5.32	0.021
MS 58	98/135	0.0001	68/135	0.44	13.15	0.0001
S12 51	63/75	0.0001	53/75	0.0001	3.08	0.079
S13 53	53/75	0.0001	51/75	0.0006	0.03	0.859
S14 58	64/75	0.0001	47/75	0.02	8.87	0.003
Inside the scanner						
DF 52	30/75	0.95	43/75	0.08	3.84	0.05
MS 58	54/75	0.0001	34/75	0.76	9.92	0.002
S12 51	55/75	0.0001	49/75	0.003	0.01	0.934
S13 53	52/65	0.0001	35/65	0.23	8.90	0.003
S14 58	54/65	0.0001	36/65	0.17	10.44	0.001

Note: The chi-square statistic was used to compare performance accuracy in shape and texture trials. The binomial distribution was used to test whether the performance was significantly above chance.

texture did not reach significance (χ_1^2 = 1.71, P = 0.19). As shown in Figure 6 and Table 2, performance in the texture discrimination task was less good in the scanner, with DF reaching only marginal significance (P < 0.083) and 2 of the 3 age-matched controls failing to reach significance (S13, P < 0.23 and S14, P < 0.17). This less good performance might be due to small imperfections in the acrylic screen used in the scanners. Although they all claim perfect sight, it is possible that the older participants might have been affected more by these imperfections than the young ones. It is unlikely, however, that this low accuracy for texture would have compromised the imaging results because participants were still paying full attention to the texture of the stimuli. As shown for the young controls in the previous section, correct versus incorrect trials were not associated with differential brain activity within LO or pCoS. Unless compromised by a lesion, brain areas sensitive to a given visual feature may be assumed to respond to that feature even when the stimuli are not well discriminated. Indeed, brain activity in early visual cortex (measured in terms of BOLD signal and neural activity) has been found not to differ between alert and anesthetized states (Goense and Logothetis 2008).

It is unlikely that MS's difficulty in discriminating textures is purely the result of poor contrast sensitivity at high spatial frequencies. First, MS's visual acuity (Snellen acuity, measured using high-contrast letters: Heywood et al. 1996) is within the normal range, enabling him to discriminate high spatial frequencies as well as DF and neurological intact controls. Second, MS was well able to report the presence/absence of indentations on the surface of the experimental stimuli when asked about them. Finally, MS's severe impairment in texture discrimination remained present when he was tested with coarse texture stimuli (e.g., tree bark, stone walls, and plaster). His performance remained at chance and significantly lower than that of DF (Fig. 5, Supplementary material).

Imaging Results: Shape Task
Overlaid activation maps for shape versus texture trials in patients DF and MS are shown in Figure 7. We focused our single-subject analyses on area LOC, given its well-known role in form perception (Grill-Spector et al. 2001). All brain areas

active for shape contrasted with texture in the 2 patients are reported in Table 3.

Patient MS showed 2 foci of activation within the left LOC (Fig. 7*b*). Talairach coordinates for the posterior and anterior foci overlap well with the 2 well-known major subdivisions of LOC, namely areas LO and the posterior fusiform sulcus area (pFs), respectively. Brain activity, in terms of beta weights, averaged across the 2 foci was higher for shape than for texture discrimination showing a clear preference for the geometry of the stimuli. No activation was found in the right hemisphere. MS's activation pattern in terms of both location and beta weights is very similar to the results found in the left hemisphere of the control participants (at the level of both single subjects and averaged data—Fig. 7*d*; Fig. 2, Supplementary material).

Patient DF showed no activation within LOC or any other part of occipitotemporal cortex. This result is not surprising given that her lesion (highlighted by pink arrows in Fig. 7*a*) overlaps quite well with the locus of activation in both control participants and patient MS.

Imaging Data: Texture Task
Overlaid activation maps for texture versus shape trials in patients DF and MS are shown in Figures 8 and 9. We focused our single-subject analyses on the occipital cortex given its reliable activation for texture but not for task difficulty. All brain areas active for texture versus shape in the 2 patients are reported in Table 3.

