

Separate Channels for Processing Form, Texture, and Color: Evidence from fMRI Adaptation and Visual Object Agnosia

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Previous neuroimaging research suggests that although object shape is analyzed in the lateral occipital cortex, surface properties of objects, such as color and texture, are dealt with in more medial areas, close to the collateral sulcus (CoS). The present study sought to determine whether there is a single medial region concerned with surface properties in general or whether instead there are multiple foci independently extracting different surface properties. We used stimuli varying in their shape, texture, or color, and tested healthy participants and 2 object-agnosic patients, in both a discrimination task and a functional MR adaptation paradigm. We found a double dissociation between medial and lateral occipitotemporal cortices in processing surface (texture or color) versus geometric (shape) properties, respectively. In Experiment 2, we found that the medial occipitotemporal cortex houses separate foci for color (within anterior CoS and lingual gyrus) and texture (caudally within posterior CoS). In addition, we found that areas selective for shape, texture, and color individually were quite distinct from those that respond to all of these features together (shape and texture and color). These latter areas appear to correspond to those associated with the perception of complex stimuli such as faces and places.

Keywords: color processing, fMRI, shape processing, texture processing, visual agnosia

Introduction

Although surface features such as texture and color allow the brain to infer the material of which an object is composed—a facility that is crucial for classifying objects in the natural world (Adelson 2001)—current research on the neural correlates of object recognition has focussed mainly on the role played by geometric features such as shape (Kourtzi and Kanwisher 2000; Murray et al. 2003), size (Murray et al. 2006; Cavina-Pratesi et al. 2007), and orientation (Valyear et al. 2006; Rice et al. 2007).

Surface cues can be highly diagnostic for object identification in natural versus 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), 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).

Brain areas associated with surface color (Lueck et al. 1989; McKeefry and Zeki 1997; Hadjikhani et al. 1998), texture (Peuskens et al. 2004), and pattern (Barrett et al. 2001) have been localized within the temporal-occipital region in humans, yet their role in object recognition is still poorly understood. A major step forward has been taken by Goodale and coworkers (Cant and Goodale 2007; Cant et al. 2009) who proposed the

existence of a division of labor between lateral and medial occipital cortices for discriminating geometric versus material properties of objects, respectively. They showed that although geometric properties of meaningless objects activated the lateral occipital cortex (LOC), surface properties of the same objects activated more medial areas near the collateral sulcus (CoS). In line with these results, we recently provided evidence that areas activated by shape and texture, respectively, play a causally necessary role in the perceptual discrimination of these features (Cavina-Pratesi et al. 2009). We tested 2 patients with visual object agnosia, one of whom (DF: Milner et al. 1991) performed well on our texture discrimination task but at chance on the shape discrimination task, whereas the other (MS: Newcombe and Ratcliff 1975) showed the converse pattern. We were able to match this behavioral double dissociation with a parallel neuroimaging dissociation, finding activation in medial occipitotemporal cortices only in patient DF during texture discrimination and activation in lateral occipitotemporal cortex only in patient MS during shape discrimination.

The evidence thus suggests that medial occipitotemporal mechanisms are specialized for resolving the surface features that can signal the material of which an object is composed. It should be noted, however, that although Goodale and coworkers varied the surface features of their stimuli in terms of texture and color, they failed to demonstrate the existence of independent brain modules for texture and color within the medial occipitotemporal cortex (Cant et al. 2009).

The aim of the present study was 3-fold: First, we planned to investigate whether the medial occipitotemporal cortex processes surface properties in general (including both texture and color) or whether it houses separate foci that extract different surface features (texture vs. color). Second, we planned to investigate whether separate information about geometric and surface features would converge in “higher” areas of the occipitotemporal cortex, which might combine shape, texture, and color features as conjoint “objects.” Third, we aimed to replicate our previous results on the necessary role played by lateral and medial occipitotemporal cortices in discriminating geometric and surface features, respectively, by using a novel set of stimuli and a different experimental paradigm. We used images of virtual 3D stimuli varying in their geometric (shape) or surface (texture or color) features and asked neurologically healthy participants, and 2 object-agnosic patients, to perform a behavioral discrimination task (Experiment 1), and a functional magnetic resonance adaptation (fMRI) task (Experiment 2). The 2 patients (MS and DF) suffer from visual agnosia as a consequence of selective lesions of their visual ventral streams. However, although patient DF’s perceptual deficit focuses on the geometric features of objects, leaving her ability to extract texture and color spared (Milner et al. 1991; Humphrey et al. 1994), patient MS’s perceptual deficit is centered on color (achromatopsia: Heywood and Kentridge 2003) and texture

(Cavina-Pratesi et al. 2009). Quite unlike DF, MS's perception of geometric structure (when the contours are clearly defined) remains intact (Kentridge et al. 2004).

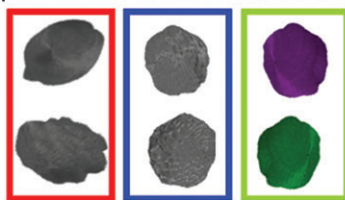
Material and Methods

Images of virtual 3D objects resembling furry balls that could vary in shape or in the surface dimensions of texture or color (Fig. 1) were used with neurologically intact participants and 2 object-agnosic patients (MS and DF) both behaviorally (Experiment 1) and in the magnetic resonance imaging (MRI) scanner (Experiment 2).

In Experiment 1, behavioral data were collected for patients DF and MS, and 8 age-matched controls, performing same-different discrimination tasks between pairs of stimuli differing only in either shape, or color, or texture (Fig. 1*a*).

In Experiment 2, 12 neurologically intact participants, along with patients DF and MS, took part in an fMRI experiment in which no-change (NC), shape-change (SC), texture-change (TC), and color-change (CC) blocks of trials (Fig. 1*b*) were intermingled with periods of fixation. To maintain their attention throughout the experimental session, we asked participants to perform a one-back task, by pressing a button with the right index finger whenever an image was immediately repeated. This implies that even within the "change" blocks, a stimulus was sometimes presented twice. The logic of the fMRI technique assumes that neuronal populations within a given cortical region are sensitive to specific aspects of a stimulus. This sensitivity is assessed by measuring the attenuation (reduction) or rebound (increase) of the blood oxygenation level-dependent (BOLD) signal in response to a pair of stimuli in which the second stimulus has been modified in one dimension only. If the BOLD signal is attenuated, then it is inferred that the neuronal population is not sensitive to the changed dimension (because it responds as if the stimulus is repeated identically). If the BOLD signal shows a rebound, then it is inferred that the neuronal population is sensitive to the changed dimension.

a. Experiment 1: same/different discrimination task



b. Experiment 2: fMRI

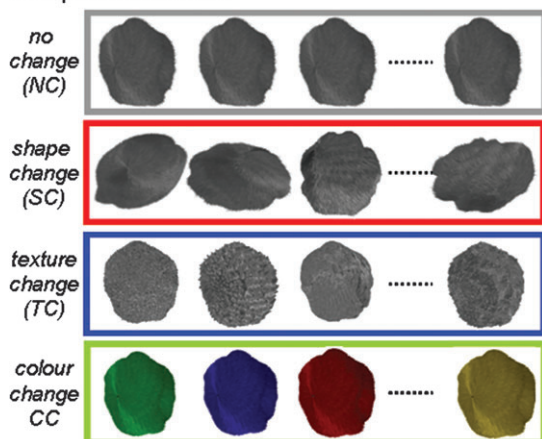


Figure 1. Visual stimuli for Experiments 1 and 2 were assembled using virtual 3D textured irregular objects resembling furry balls. (a) In Experiment 1, participants were asked to perform same-different judgments on objects that could vary in shape, texture or color only. Examples of trials are shown for the "different" condition only. (b) In Experiment 2, objects were assembled in order to create blocks of NC, SC, TC, and CC stimuli.

Participants: Experiments 1 and 2

Two brain-damaged patients (DF and MS) participated in both experiments. DF is right handed, and MS is left handed.

Patient DF has a profound visual form agnosia as a consequence of a hypoxic episode that damaged her LOC bilaterally (Milner et al. 1991). Structural MRI shows that DF's most clearly defined lesions overlap well with the location of area LOC in the ventral stream of healthy subjects, along with a further 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 relatively well-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 ventromedial occipitotemporal cortex bilaterally. His 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 the left homonymous hemianopia). For a more extensive case description of MS, see Newcombe and Ratcliff (1975) and Heywood et al. (1994). Although MS has a profound object agnosia, he does not have visual form agnosia, because he can readily discriminate between different shapes.

