RESEARCH ARTICLE

fMR-adaptation reveals separate processing regions for the perception of form and texture in the human ventral stream

Jonathan S. Cant · Stephen R. Arnott · Melvyn A. Goodale

Abstract We recently demonstrated that attending to the form of objects and attending to their surface properties activated anatomically distinct regions of occipito-temporal cortex (Cant and Goodale, Cereb Cortex 17:713–731, 2007). Specifically, attending to form activated the lateral occipital area (LO), whereas attending to texture activated the collateral sulcus (CoS). Although these regions showed preferential activation to one particular stimulus dimension (e.g. texture in CoS), they also showed activation to other, non-preferred stimulus dimensions (e.g. form in CoS). This raises the question as to whether the activation associated with attention to form in CoS, for example, represents the actual processing of object form or instead represents the obligatory processing of object texture that occurred when people attended to form. To investigate this, we conducted an fMR-adaptation experiment which allowed us to examine the response properties of regions specialized for processing form, texture, and colour when participants were not explicitly attending to a particular stimulus dimension. Participants passively viewed blocks where only one dimension varied and blocks where no dimensions varied, while fixating a cross in the centre of the display. Area LO was most sensitive to variations in form, whereas the CoS was most sensitive to variations in texture. As in our previous study, no regions were found that were *most* sensitive to variations in colour, but unlike the results from that study, medial regions of the ventral stream along the fusiform gyrus and CoS showed *some* selectivity to colour. Taken together, these results replicate the findings from our previous study and provide additional evidence for the existence of separate processing pathways for form and surface properties (particularly texture) in the ventral stream.

Keywords Form perception · Texture perception · Functional magnetic resonance imaging adaptation · Ventral visual stream

Introduction

Most studies of object recognition, particularly in the neuroimaging literature, have concentrated on the role played by shape and form cues and have largely ignored the contribution of surface properties, such as colour and visual texture (for review, see Cant and Goodale 2007). Those fMRI studies, for example, that have identified the lateral occipital area (area LO) as important for object recognition have focused almost entirely on the geometric properties of objects (e.g. Grill-Spector et al. 1998). There has been little exploration of the role of this area and other regions of the ventral stream in processing the surface properties of objects. In a recent study, however, we showed that attending to the surface properties of objects and attending to their form activated quite different regions of the ventral stream (Cant and Goodale 2007). Like others, we showed

J. S. Cant · S. R. Arnott · M. A. Goodale
CIHR Group on Action and Perception,
University of Western Ontario, London, ON, Canada

J. S. Cant · M. A. Goodale
Neuroscience Program, University of Western Ontario,
London, ON, Canada

J. S. Cant · S. R. Arnott · M. A. Goodale (✉)
Department of Psychology, University of Western Ontario,
London, ON N6A 5C2, Canada
e-mail: mgoodale@uwo.ca

that attending to object form activated area LO. But when participants attended to the surface properties of the same objects, activation was present in more medial and anterior regions in the collateral sulcus (CoS) and the inferior occipital gyrus (IOG). We went on to demonstrate that attending explicitly to texture activated regions in the IOG and the CoS, as well as regions in the lingual sulcus (LS) and the inferior temporal sulcus (ITS). To our surprise, we found no evidence of colour-specific cortical areas in the brain, although regions in early stages of visual processing in the primary visual cortex (V1) and the cuneus yielded more activation when people attended colour compared to when they attended texture—but this activation was never higher than the activation yielded when people attended form. In other words, the processing of object form and the processing of surface properties engages anatomically distinct regions in the ventral stream. This finding is in agreement with an elegant study by Giovanni Berlucchi and his colleagues, who showed a dissociation between shape and colour processing in a patient (PB) who was left virtually blind as a result of an electric shock that led to vascular insufficiency (Zeki et al. 1999). Specifically, patient PB is perimetrically blind, lacks visual acuity, and has extremely poor shape perception but nevertheless demonstrates conscious colour perception. Psychophysical testing with pictures of common objects (e.g. car, boat) revealed that Patient PB can accurately name the colours of objects that are presented to him, but has a complete inability to recognize those objects based on shape. Moreover, an fMRI experiment revealed areas V1 and V2 as the potential loci of PB's spared colour processing. In summary, while the psychophysical testing revealed a striking dissociation between shape and colour processing, these latter imaging results, combined with our recent fMRI results, also suggest that information about an object's colour is extracted relatively early in visual analysis as compared to the extraction of its surface texture, perhaps because the latter requires more complex processing.