Patient DF showed several foci of activation within the occipital cortex. One focus was located at the posterior end of the right CoS (Fig. 8*b*), and others were found bilaterally in posterior lingual gyrus (pLG, Fig. 9*b*) and in the right medial LG (mLG, Fig. 9*b*). Brain activity, in terms of beta weights for the activated areas in the CoS, pLG, and mLG, was higher for texture than for shape discrimination, showing a clear preference for the surface properties of the stimuli (for the pCoS, see Fig. 8*c*). DF's activation pattern in terms of both location and percent of BOLD signal chance (%BSC) is similar (with the exception of extended bilateral activations within the LG) to the results found in the control participants at the level of single subjects and in averaged data (see Supplementary material, Figs 3 and 4).

Patient MS showed no activation within the occipital lobe (Figs 8*a* and 9*a*). This result is unsurprising given that his lesion encompasses all the medial aspect of the occipital lobe, including all the active foci found for texture versus shape discrimination in control participants and in patient DF.

Discussion

In the present study, we first confirmed the existence of a specific division of labor between the lateral (LOC) and medial (pCoS) occipital cortices within the ventral stream for the processing of geometric (shape) versus surface (texture) properties of objects (Experiment 1). We then showed in 2 patients with different object recognition difficulties that disruption of one of these areas while sparing the other was associated with a loss of discrimination on the corresponding feature (shape or texture) along with successful discrimination on the other (Experiment 2). Experiment 2 thus provides presumptive evidence that the areas activated by a given feature during fMRI in Experiment 1 play a causally necessary role in successful perceptual discrimination of that feature.
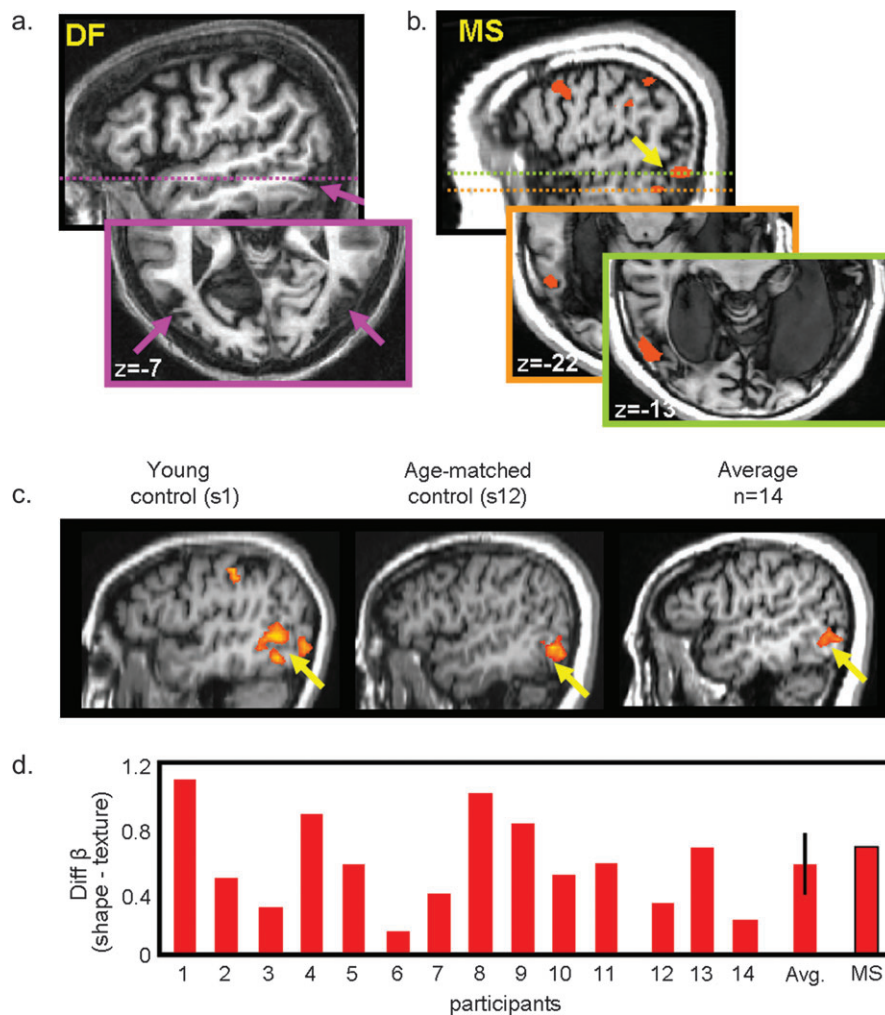
Figure 7. Individual activations for shape versus texture in patient DF, patient MS, age-matched controls, and young controls. The exact position of left LOC localized by contrasting shape versus texture discrimination is shown (yellow arrows) in the clearest parasagittal and/or axial slices for patient MS (*b*), young subject #1 (*c*, leftmost panel), age-matched control #12 (*c*, middle panel), and the control group average data (*c*, rightmost panel). DF (*a*) shows no activation for this contrast, but her lesion (highlighted by pink arrows) overlaps with the locus of activation found in patient MS and control subjects. The higher brain response for shape trials in terms of beta weights differences (diff shape minus texture) for patient MS (*d*, rightmost plot) is very similar to that found in controls (young: 1–11 and age matched: 12–14) at the level of single subjects and in the group average (*d*, second rightmost plot). Bars represent 95% confidence interval.