Eight age-matched controls (4 females; age range 51–60) also participated in Experiment 1, and 10 young participants (6 female; age range: 22–42) and 2 older males (age 51 and 60) participated in Experiment 2. All of them were right handed as measured by the Edinburgh Handedness Inventory (Oldfield 1971), all had normal or corrected-to-normal vision, and none had any history of neurological disorder. All participants (patients and intact controls) underwent repeated functional scans as well as one anatomical scan during the same session and gave informed consent before beginning the experiment, which was approved by the Ethics Committees of Durham University and York Neuroimaging Centre (YNIC).

Stimuli: Experiments 1 and 2

The virtual 3D stimuli used in the experiment were created using the software package Autodesk Maya Unlimited 2008 (Autodesk, San Rafael, CA). Shapes can be created in this package by stretching a "skin" over a skeleton defined by a set of lines in 3D space. Objects with random shapes were created by a custom program that built random skeletons constrained to fit within virtual boxes with predefined minimum and maximum sizes. The package also provides texturing options ("Maya Fur") that can be controlled by a wide range of parameters (e.g., texture element density, length, correlation, orientation, and curl). A custom program generated objects with random textures by varying these parameters randomly within predefined limits. The pigments of the underlying skin and of all of the texture elements were defined to be identical. Objects with random colors were produced by varying the red, green, and blue reflectances of these pigments randomly between predefined limits. One shape, texture, and color was chosen as the arbitrary standard object used in the NC condition. Sets of objects that departed from this standard in terms of one feature only, either shape, texture, or color, were created using the procedures outlined above (a total of 115 prototypes for each category). The same sets of objects were used in both Experiments 1 and 2. It is worth noting that it is inevitable that the textures covering objects that differ in shape in the SC condition will be different instances of a common type of texture. It would be possible to generate different instances of the same type of texture in the CC and NC sets. There is, however, no obvious way of applying the same logic to color. As we are particularly concerned with equating change in the TC and CC sets, we therefore chose to retain identical unchanging tokens of texture in the CC set and unchanging tokens of color in the TC set.

Apparatus and Procedures

Experiment 1

Experimental stimuli were created by arranging images of the objects from the sets described above into pairs vertically aligned on the right side of the screen, centered at an eccentricity of 6.65° of visual angle. The stimuli measured 15×6 cm at a viewing distance of 60 cm. Lateralized presentation was chosen to facilitate object discrimination for patient MS, who has a left hemianopia. In half of the trials, the pair of objects was identical, and in the other half, it was different. Same-different judgments were performed within the same visual feature (i.e., between 2 shapes, 2 textures, or 2 colors). For both same and different trials, stimuli were not perfectly aligned vertically and were left/right flipped in order to avoid visual discrimination based on symmetry. To reduce cognitive demands caused by frequent task changes, shape, texture, and color discriminations were performed in blocks of 30 trials. Participants were informed at the beginning of each block as to the feature they were about to discriminate. In each trial, stimuli were presented for 4 s, and subjects were required to perform a discrimination by signaling verbally whether the stimuli were “same” or “different.” Verbal report was chosen over manual report to avoid confounds associated with difficulties the patients might have learning/remembering the correct stimulus-response associations. Age-matched controls were tested in one session, whereas DF and MS underwent 2 separate sessions.

Experiment 2

Subjects lay comfortably supine inside the bore of the scanner, with their head fixed in order to minimize movements. Stimuli were backprojected (Dukane 8942 ImagePro 4500 lumens LCD projector) onto a custom in-bore acrylic rear projection screen and were viewed through a mirror mounted on the head coil.

We used a block design experiment where stimuli were organized into SC, TC, CC, and NC blocks. In each block, a series of stimuli were presented for 800 ms each, with a 200-ms inter-stimulus interval (blank screen). SC blocks consisted of 13 unique objects that differed in their geometric shape but not in their texture or color. TC blocks consisted of 13 unique objects differing in the type of surface texture but identical in underlying shape and color. CC blocks consisted of 13 unique objects that varied in color but maintained the same texture and shape. In NC blocks, we presented an identical stimulus (which was different from those used in the other blocks) 14 times. Each block of stimuli was intermingled with a period of fixation (which was used as a baseline condition). Because we asked our participants to perform a one-back task, during SC, TC, and CC blocks, one of the stimuli, and its location within the block, was randomly repeated.

Each run was organized into a series of 16 blocks of stimuli (4 blocks per condition) and 17 blocks of fixation, each one lasting 14 s, for a total duration of 7:42 min. During the fixation period, a $0.54^\circ \times 0.54^\circ$ black cross was presented on a white background. Each subject performed 4 experimental runs.

Stimuli were presented in the center of the screen and measured 6×6 cm at a viewing distance of 60 cm. Participants were 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.¹ They were also asked to perform a one-back task by pressing a button with the right index finger. Stimuli were controlled by Presentation software (version 9; Neurobehavioral Systems Inc, Albany). Manual responses were collected via keypads (“Lumitouch” pads—Photon Control, Inc, Burnaby, BC, Canada).

¹Free viewing was allowed to equate the experimental setting for patient MS who, having a left hemianopia, needed to move his eyes to see the stimuli entirely. Following the arguments of Cant and Goodale (2007), we believe that the deployment of attentional resources to the geometric versus surface features of the object would not grossly affect the viewing strategy applied by participants during the discrimination task.

Imaging Parameters

All participants were tested at the YNiC (York, UK), using a 3-T whole-body GE “Excite” MRI system. A High Density Brain Arrays 8 channels head coil was used in all experiments. BOLD-based functional MRI volumes were collected using optimized T2*-weighted segmented gradient echo planar imaging (26 cm field of view [FOV], with a 64×64 matrix size for an in-plane resolution of 3 mm, repetition time [RT] = 2 s, time echo [TE] = 30 ms, flip angle [FA] = 90 deg). Each volume was composed of 40 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 T1-weighted anatomic reference volume was acquired along the same orientation as the functional images using a 3D acquisition sequence (scan parameters: RT = 7.8 ms, TE = 3 ms, FA = 20° , matrix size = 256×256 , FOV = 256×256 mm², 176 slices, slice thickness = 1 mm, no gap, and total scan time = 5 min 3 s).

Data Analysis

Behavioral Data

In Experiment 1, accuracy scores of the age-matched controls were analyzed using a repeated-measures analysis of variance (ANOVA) and paired-comparison *t*-tests. Single-subject data for MS and DF were analyzed using binomial and χ^2 tests.

In Experiment 2, accuracy scores of the controls during the SC, TC, and CC conditions were analyzed using a repeated-measures ANOVA on the number of correct reports. For DF and MS, accuracy data were gathered but not analyzed, because some of the experimental conditions did not exceed the minimum 5 values difference required by χ^2 tests.

Imaging Data (Experiment 2)

Data were analyzed using “Brain Voyager QX” software (version 1.9; Brain Innovation, Maastricht, Netherlands). For each subject, functional data underwent 3D motion correction algorithms. 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 functional MRI (fMRI) data were analyzed using a general linear model (GLM), and a random-effect GLM was used for the group average analysis. The model included 4 experimental predictors (SC, TC, CC, and NC) and 6 motion correction predictors (*x*, *y*, *z* for translation and for rotation). The period of fixation (14 s) was used as a baseline. The experimental predictors were modeled as a transient (14-s) epoch where the square-wave function for each phase was convolved with the default Brain Voyager 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 ($P < 0.001$, minimum cluster size = 373 mm³) using Monte Carlo simulations (performed using BrainVoyager QX) to verify that our regions of interest were unlikely to have arisen by chance as a consequence of multiple comparisons.

After identifying the areas that were activated by a comparison of interest using odd runs only (runs 1 and 3), we performed analyses on the beta weights (β) extracted from the even runs only (runs 2 and 4). The use of separate data sets to localize the activated brain areas and to evaluate the different patterns of activity within them circumvents the problem of “circular analysis” (Kriegeskorte et al. 2009), where the independence of statistical tests for selective analysis (in this case “ β values”) is invalidated by the bias present in the comparisons used to select the areas (procedures sometimes called “double dipping”). “Beta”

values (β) for even runs only were extracted for each area, each subject and each condition separately and were analyzed using repeated-measures ANOVAs and corrected post hoc comparisons. Although Sidak adjustments for multiple comparisons were used for the main effects, 2-tailed *t*-test statistics (corrected for the numbers of planned comparisons) were used to scrutinize significant interactions. The *t*-test statistics were computed using subject-related variability as error estimates.

Single-subject imaging data on MS and DF were preprocessed and analyzed as described above. Significant activations 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. Patients MS and DF performed the main fMRI adaptation experiment for less than 4 runs (DF a total of 2 runs and MS a total of 3 runs); therefore, separate data sets could not be used for the selection and selectivity analyses, as they were for the control subjects.

Results

Experiment 1

In a repeated-measures ANOVA on the accuracy of the age-matched controls, TASK (shape vs. texture vs. color) did not reach significance ($F_{(2,14)} = 2.384$, $P = 0.129$), showing that performance did not differ across the 3 discrimination tasks (shape = 87%, texture = 90%, and color = 91%; Fig. 2). In contrast, our patients DF and MS obtained performance scores that differed markedly across the 3 discriminations, and they showed an opposite pattern of results from each other. DF's performance rose above chance only for the texture (74% [53/72], $P = 0.0001$) and color (85% [61/72], $P = 0.0001$) discriminations, which were significantly more accurate ($\chi^2(1) = 5.9$, $P = 0.015$ and $\chi^2(1) = 15.8$, $P = 0.0001$) than her shape discrimination (54% [39/72]). DF's scores on texture and color discrimination were not statistically distinguishable ($\chi^2(1) = 2.7$, $P > 0.10$). Conversely, patient MS performed above chance only for shape discrimination (81% [58/72], $P = 0.0001$), which was significantly more accurate than his texture ($\chi^2(1) = 12.5$, $P = 0.0001$) and color ($\chi^2(1) = 11.4$, $P = 0.001$) discrimination (52% [38/72] and 54% [39/72], respectively), which again were not statistically distinguishable ($\chi^2(1) = 0.03$, $P = 0.87$) from one another.

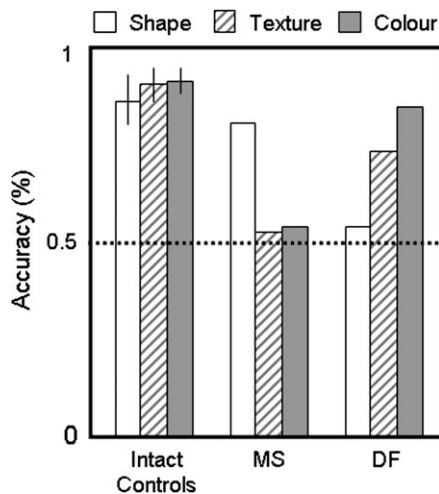


Figure 2. Percent correct responses for shape (white), texture (lined), and color (gray) trials plotted separately for intact age-matched controls, patient DF and patient MS. Bars represent standard errors. The horizontal dotted line represents chance level.

When DF and MS were compared with each other, we found that shape discrimination was significantly better in MS ($\chi^2(1) = 11.4$, $P = 0.001$), whereas texture ($\chi^2(1) = 6.7$, $P = 0.01$) and color ($\chi^2(1) = 15.8$, $P = 0.0001$) discrimination were significantly better in DF.

Experiment 2

In order to isolate the neural correlates of shape, texture, and color discrimination, we carried out conjunction analysis and standard pair comparisons analysis. Although standard subtraction logic can be usefully applied to experiments involving 2 conditions that differ in one or more cognitive components, in our paradigm, the investigated differences should emerge most clearly by the comparison of multiple experimental conditions. For example, shape selective voxels should rebound only when shape is changed (SC) and not when there is no change (during NC, TC, and CC blocks). It follows that shape selective voxels should respond more strongly for SC as compared with NC, for SC as compared with TC and for SC as compared with CC. In conjunction analyses, multiple paired comparisons are adjoined with an "and" function assuring that only those voxels that significantly satisfy all contrasts simultaneously are selected (Cavina-Pratesi et al. 2006). As such, they can provide more rigorous evidence with respect to the neural substrates of the presumptive cognitive process than single contrasts alone (Price and Friston 1997). Just as for shape voxels, we expect texture and color-selective voxels to respond only when texture (TC) or color (CC) is changed as compared with when it is not changed (NC, SC, and CC for texture and NC, SC, and TC for color).

For all comparisons, we will focus our results and discussion within the occipitotemporal cortices, while reporting stereotaxic coordinates for all active foci in Tables 1 and 2.

Table 1

Brain areas active in the contrasts of interest

Brain areas	Hemisphere	Talairach coordinates			Volume (mm ³)
		x	y	z	
Shape change ([SC > NC]∩[SC > TC]∩[SC > CC])					
LO	Left	-44	-75	-5	1501
	Right	43	69	-4	3734
pIPS	Left	-23	-85	24	374
	Right				
Texture change ([TC > NC]∩[TC > SC]∩[TC > CC])					
pCoS	Left	-23	-84	-13	1652
	Right	16	-88	-12	2609
Color change ([CC > NC]∩[CC > SC]∩[CC > TC])					
aCoS	Left	-30	-50	-13	376
	Right	28	-50	-13	1082
LG	Left	-10	-76	-8	727
	Right				
Anterior insula	Left	-31	20	9	1252
	Right				
DLPFC	Left	-38	1	27	1911
	Right	32	-2	32	565
mIPS	Left	-29	-60	39	730
	Right	27	-48	34	390
preSMA	Left				
	Right	-5	18	47	753
Shape and color and texture ([SC > NC]∩[TC > NC]∩[CC > NC])					
aFG	Left	-35	-50	-14	492
	Right	33	-44	-14	441
pFG	Left	-32	-73	-12	1217
	Right	25	-73	-11	390

LO = lateral occipital cortex; pIPS = posterior intraparietal sulcus; pCoS = posterior collateral sulcus; aCoS = anterior CoS; LG = lingual gyrus; FG = fusiform gyrus; DLPFC = dorsolateral prefrontal cortex; mIPS = medial intraparietal sulcus; preSMA = presupplementary motor area; a = anterior; p = posterior. SC=shape change, TC=texture change, CC=color change, and NC=no change.

Imaging Results in Neurologically Intact Participants

Behavioral Results for One-Back Task

In a repeated-measures ANOVA on the accuracy of the neurologically intact participants, TASK (shape vs. texture vs. color) did not reach significance ($F_{(2,22)} = 0.042$, $P = 0.96$). Performance in the scanner was equally accurate across the 3 discriminations (shape = 97%, texture = 97%, and color = 97%).

Separate Activations for Shape, Texture, and Color processing

Conjunction analysis. To extract voxels selectively responsive to shape, we compared SC trials with NC trials in a conjunction analysis using odd runs only (see Materials and Methods) as follows: $([SC > NC] \& [SC > TC] \& [SC > CC])$. We found bilateral foci of activation along the lateral occipitotemporal cortex and one focus of activation in the left dorsal extrastriate visual cortex (Table 1). As shown in Figure 3*a* (highlighted in red), the bilateral activations were congruent with the more dorsolateral portion of the lateral occipital complex (e.g., Malach et al. 2002), named LO. The more dorsal activation (not shown in the figure) was located at the very posterior end of the left intraparietal sulcus (pIPS), and it may correspond to area V3A (Tootell et al. 1997).

To extract voxels selectively responsive to surface texture, we compared TC trials with no TC trials in a conjunction analysis using odd runs only (see Materials and Methods) as follows: $([TC > NC] \& [TC > SC] \& [TC > CC])$. As reported in Table 1 and Figure 3*a* (highlighted in light blue), there were bilateral activations lying caudally to the CoS (henceforth referred to as pCoS), in congruence with the location of texture activations reported in previous literature (Peuskens et al. 2004; Cavina-Pratesi et al. 2009).

To extract voxels selectively responsive for surface color, we compared CC trials with no-CC trials in a conjunction analysis using odd runs only (see Material and Methods) as follows: $([CC > NC] \& [CC > SC] \& [CC > TC])$. As shown in Figure 3 (highlighted in green), a bilateral focus of activation was found along the anterior portion of the CoS (henceforth referred to as aCoS), whereas a single left lateralized focus lay caudally in the lingual gyrus (LG). These activations are congruent with the location of color-selective areas found in the ventral surface of both humans and macaque monkey using fMRI (Wade et al. 2008). Other active areas were found within the parietal (medial intraparietal sulcus [mIPS]) and frontal cortices (anterior insula, dorsolateral prefrontal cortex, and presupplementary motor area—pre-SMA, see Table 1).