Neural Correlates of Shape and Texture Discrimination

In Experiment 1, we found bilateral activations for shape versus texture discrimination, which were congruent with the location of LOC in previous literature (Grill-Spector et al. 2001). Area LOC, often called the "object area," has been traditionally localized by contrasting images of intact objects versus scrambled versions of the same images (Malach et al. 1995). Over recent years, it has become clear that activity in the LOC is associated more with the extraction of information about shape per se rather than with the specific contours comprising the shape (Kourtzi and Kanwisher 2000; Hasson et al. 2001; Vinberg and Grill-Spector 2008) or the visual cue (e.g., texture, motion, color, or luminance) used to define the shape (Grill-Spector et al. 1998; Self and Zeki 2005; Georgieva et al. 2008). It has also been shown that LOC responds more vigorously when the subject's attention is devoted to the geometric rather than the surface properties of objects (Cant and Goodale 2007). Our results fit neatly within this characterization, given that LOC activation was found when subjects were required to discriminate between objects of identical volume and surface texture but different in shape, as contrasted with objects of identical volume and shape, but different in surface texture. Also, in line with previous findings, activation was higher in the LOC contralateral to the visual hemifield in which the stimuli were presented, in our case the left LOC (Hemond et al. 2007; McKyton and Zohary 2007; Large et al. 2008). Shape-related activity was also found more dorsally, nearby V3A, a finding that has been reported previously (Grill-Spector et al. 1999; Hasson et al. 2003; Denys et al. 2004; Cavina-Pratesi et al. 2007). It should be pointed out that our activations for shape versus texture discrimination in the control participants do not encompass the entire extent of LOC proper (i.e., as localized by images of objects vs. their scrambled counterparts) but rather were limited to the most superior and lateral division (LO), which has recently been associated with the processing of physical (but not perceptual) shape similarity (Haushofer et al. 2008).