Although the pattern of activation between the change and NC conditions within each localized area is predicted by the specific comparisons we applied, the exact relationship between the NC conditions (including NC proper and the feature-of-no-interest change conditions) remains open. One of the criticisms made of adaptation paradigms is that the conditions where the same stimuli are constantly repeated are less interesting for the participants as compared with the ones in which the stimuli are changing continuously. This might cause the subjects to pay less attention to the same-stimulus conditions as compared with the changing ones. Such an attentional imbalance could of course explain the higher response for SC, TC, and CC trials as compared with NC trials.

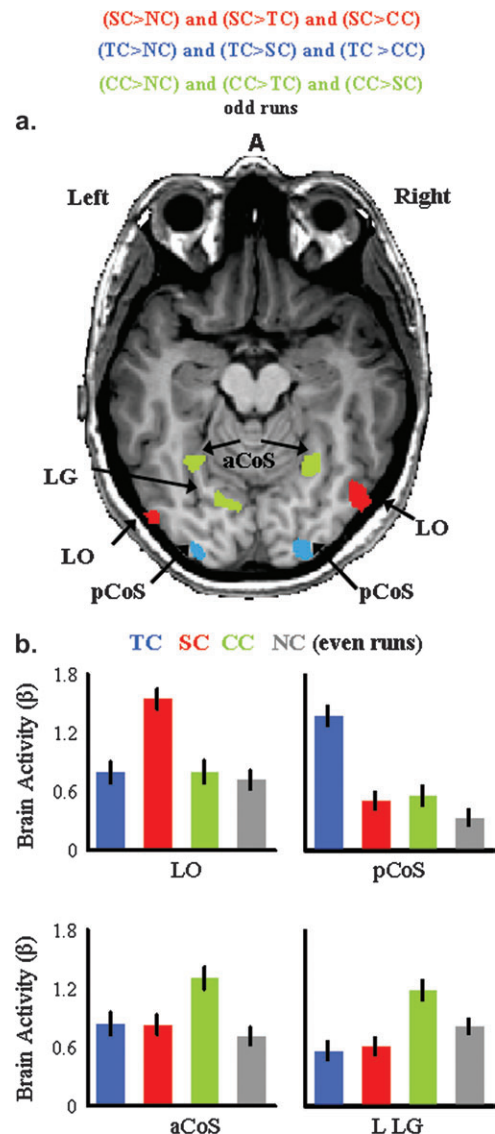


Figure 3. Group activation maps and beta weights for shape, texture, and color. (a) Rebound from adaptation for SC trials ($[SC > NC] \& [SC > TC] \& [SC > CC]$) in red, for TC trials ($[TC > NC] \& [TC > SC] \& [TC > CC]$) in blue, and for color-change trials ($[CC > NC] \& [CC > TC] \& [CC > SC]$) in green. SC activates bilateral LO. TC activates bilateral pCoS. CC activates bilateral aCoS and left LG. The group activation map is based on the Talairach averaged group results using odd runs only, shown for clarity on a single subject's anatomical scan. (b) Averaged beta weights (β) extracted from even runs only measured in each brain area for SC, TC, CC, and NC blocks. Bars represent standard errors. L = left, R = right, a = anterior, p = posterior, LG = lingual gyrus, LO = lateral occipital cortex, CoS = collateral sulcus. SC = shape change, TC = texture change, CC = color change, and NC = no change.

In order to test the exact relationship between all experimental conditions within the activated area in the ventral stream, beta weights (β) were extracted for each participant and each activated area using even runs only (see Materials and Methods) and were subjected to several ANOVAs. First, given that most of the areas were bilateral we ran a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN AREA (LO, pCoS, aCoS), and TRIAL TYPE (SC, TC, CC, and NC) as factors. Only the main effect of TRIAL TYPE ($F_{(3,33)} = 11.55$, $P < 0.0001$) and the interaction of BRAIN AREA \times TRIAL TYPE ($F_{(6,66)} = 11.8$, $P < 0.0001$) reached significance. Post hoc paired comparisons on the main effects showed that β values for NC trials were

significantly lower (P values ≤ 0.014) than SC, TC, and CC trials, which were not statistically distinguishable from each other. However, and more interestingly for our purpose, post hoc t -tests corrected for the number of comparisons in the interaction ($3 \text{ areas} \times 4 \text{ tasks} \rightarrow 0.05/12 = 0.0042$) showed that each area exhibited a specific rebound from adaptation for one feature change only, leaving all the other conditions statistically indistinguishable. More specifically, as shown in Figure 3*b*, area LO showed significantly higher β for SC than for TC ($P < 0.0001$), CC ($P < 0.0001$), or NC ($P < 0.0001$), which did not differ from each other (P values ≥ 0.676). Area pCoS showed significantly higher β for TC than for SC ($P < 0.001$), CC ($P < 0.0001$), or NC ($P < 0.0001$), which did not differ from each other (P values ≥ 0.185). Lastly, area aCoS showed significantly higher β for CC than for TC ($P < 0.0001$), SC ($P < 0.002$), or NC ($P < 0.004$), which did not differ from each other (P values ≥ 0.263). Given that differences between hemispheres did not reach significance, in a second ANOVA, we compared activations for all brain areas (including the unilateral response within LG excluded from the previous analysis) across hemispheres using BRAIN AREAS (LO, pCoS, aCoS, and LG) and TRIAL TYPE (SC, TC, CC, and NC) as factors. Again we found a significant main effect of TRIAL TYPE ($F_{(3,33)} = 3.795$, $P < 0.019$) and interaction of BRAIN AREA \times TRIAL TYPE ($F_{(9,99)} = 14.75$, $P < 0.0001$). Planned post hoc t -test comparisons on the interaction ($4 \text{ areas} \times 4 \text{ tasks} \rightarrow 0.05/16 = 0.0031$) showed that activations for LO, aCoS, and pCoS were identical to the ones reported above. More importantly, color-selective voxels within LG showed the same pattern of activation as aCoS voxels, with a significantly higher β for CC than for TC ($P < 0.0001$), SC ($P < 0.003$), or NC ($P < 0.0001$), which did not differ from each other (P values ≥ 0.209). Overall, the lack of differences between the NC and the “feature-of-no-interest” change conditions in all areas suggest that differences in activation were truly feature specific and not driven by nonspecific attentional factors.

Separate paired-comparisons analysis. It is possible to argue that using conjunction analysis to demonstrate the existence of independent subsystems might have introduced a bias, dictating to some degree the outcome as “independent” rather than “interactive” processing. We therefore carried out separate analyses using single-pair comparisons and independent localizers, to localize shape, texture, and color areas. First, following the logic of Cavina-Pratesi et al. (2009), we compared SC versus TC using odd runs only. We found bilateral foci of activation along the more lateral and dorsal parts of the lateral occipitotemporal cortex (LO, see Fig. 6*a*, supplementary materials, depicted in red). Second, using a similar logic, we compared TC versus SC using odd runs only and found bilateral activations lying within the pCoS (Fig. 6*a*, supplementary materials, depicted in blue). For completeness, we also compared SC versus CC and TC versus CC, and again, we found bilateral activations within LO and pCoS, respectively (see Fig. 6*a* supplementary material, depicted in orange and light blue, respectively). Given the importance of the comparison between texture and color in the present investigation, brain activity for pCoS was extracted from the voxels localized using TC versus CC. Third, we used an independent color localizer contrasting color versus grayscale paintings (see supplementary materials: independent localizer 1) and found significant activations bilaterally within the aCoS and within the left LG (Fig. 6*a*, supplementary materials, depicted in dark

green). For completeness, brain activity for color is also reported for the paired comparisons of CC versus TC (Fig. 6*a*, supplementary materials, depicted in light green) and CC versus SC (Fig. 6*a*, supplementary materials, depicted in bright green) using odd runs only. Talairach coordinates for all active areas are reported in Table 3, supplementary materials. Brain activity (in terms of β , extracted for the even runs only) was analyzed using repeated-measures ANOVAs. Brain activity for color was extracted from the areas localized by the independent comparison of color $>$ grayscale paintings. First, given that most of the areas were bilateral, we ran a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN AREA (LO, pCoS, and aCoS), and TRIAL TYPE (SC, TC, CC, and NC) as factors. Only the main effect of TRIAL TYPE ($F_{(3,33)} = 13.34$, $P < 0.0001$) and the interaction of BRAIN AREA \times TRIAL TYPE ($F_{(6,66)} = 10.42$, $P < 0.0001$) reached significance. Corrected post hoc paired comparisons on the main effects showed that β values for NC trials were significantly lower (P values ≤ 0.028) than SC, TC, and CC trials, which were not statistically distinguishable from each other. However, and more interestingly for our purpose, post hoc t -tests corrected for the number of comparisons in the interaction ($3 \text{ areas} \times 4 \text{ tasks} \rightarrow 0.05/12 = 0.0042$) showed that each area exhibited a specific rebound from adaptation for one feature change only, leaving all the other conditions statistically indistinguishable. More specifically, as shown in Figure 3*b*, area LO showed significantly higher β for SC than for TC ($P < 0.0001$), CC ($P < 0.0001$) or NC ($P < 0.0001$), which did not differ from each other (P values ≥ 0.736). Area pCoS showed significantly higher β for TC than for SC ($P < 0.0034$), CC ($P < 0.001$), or NC ($P < 0.002$), which did not differ from each other (P values ≥ 0.526). Lastly, area aCoS showed significantly higher β for CC than for TC ($P < 0.001$), SC ($P < 0.0001$), or NC ($P < 0.001$), which did not differ from each other (P values ≥ 0.131). For the conjunction analysis, given that no differences between hemispheres reached significance, we compared activations for all brain areas (including the unilateral response within LG excluded from the previous analysis) across hemispheres, in a second ANOVA using BRAIN AREAS (LO, pCoS, aCoS, and LG) and TRIAL TYPE (SC, TC, CC, and NC) as factors. Again, we found a significant main effect of TRIAL TYPE ($F_{(3,33)} = 8.90$, $P < 0.0001$), and interaction of BRAIN AREA \times TRIAL TYPE ($F_{(9,99)} = 19.08$, $P < 0.0001$). Planned post hoc t -test comparisons on the interaction ($4 \text{ areas} \times 4 \text{ tasks} \rightarrow 0.05/16 = 0.0031$) showed that activations for LO, aCoS, and pCoS were identical to those reported above. Most importantly, color-selective voxels within LG showed the same pattern of activation as aCoS voxels, with a significantly higher β for CC than for TC ($P < 0.0025$), SC ($P < 0.0001$), or NC ($P < 0.0022$), which did not differ from each other (P values ≥ 0.099).

Common activations for shape, texture, and color. Conjunction analyses can also be used to identify brain areas that are jointly activated by shape, texture, and color together. It is possible that some neurons might be driven by a conjunction of features and would therefore record a rebound from adaptation for all types of feature change, relative to NC. The logic is identical to the one applied above: If one voxel is selective for shape, texture, and color, then it should significantly rebound from adaptation for SC versus NC, for TC versus NC, and for CC versus NC. We performed a conjunction analysis using even runs only (see Materials and Methods) ($[TC > NC] \& [SC > NC] \& [CC >$

NC]), and activations were found bilaterally along the fusiform gyrus (FG), both anteriorly (aFG) and posteriorly (pFG, Table 1 and Fig. 4—highlighted in yellow). β Values from these areas (depicted in Fig. 4b) were subjected to a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN LOCATION (anterior, posterior), and TRIAL TYPE (SC, TC, CC, and NC) as factors. All the main effects reached significance, showing lower levels of activation in the left hemisphere ($F_{(1,11)} = 6.25, P < 0.029$), in the more anterior portion of FG ($F_{(1,11)} = 31.43, P < 0.0001$) and for the NC blocks ($F_{(3,33)} = 20.56, P < 0.0001$) as compared with all the others (SC, TC, CC; P values ≤ 0.001), which were not statistically distinguishable from each other (P values = 1.0).

Although activations along the FG could arguably be driven by the higher attentional resources devoted to the more difficult one-back task performed on the change blocks as compared with the NC blocks, we do not consider this to be likely. If the common activated areas along the bilateral FG were indeed driven by attention, then it is not clear why the frontoparietal “attentional network” (Corbetta and Shulman 2002; Corbetta et al. 2008) was not active as well (no frontal or parietal areas were active for the conjunction analysis of $([TC > NC] \& [SC > NC] \& [CC > NC])$ in Table 1). It is unlikely that top down attentional effects due to task load would activate voxels in visual areas but not in parietal and frontal cortices. We hypothesize instead that the activations along the FG reflect the activity of neurons that are truly responsive to the 3 features jointly, perhaps neurons receiving information from geometric and surface areas that are selective for higher-level stimuli such as faces and places. Figure 4a shows that activations along the FG partially overlapped with some of the voxels selectively responsive for faces versus places in the fusiform face area (FFA, anterior pink dotted lines, Fig. 4a) and for places versus faces in the posterior lingual gyrus (pLG, posterior brown dotted lines, Fig. 4a), mapped by the use of an independent localizer (see supplementary material: independent localizer 2). The locations of these areas agree well with those previously reported for some of the foci associated with face and place stimuli (Kanwisher et al. 1997; Epstein et al. 2007). To verify that the overlap was truly driven by the conjunction of shape, texture and color, we extracted brain activity (β) for SC, TC, CC, and NC from the voxels that were activated by both the face and place independent localizers and by the conjunction analysis of $([TC > NC] \& [SC > NC] \& [CC > NC])$. Brain activity extracted from the voxels in which the conjunction analysis overlapped with left FFA (14 voxels), right FFA (64 voxels), left pLG (180 voxels), and right pLG (275 voxels), were then subjected to a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN LOCATION (FFA, pLG), and TRIAL TYPE (SC, TC, CC, and NC) as factors. Only the main effects of HEMISPHERE ($F_{(1,11)} = 66.2, P < 0.0001$) and TRIAL TYPE ($F_{(3,33)} = 27.3, P < 0.0001$) reached significance, showing lower activity within the left hemisphere, and more importantly, for the NC as compared with all the change tasks (all P values < 0.0001). In addition SC, TC, and CC were mutually indistinguishable (all P values ≥ 0.45).

Common activations for texture and color. In order to test for the existence of brain areas jointly activated by texture and color but not by shape, we performed a conjunction analysis using odd runs only as follows: $([TC > NC] \& [CC > NC] \& [CC >$

$SC] \& [TC > SC])$. No significant active voxels were found at the selected threshold.

Imaging Results for Patients DF and MS

Behavioral results for one-back task. DF's and MS's accuracy in the scanner was similar to those recorded for the behavioral task. DF performed better for texture (6/8 correct; 75%) and color (6/8 correct; 75%) than for shape (4/8 correct; 50%). MS showed the opposite trend: he could discriminate between shapes (9/12 correct; 75%) but not between textures (5/12 correct; 41%) or colors (6/12 correct; 50%).

Separate Activations for Shape, Texture, and Color Processing

Conjunction analysis. Overlaid activation maps for SC trials as compared with no-SC trials using a conjunction analysis ($[SC > NC] \& [SC > TC] \& [SC > CC]$) are shown in Figure 5 (highlighted in red). We focused our single-subject analyses around area LOC, given its well-known role in form perception (Grill-Spector et al. 2001) and our results on neurologically intact participants. Talairach coordinates for all brain areas active for the above comparison in the 2 patients are reported in Table 2.

Patient MS showed one focus of activation within the left LOC (Fig. 5c) and one focus of activation within the dorsal bank of the calcarine sulcus (calcD). Talairach coordinates overlapped well with the dorsal subdivision of LOC, namely, the lateral occipital area (LO). The level of brain activity (β), reported here for completeness but not analyzed quantitatively, was higher for SC than for NC, TC, or CC, indicating

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

Brain areas	Hemisphere	Talairach coordinates			t Value
		x	y	z	
Shape change ($[SC > NC] \& [SC > TC] \& [SC > CC]$)					
Patient MS					
LO	Left	-58	-56	-4	3
calcD	Right	5	-80	7	3
mIPs	Left	-30	-60	53	3
	Right	26	-67	48	3
Patient DF					
n.a.					
Texture change ($[TC > NC] \& [TC > SC] \& [TC > CC]$)					
Patient DF					
pCoS	Left	-16	-87	-20	3
pLG	Right	21	-91	-5	3
Patient MS					
n.a.					
Color change ($[CC > NC] \& [CC > SC] \& [CC > TC]$)					
Patient DF					
aCoS	Left	-32	-60	-20	3
	Right	33	-52	-20	3
LG	Left	-30	-74	-23	3
Anterior insula	Left	-30	15	10	3
DLPC	Left	-43	23	30	3
	Right	45	27	25	3
mIPs	Left	-43	-51	32	3
	Right	39	-52	30	3
preSMA		-2	8	47	3
Patient MS					
n.a.					
Shape & color & texture ($[SC > NC] \& [TC > NC] \& [CC > NC]$)					
Patient MS					
Cu	Left	-4	-83	-14	3
Patient DF					
Cu	Right	8	-92	-9	3

LO = lateral occipital area; calcD = dorsal calcarine; and Cu = cuneus. Other abbreviations as in Table 1.