In contrast to these findings for shape discrimination, when subjects were required to differentiate stimuli according to their texture, we found several foci of activation lying more

Table 3
Brain areas active in the 2 contrasts of interest for patient MS and patient DF

	Hemisphere	Talairach coordinates			t
		x	y	z	
Shape versus texture discrimination					
Patient MS					
PFs	Left	−54	−55	−23	3
LO	Left	−53	−68	−13	3
V3A	Left	−21	−81	26	3
Anterior insula	Right	35	18	5	3
IPL	Left	−59	−33	23	3
Middle IPS	Left	−48	−53	42	3
	Right	38	−37	38	3
vPM	Left	−55	2	37	3
dPM	Left	−28	−2	55	3
SMA	Left	−5	1	50	3
	Right	4	17	44	3
Patient DF					
NA					
Texture versus shape discrimination					
Patient MS					
SPL	Left	−37	−47	52	2.7
Patient DF					
pCoS	Left	−15	−76	−22	3
pLG	Left	−6	−91	−8	3
	Right	13	−91	−8	3
mLG	Left	−16	−46	−8	3
	Right	23	66	−8	3
Anterior insula	Left	−36	10	15	3
	Right	33	12	12	3
cIPS	Right	24	−71	29	3
Middle IPS	Right	39	−50	32	3
vPM	Left	−51	2	20	3
dPM	Left	35	−15	57	3
SMA	Left	−2	18	44	3
	Right	3	8	44	3

Note: pFs, posterior fusiform sulcus; IPL, inferior parietal lobe; vPM, ventral premotor cortex, dPM, dorsal premotor cortex; NA, no activation found; SPL, superior parietal lobe; pCoS: posterior collateral sulcus.

medially in the ventral stream, in the posterior portion of the lateral occipital sulcus, caudal to the CoS. These foci fit well with previous reports of surface pattern–related (but not strictly texture related) activity in humans (Peuskens et al. 2004). Unlike previous studies (Peuskens et al. 2004; Cant and Goodale 2007), we did not find activations within the lingual sulcus/LG nor the medial CoS. This may be because unlike the stimuli used in those previous studies, our texture stimuli did not include color: they were all constructed as purely grayscale images. It is possible that when asked to make judgments about surface textures (Peuskens et al. 2004) or material properties (Cant and Goodale 2007), subjects would have found it difficult to ignore the associated colors. If so, then the range of activations found within the medial occipital cortex in previous studies would not reflect the processing of texture per se, but rather the processing of a variety of features, all of which can contribute to the appearance of an object's surface, including color, smooth surface pattern, and lightness. This interpretation would fit with the fact that the putative color areas V4 and V8 are located in close proximity to the medial aspect of the CoS, thus lying more anteriorly in the medial occipital lobe than the foci localized here for texture alone.

Specially designed experiments will be needed to confirm whether surface features such as color and texture are extracted by different brain foci within the medial occipital cortex. For now, we can only state that our fMRI results suggest that a brain area selectively responsive for texture is located more caudally than the ones known to be selective for color (for a review, see Bartels and Zeki 2000). Likewise, behavioral

evidence not only confirms that form is processed independently from surface properties but also suggests that surface detail is processed independently of the processing of surface color (Cant et al. 2008). Moreover, patients have been described in the literature with texture discrimination impairments despite a sparing of color vision (Vaina 1990; Battelli et al. 1997). This apparent functional separation within the medial portion of the ventral stream suggests that individual surface features of objects are processed separately, rather than together in a common area dedicated to processing material properties (stuff) as a whole. It may be that there is no visual area that identifies material properties per se but instead a constellation of foci that independently extract the different components of visual information needed for inferring the material that constitutes a given object.