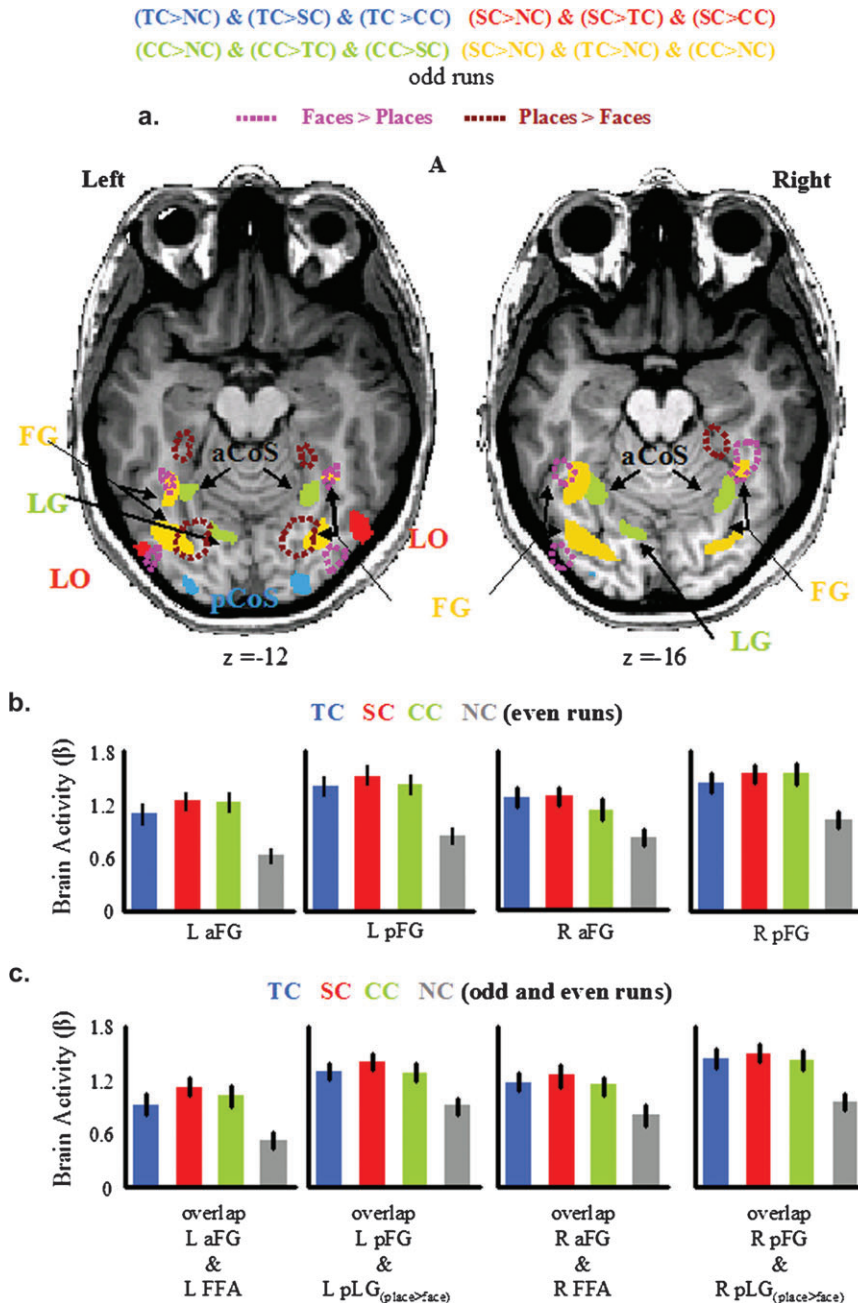


Figure 4. Group activation maps and beta weights for selective and common areas. (a) Rebound from adaptation for SC trials ($[(SC > NC) \& (SC > TC) \& (SC > CC)]$) in red, for TC trials ($[(TC > NC) \& (TC > SC) \& (TC > CC)]$) in blue, for color-change trials ($[(CC > NC) \& (CC > TC) \& (CC > SC)]$) in green and for the common activation of shape, texture, and color trials ($[(SC > NC) \& (TC > NC) \& (CC > NC)]$) in yellow. Activations for faces versus places (pink dotted lines) and places versus faces (dark brown dotted lines) from separate localizer runs are also reported. Common activations for SC, TC, and CC are localized bilaterally along the anterior and medial portion of the FG. As before, the group activation map is based on the Talairach averaged group results using odd runs only, shown for clarity on a single subject's anatomical scan. (b) Averaged beta weights (β) extracted for even runs only, measured in the common brain areas for SC, TC, CC, and NC blocks. (c) Averaged beta weights (β) extracted for even runs only from the voxels in which the common activated brain areas overlapped with the brain areas active for face versus place (left and right FFA) and for place versus face (left and right pLG). Bars represent standard error. FG = fusiform gyrus; other abbreviations as in Figure 3.

a clear preference for the geometry of the stimuli (Fig. 5*d*). No activation was found in the right hemisphere. MS's activation in terms of both location and β is similar to the results found in the left hemisphere of the control participants (see single subjects' activations in supplementary material, Fig. 7).

Patient DF showed no activation within LOC or its subdivision LO. This result is consistent with the fact that

her lesion (yellow arrows in Fig. 5*a*) overlaps greatly with the locus of activation seen in control participants and patient MS.

Overlaid activation maps for TC trials using a conjunction analysis ($[(TC > NC) \& (TC > SC) \& (TC > CC)]$) are shown in Figure 5 (highlighted in blue).

Patient DF showed 2 foci of activation: One was located at the posterior end of the left CoS (Fig. 5*a*), and the second was

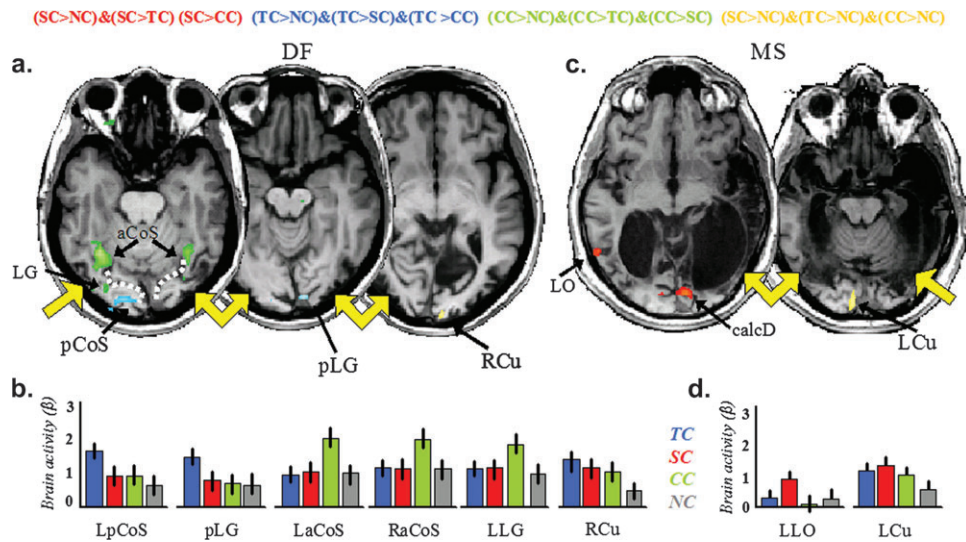


Figure 5. Activation maps and beta weights for shape, texture, and color in patients. Rebound from adaptation for SC trials ($(SC > NC) \& (SC > TC) \& (SC > CC)$) in red, for TC trials ($(TC > NC) \& (TC > SC) \& (TC > CC)$) in blue, for CC trials ($(CC > NC) \& (CC > TC) \& (CC > SC)$) in green and for the common activation of shape, texture, and color trials ($(SC > NC) \& (TC > NC) \& (CC > NC)$) in yellow. SC activates left LO in patient MS only (c). TC activates right pCoS and left pLG in patient DF only (a). CC activates bilateral aCoS and left LG in DF only (a). Common activations for SC, TC, and CC are localized within LCu in MS (c) and RCu in DF (a). (b,d) Averaged beta weights (β) measured in each brain area for SC, TC, CC, and NC blocks. Yellow arrows highlight principal brain lesions. calcD = dorsal calcarine; Cu = cuneus; other abbreviations as in Figure 3.

found in the right pLG. The level of brain activity (β) for the activated area in pCoS, reported here for completeness but not analyzed quantitatively, was higher for TC than for NC, SC, or CC, which showed comparable overall responses (Fig. 5b). DF's activation pattern in terms of both location and β is similar to the results found in control participants (see single-subject activations in the supplementary material, Fig. 7).