Net brain activity for texture as contrasted with shape processing was found beyond the ventral visual stream as well, notably within parietal and frontal areas. However, only activation within the cIPS was associated with the extraction of texture per se. Analysis of the error trials showed that the other activations—in the anterior insula, mFG, and SMA—were modulated by the difficulty of the shape discrimination task. It is unlikely that brain areas dedicated to texture processing would show task difficulty modulations associated with the processing of a nonrelevant stimulus feature. Activations in dorsal and ventral frontal areas have, however, been repeatedly associated with manipulations of task load in general (Lehmann et al. 2006; Liu et al. 2006; for a review, see Rees and Lavie 2001) and with manipulation of task difficulty in the visual discrimination domain more specifically (Sunaert et al. 2000). Activity within cIPS has been previously reported during judgments of surface orientation (Shikata et al. 2001, 2003; Vinberg and Grill-Spector 2008). In our texture task, subjects were asked to discriminate the grain of textured stimuli, 2 of which were identical. Identical texture, however, did not imply physical identity because all 3 textured spheres were randomly rotated in space. In other words, to perform the texture discrimination task successfully, subjects needed to isolate the texture perceptually, allowing for object orientation in 3D. The shape stimuli were each differently rotated as well, and area cIPS was activated by these stimuli likewise, although to a lesser extent. Several experiments have shown that cIPS is sensitive to orientation of stimuli regardless of texture (James et al. 2002; Valyear et al. 2006; Rice et al. 2007), but distortions and gradations of a textured surface when present would provide very efficient cues to orientation.

Causal Roles of LOC in Shape Processing and pCoS in Texture Processing

In Experiment 2, we tested 2 patients suffering from visual agnosia as a consequence of brain lesions affecting different portions of their ventral visual system. Patient DF developed visual agnosia after bilateral lesion of her LOC, whereas patient MS developed visual agnosia and achromatopsia after a lesion affecting the medial portion of his occipitotemporal cortex bilaterally and the LOC in the left hemisphere only. If the fMRI activations in Experiment 1 truly reflect a division of labor for the extraction of surface and geometric features of objects, respectively, then DF's spared medial occipitotemporal areas might underlie her ability to use surface features to recognize
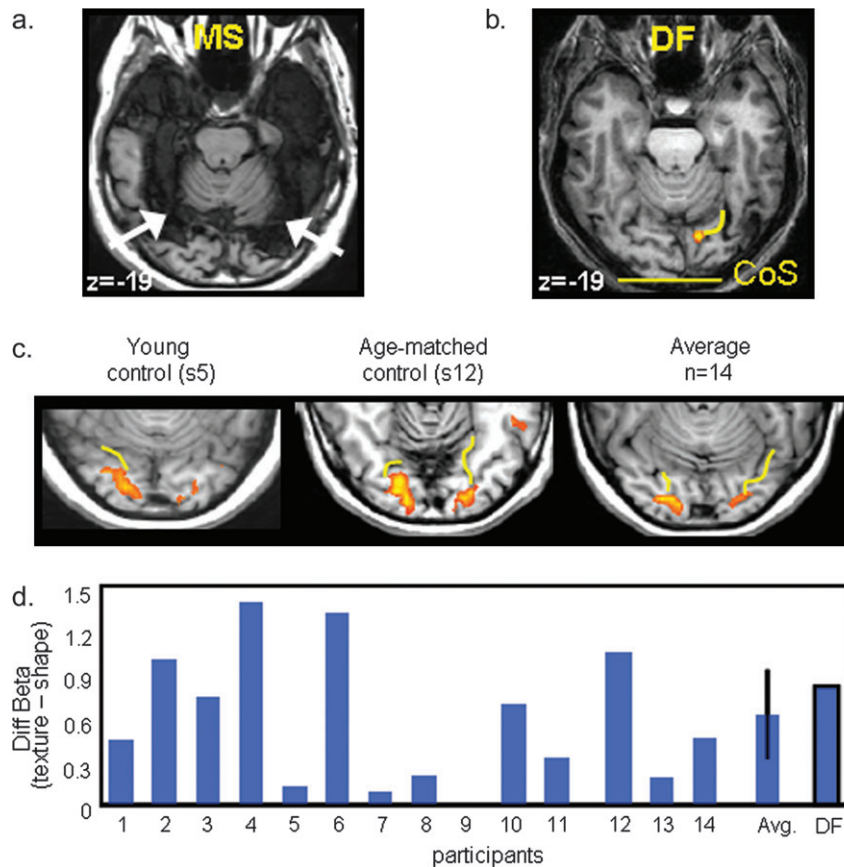
Figure 8. Individual activations for texture versus shape in patient DF, patient MS, and controls: CoS. The exact position of pCoS activations, localized bilaterally by contrasting texture versus shape discrimination, is shown in the clearest parasagittal and/or axial slices for patient DF (*b*), young subject #5 (*c*, leftmost panel), age-matched control #12 (*c*, middle panel), and the group average (*c*, rightmost panel). MS (*a*) shows no activation for this contrast, but his lesion overlaps completely with the locus of activation found in patient DF and control subjects (see white arrows). The higher brain response for texture trials in terms of beta weight differences (diff texture minus shape) for patient DF (*d*, rightmost plot) is very similar to that found in controls (young: 1–11 and age matched: 12–14) at the level of single subjects and the group average (*d*, second rightmost plot). Bars represent 95% confidence interval.