Patient MS showed no activation within the occipital lobe. This result is consistent with the fact that his lesion encompasses all of the medial aspects of the occipital lobe (yellow arrow, Fig. 5d), including the active foci found in control participants and in patient DF.

Overlaid activation maps for color-change trials using a conjunction analysis ($(CC > NC) \& (CC > SC) \& (CC > TC)$) are shown in Figure 5 (highlighted in green). As before, we focused on the temporo-occipital cortex, but stereotaxic coordinates for all active areas are reported in Table 2.

Patient DF showed bilateral activations within the aCoS and one focus of activation slightly caudally within the left LG (Fig. 5a). Beta values, again reported for completeness but not analyzed quantitatively, were higher for CC than for NC, SC, or TC (which showed comparable overall responses) in all 3 areas (Fig. 5b). DF's activations in terms of both location and β are similar to the results found in the control participants (see single-subject activations in supplementary material, Fig. 7).

Patient MS showed no activation for color (Fig. 5c). As before, this result is consistent with the fact that his lesion encompasses all of the medial aspect of the occipital lobe, including all the active foci found in control participants and in patient DF

Separate Paired-Comparisons Analysis

Just as for the controls, we localized shape, texture, and color areas using single-paired comparisons and independent localizers. First, we compared SC versus TC and SC versus CC and found for both contrasts a left lateralized activation along the more lateral and dorsal portions of the lateral occipitotem-

poral cortex in patient MS only (LO, see Fig. 8a, supplementary materials, depicted in red and orange, respectively). Second, we compared TC versus SC and TC versus CC and found for both contrasts a left lateralized activation lying within the pCoS of patient DF only (see Fig. 8a, supplementary materials, depicted in light blue and dark blue, respectively). Third, we used an independent color localizer contrasting color versus grayscale paintings (see supplementary materials) and found significant activations bilaterally within the aCoS and within the left LG, in patient DF only (see Fig. 8a, supplementary materials, depicted in dark green). The level of activity (β) for left LO and pCoS and aCoS bilaterally (reported for completeness but not analyzed quantitatively) reflected the pattern of activity found previously in the conjunction analysis. For completeness, we have also reported brain activity for the paired comparison of CC versus TC (Fig. 8a, supplementary materials, depicted in light green). Talairach coordinates for all active areas are reported in Table 4, supplementary materials.

Common Activations for Shape, Texture, and Color processing

Just as for the neurological intact participants, we ran conjunction analyses to isolate areas that are jointly activated by shape, texture and color, using $([TC > NC] \& [SC > NC] \& [CC > NC])$. Unilateral activations were found only within the right cuneus (Cu) of patient DF and the left Cu of patient MS, perhaps in correspondence with early visual areas. Activation maps, β values and Talairach coordinates are shown in Figure 5 (highlighted in yellow) and Table 2.

Common Activations for Texture and Color

As for the intact control participants, we performed a conjunction analysis using $([TC > NC] \& [CC > NC] \& [CC > SC] \& [TC > SC])$ to test for the existence of brain areas activated

by surface features in general. No significant active voxels were found at our chosen threshold.

Discussion

In the present study, we confirmed previous evidence of the role played by lateral and medial occipitotemporal cortices in discriminating geometric (shape) and surface (color and texture) features, respectively (Experiments 1 and 2). More importantly, we found that the medial occipitotemporal cortex contains separate foci for processing different surface features of a given object. In particular, although color-related activity was localized anteriorly within the CoS and the LG, texture-related activity lay more caudally within the CoS (Experiment 2). We also showed that areas selective for shape, texture, and color were quite distinct from those areas that respond to all of these features (shape and texture and color) together. The latter were found to correspond closely with some of those associated with the perception of more complex stimuli such as faces and places. Finally, we tested 2 patients with object recognition difficulties following different patterns of ventral-stream damage. We showed that a disruption or sparing of the surface-feature selective areas, versus a reciprocal sparing or disruption of area LO, was associated with a loss of discrimination for the corresponding feature/s (texture or color vs. shape) along with successful discrimination on the other/s (Experiments 1 and 2).

Shape

A selective rebound from adaptation for object shape was found in an area identifiable with LO. This area is part of the so-called “object area” (LOC), which has been traditionally localized by contrasting images of intact objects versus scrambled versions of the same images (Malach et al. 1995). Recent findings have refined the function of this area, which is now associated specifically with the extraction of shape per se, rather than with either the specific contours comprising the shape (Kourtzi and Kanwisher 2000; Vinberg and Grill-Spector 2008), or the visual cue (texture, motion, color, or luminance) used to define the shape (Grill-Spector et al. 1998; Self and Zeki 2005; Georgieva et al. 2008). This definition fits perfectly with the idea that the LO subdivision of LOC responds more vigorously when asked to deal with the geometric rather than the surface properties of objects in the present and previous (Cant et al. 2009) adaptation experiments.

Texture

A selective rebound from adaptation for texture was localized more medially, within the pCoS bilaterally. These foci fit with previous reports of texture (Cavina-Pratesi et al. 2009) and surface pattern related (but not strictly texture related) activations (Peuskens et al. 2004). However, unlike previous studies (Peuskens et al. 2004; Cant and Goodale 2007; Cant et al. 2009), we did not find activations within the lingual sulcus/gyrus nor in the anterior CoS. This may be because unlike the stimuli used in those previous studies, our texture stimuli did not include color variation (being constructed as purely grayscale images), and their texture was defined solely through local small-scale variations of the structure of their surfaces. Unlike the stimuli used in those previous studies, our textural stimuli only varied in the microgeometry of their

surfaces (not to be confused with the macrogeometry of their overall shape). In other words, they differed in texture defined as a 3D property that could be detected by touch as well as by vision (Koenderink et al. 2007; Ho et al. 2008). We would draw a distinction between “texture” as a microgeometric property of surfaces, and “pattern” as a property in which coloration varies in some recognizable fashion over the surface of an object. A zebra, for example, has a more or less uniform horse-hair texture but a pattern of irregular black and white stripes. Some of the objects used in previous studies varied in both pattern and texture in our terms, which may account for the differences between the activations we found and those reported in those earlier studies.

One might reasonably have concern about this result in pCoS if the stimuli in the TC blocks differed from the other blocks in terms of low-level visual properties such as spatial frequency content. One might intuit that the TC would vary more than the others in terms of contrast and therefore it would activate the pCoS more given its location near retinotopic cortices. To address this issue, we computed the power spectra across spatial frequencies for the luminance component of all of our images. We then computed the coefficient of variation (the standard deviation of power divided by the mean) at all frequencies for each stimulus type as the coefficient of variation should best predict the extent of adaptation to variation in low-level properties of the stimuli. It turned out that the shape stimuli (SC block) produced higher average power than CC and TC. Importantly, the coefficient of variation is remarkably similar across nearly all frequencies for TC and SC. At the lowest frequencies, the coefficient of variation for TC and CC are similar (a graph of the coefficients of variation is presented in the supplementary Fig. 10). This pattern of variability rules out the possibility that TC adaptation in pCoS is attributable to a confounding effect of contrast activating retinotopic areas.

Color

A selective rebound from adaptation for surface color was found medially within the left LG and the aCoS (bilaterally). These locations fit well with color-related areas V4/V8 (McKeefry and Zeki 1997; Hadjikhani et al. 1998) or VO1 (Brewer et al. 2005) and V4 α (Bartels and Zeki 2000) or the anterior color area (Murphey et al. 2008), respectively.