objects. Similarly, MS's spared right LOC might account for his intact ability to distinguish shapes. Our behavioral results confirmed a double dissociation between patients DF and MS in performing these visual discriminations. Whereas DF showed above-chance texture discrimination but no significant shape discrimination, MS showed the converse pattern, performing above chance only for shape discrimination. In parallel with this behavioral double dissociation, DF's lesion overlapped the region where brain activity was higher for shape than texture in our control subjects and in patient MS, whereas conversely, MS's lesion overlapped the region where brain activity was higher for texture than shape in the controls and in patient DF. In other words, the brain areas active for shape discrimination in control participants and in MS were compromised in DF's brain, whereas conversely, the brain areas active for texture discrimination in control participants and in DF were compromised in MS's brain.

This pattern of results argues for parallel "causal" roles of the LOC in shape discrimination and the pCoS in texture discrimination. The necessary participation of LOC in object discrimination confirms previous work (Heider 2000; James et al. 2003; Ellison and Cowey 2006). The novelty of our results lies in the fact that we have narrowed the causal role of LOC to geometric shape rather than the surface texture of objects. Because the nature of an object is defined by more than simply

its global geometry, it follows that area LOC can no longer be regarded as the single pivotal area for object recognition. Texture-related impairments have been previously reported in the literature, but the exact location of the critical lesion has never been clearly shown (Vaina 1987; Battelli et al. 1997). Patient DM (Vaina 1990), for example, had a clear lesion in the posterior portion of the right CoS, but the damage also extended into the adjacent medial and lateral occipitotemporal gyri, and DM was impaired in shape as well as texture discrimination.

Studying the neural correlates of spared functions in brain-damaged patients using neuroimaging is potentially highly informative but presents particular challenges. In this study, we took care to use stimuli that differed in the shape or in the texture dimension only. In this way, neither the behavioral nor the neural responses in the "impaired" task could be contaminated by an attempt by the patients to use their intact visual processing (texture for DF and shape for MS), thereby devoting their attention to the "wrong" stimulus dimension.