Previous studies have failed to isolate brain areas truly selective for color as opposed to texture. Common activations for all combinations of color, texture, and shape have been reported within several ventral areas, mostly within anterior and medial portions of the FG (Cant and Goodale 2007; Cant et al. 2009). Not surprisingly, these locations are very similar to the joint activations that we found for TC, SC, and CC in the present study. The absence of specific activations in known color areas in Cant and coworkers' results might be related both to the nature of their visual stimuli and the task demands they used. As we noted above, they used stimuli with complex surface features varying in both texture and pattern resembling real materials such as laminated oak, metallic paint, marble, and tinfoil, whereas our texture stimuli simply varied in surface microgeometry. Their stimuli may also have differed more than ours in other surface properties such as reflectance and specularly. As a consequence of these differences, it is possible that the processing areas localized by Cant and coworkers were

responsive to combinations of features (including color), rather than to individual surface features per se. For example, behavioral studies have clearly shown that the surface feature of glossiness can be represented in conjunction with other surface features such as coarser scales of 3D texture (Ho et al. 2008).

Another factor that might have facilitated the identification of color areas in our study is the task. Although Cant et al. (2009) used a passive viewing paradigm, we asked our participants to perform a one-back task and therefore to pay attention to each stimulus feature. Attentional modulation has been widely found within color areas (Maunsell and Treue 2006) and may have contributed to the activations we observed.

Common Neural Activations During Shape, Color, and Texture Discrimination

Brain areas showing single-feature selectivity for shape, color, or texture sit beside other areas that respond to all of the features together. These multifeature areas lie within the FG, extending toward both the anterior and the posterior portions of the gyrus. Neurons selective for multiple features of objects have been reported in the inferior temporal (IT) cortex of macaque monkey. Although some neurons respond to either shape or color (Komatsu et al. 1992), others are modulated by different combinations of shapes, colors, and patterns (Komatsu and Ideura 1993). IT neurons have been found to show either selective responses to 3D texture or to a combination of these same textures and shapes (Koteles et al. 2008). It should be noted however that within a single voxel, there are thousands of neurons, and therefore, it is not possible for us to trace back our conjunction activations to either neurons selective to all features simultaneously or to overlapping populations of neurons each singly selective for color, texture, and shape. Areas of common activation for shape, color, and texture along the FG overlap quite well with voxels selective for more complex visual stimuli such as scenes (pLG, Epstein et al. 2007) and faces (FFA, Kanwisher et al. 1997). Cant and Goodale (2007) similarly found a compelling overlap between areas selective for material properties and areas selective for places and faces. Presumably, the identification of such complex stimuli relies on combinations of features including shape, color, and texture. Indeed, current models of scene recognition postulate the use of surface cues such as color (Oliva and Schyns 1997) and texture (Renninger and Malik 2004) in the rapid categorization of scenes (scene “gist”). Similarly, when asked to discriminate faces, observers do not use only shape (local/global, Schiltz and Rossion 2006; Liu et al. 2010) but rely also on surface features such as skin color and pigmentation (Bruce and Langton 1994; Vuong et al. 2005; Nestor and Tarr 2008).

Causal Roles of Lateral and Medial Occipitotemporal Cortices in Geometric and Surface Feature Processing

If the fMRI activations within lateral and medial occipitotemporal cortices 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 color and texture to help recognize objects (Humphrey et al. 1994). Similarly, MS's spared right LOC might account for his intact ability to distinguish shapes. Our behavioral results in Experiment 1

confirmed a double dissociation between patients DF and MS. Although DF showed above-chance texture and color 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, Experiment 2 showed that DF's lesion included the region where brain activity was higher for shape than texture and color in our control subjects and in patient MS, whereas, conversely, MS's lesion included the region where brain activity was higher for texture and color 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 and, conversely, the brain areas active for texture and color discrimination in control participants and in DF were compromised in MS's brain. This pattern of results argues for specific causal roles of LO in shape discrimination and pCoS and aCoS in the discrimination of surface features such as texture and color. The necessary participation of LO in object discrimination confirms previous work (James et al. 2003; Ellison and Cowey 2006; Cavina-Pratesi et al. 2009). The novelty of our results lies in the fact that we have narrowed the causal role of LO to overall macrogeometry, specifically excluding the surface indentations or colors of objects. Similarly, perceptual impairments have been previously reported in the neuropsychological literature for both texture (Vaina 1987; Battelli et al. 1997; Cavina-Pratesi et al. 2009) and color (Bouvier and Engel 2006), though the extent of their independence from shape discrimination impairments has remained unclear. The present data confirm clearly that the discrimination of surface features is carried out by systems quite separate from those underlying shape discrimination.

Of course our brain lesion data alone do not allow us to argue also for mutually independent mechanisms for texture and color discrimination, because both types of discrimination are spared in DF, and both are impaired in MS. Nevertheless, our fMRI data lead us to predict that patients with sufficiently selective lesions to medial occipitotemporal cortex might present a “triple dissociation” between shape, texture, and color deficits. Unfortunately, transcranial magnetic stimulation, currently the only viable tool to create virtual lesions in the human brain, cannot reach such medial parts of occipitotemporal cortex, so that the testing of patients with selective brain lesions remains the only method available to assess the causal role played by posterior and anterior portions of the CoS.

MS's lesion includes the anterior portion of the CoS and the LG, near to the well-known color areas V4/V8 (VO1), and V4 α (anterior color area), which have been associated with achromatopsia (Heywood and Kentridge 2003) since the late 1970s (Poppel et al. 1978). Although our data clearly show that areas in the anterior portion of the CoS and the LG are necessary to discriminate colors, it is not yet clear whether these areas are involved in color vision only (Bouvier and Engel 2006). MS's lesion is extensive, and his deficit also includes hemianopia and prosopagnosia, the latter according well with the lack of activity within face-selective areas in his data presented here in Figure 9 of the supplementary material (OFA and FFA). As also depicted in Figure 9, however, DF does show active voxels within FFA, though activation is completely missing more posteriorly in OFA (see also Steeves et al. 2009). Separate clusters of voxels selective for faces within FFA/OFA

and for color in aCoS/LG in control participants confirm previous studies (Clark et al. 1995) and suggest that the common association of achromatopsia and prosopagnosia might be because the CoS and the FG share the same vascular substrate.

The lack of common activity for SC, TC, and CC in patients MS and DF suggests that these areas might play a fundamental role in combining multiple stimulus characteristics to achieve a fully unified representation of particular objects and scenes. Although these common areas of activity along the FG seem to be spared in DF, they would presumably not receive the full range of stimulus information needed for a unified multidimensional representation.

Surface Features

Our data demonstrate for the first time that a brain area selective for texture is located more caudally than the areas selective for color and that they both lie within the medial portion of the occipitotemporal cortex. This clear functional separation within the medial portion of the ventral stream suggests that individual surface features of objects are processed separately. This is confirmed by behavioral evidence showing not only that form is processed independently from surface properties but also that surface texture is processed independently from surface color (Cant et al. 2008). Likewise, patients have been described in the literature with texture discrimination impairments despite a sparing of color vision (Vaina 1990). It is likely that yet other surface properties of objects are processed within the medial occipitotemporal cortex, one example being a specific brain area responsive for light-emitting as compared with light-reflecting objects within the LG (Leonards et al. 2005). This area might be associated with the perception of glossiness that has been identified as a critical feature in guiding our oculomotor behavior while exploring paintings (Leonards et al. 2007).

We have found no evidence for any single visual area that identifies surface properties in general, and we suggest instead that a constellation of foci independently extract the different surface features needed for inferring the material that constitutes a given object.

Conclusion and Future Directions

The existence of separate and common brain foci associated with the perception of objects in terms of shape, color, and texture, enriches the realm of possibilities with which we can describe the functional organization of the ventral visual stream. So far, visual information has been mapped onto the cerebral cortex depending on its exact location in the visual field (retinotopic mapping) or on the stimulus category it belongs to (objects, faces, places, bodies, and words). Our work brings further evidence for an intermediate level of visual mapping, based on the type of visual feature that is being processed. This further level of analysis sits midway between the low and high level processing represented by retinotopic and stimulus category mapping, respectively. Studies directly investigating the relationships between these 3 different levels of visual mapping, within a single experiment and with the same subjects, will be needed to clarify their respective roles in constructing complete representations of the visual world in the ventral visual cortex.

Supplementary Material

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

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