Role of LOC and Posterior CoS in Object Recognition
Whereas DF can use her spared texture processing for the purpose of recognition, MS does not seem able to use his ability to discriminate shapes to correctly identify objects. Of course, MS has a very extensive lesion, and therefore, it is reasonable to
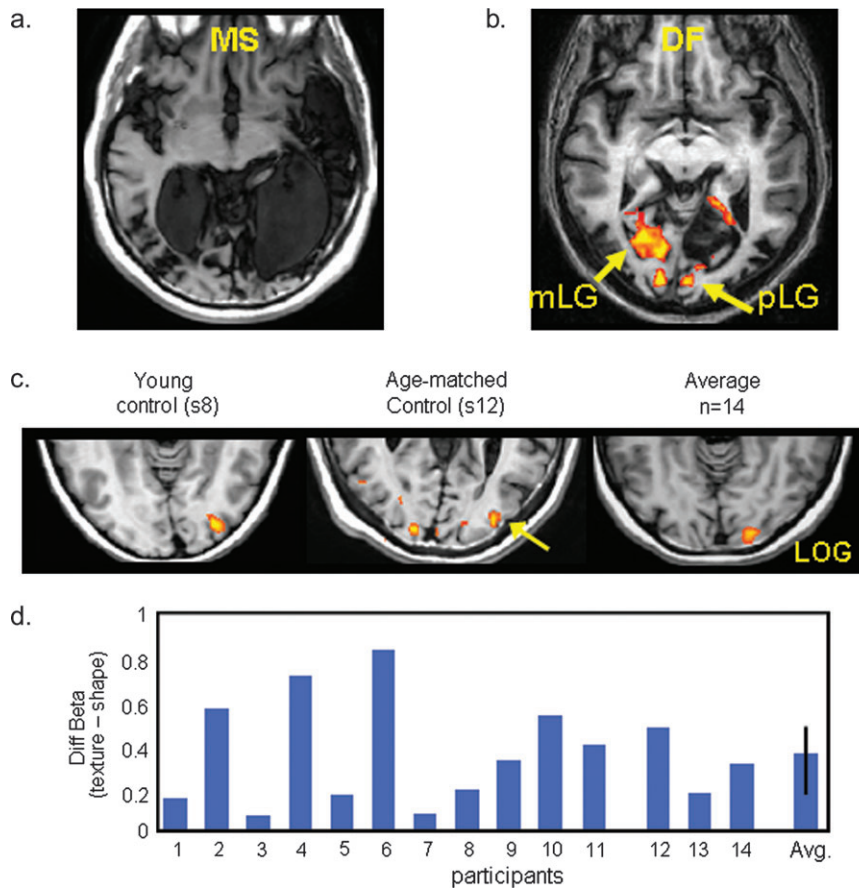
Figure 9. Individual activations for texture versus shape in patient DF, patient MS, and controls: LOG and pLG. The exact position of right LOG is shown in the clearest sagittal and/or axial slices for young subject #8 (*c*, leftmost panel), age-matched control #12 (*c*, middle panel), and the group average (*c*, rightmost panel). Activation within the LG (posterior and medial) is shown in the clearest sagittal and/or axial slices for patient DF (*b*). MS (*a*) again shows no activation for this contrast. The higher brain response for texture trials in terms of beta weight differences (diff texture minus shape) is reported for controls (young: 1–11 and age matched: 12–14) at the level of single subjects and the group average (*d*, rightmost plot). Bars represent 95% confidence interval. Differences in beta weights were found significant for DF in bilateral posterior and left mLG (data not shown).

expect other, perhaps higher level, factors to have compromised his visual recognition. Certainly, the fact that MS shows activation in LOC but yet cannot recognize or name objects indicates that LOC activation alone is insufficient for object recognition. The present results also suggest that LOC is not strictly necessary for object recognition, either: DF can identify objects by the use of features extracted elsewhere (such as color and texture). Nonetheless, her recognition is inferential rather than direct. This is in line with the fact that fMRI findings have been inconsistent in demonstrating the role of LOC in object recognition.

A similar question may be asked as to the role of pCoS in visual recognition. Patient MS, as well as the previous texture-impaired patients MD (Vaina 1990) and AB (Battelli et al. 1997), was impaired when asked to extract textural features at a global level. It is well known that early texture processing is used for the extraction of figure from ground, which in turn is necessary for segmenting scenes and reconstructing object boundaries (Vaina 1987). Given that patient MS is capable of figure–ground segregation based purely on color (Heywood et al. 1998a, 1998b; Kentridge et al. 2004) and that this probably depends upon processing in his intact striate cortex (Kentridge et al. 2007), we suggest that his deficit in

perceiving texture lies beyond the early stage of figure/ground segregation.

Funding

Supplementary Material

Supplementary material can be found at http://www.cercor.oxfordjournals.org/

Notes

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