Although our study appeared to suggest that particular regions were selective for processing a single stimulus dimension (e.g. form in area LO), these same regions also showed at least some activation to the other, non-preferred stimulus dimensions (e.g. activation to texture in area LO). This raises the question as to whether the activation to texture in area LO represented texture processing per se, or simply the obligatory processing of form while people were explicitly attending to texture. After all, the form of the objects was not held constant while participants made texture discriminations (and vice versa when people were attending to form). Thus, although the results of the Cant and Goodale (2007) study provide convincing evidence that extra-striate regions are specialized for the processing of different object attributes, the question remained as to *how*

specialized these regions are. To investigate this question in the present study, we used a complementary paradigm, functional magnetic resonance adaptation (fMRA). By using fMRA, we could now investigate the processing associated with changes in a single stimulus property (e.g. form) without the confounding effects of changes in other stimulus properties (e.g. texture and colour).

In the fMRA paradigm, the blood oxygen-level dependent (BOLD) signal in different brain regions will be reduced when the same stimulus is repeatedly presented to the participant, a phenomenon known as repetition suppression or repetition attenuation (Grill-Spector et al. 1999, 2006 Grill-Spector and Malach 2001; Henson 2003; Schacter and Buckner 1998; Wiggs and Martin 1998). If a particular property of the stimulus is then changed, recovery of the BOLD signal might be observed in some regions but not others. If there is no recovery from adaptation, then one can conclude that the neurons in this region do not participate in the processing of this stimulus property. If, however, there is recovery from adaptation (as evidenced by a rise in the BOLD signal), then one can conclude that neurons in this region do play a role in the processing of that stimulus property. For example, if a release from adaptation is observed in a specific cortical region when one changes the texture of an object (but not the form or colour), then one can surmise that this region participates in the processing of at least some aspect of surface texture. Moreover, it has been argued that the fMRA paradigm offers greater spatial resolution in the delineation of different functional regions than more conventional paradigms (for review, see Grill-Spector et al. 2006).

In the present study, we used fMRA to examine the response properties of ventral-stream cortical regions specialized for processing form, texture, and colour when participants were not explicitly attending to any particular stimulus dimension. Other investigations of ventral-stream processing have used this technique to great effect in establishing the functional selectivity of different visual areas (Andrews and Ewbank 2004; Grill-Spector et al. 1999; Kourtzi and Kanwisher 2001; Ewbank et al. 2005). Thus, we felt confident that fMRA would enable us to establish whether form, colour, and surface texture are processed selectively by different ventral-stream areas. Moreover, the potential for greater spatial resolution and the increased methodological control over stimulus presentation associated with fMRA are compelling reasons to follow up on our previous neuroimaging results (Cant and Goodale 2007) by using the fMRA paradigm.

In our study, participants passively viewed stimulus blocks where only one dimension varied (form, texture, or colour) and stimulus blocks where no dimensions varied (baseline adaptation blocks). We used the same stimulus set that was used in our previous study, but this time placed a

fixation cross in the centre of the display. The participants' only task was to maintain fixation on this cross while the stimuli were presented to them. The motivation for using fixation as our primary experimental task was to examine the response properties of regions in occipito-temporal cortex while controlling for possible differences in eye movements and deployments of attention across conditions. We felt confident in using fixation as our primary experimental task as previous fMRA studies have demonstrated robust results in occipito-temporal cortex in the absence of tasks requiring explicit deployments of attention (e.g. Kourtzi and Kanwisher 2000, 2001; Valyear et al. 2006). Nevertheless, in order to validate the use of this fixation task, we monitored activity in the lateral intraparietal area (LIP, an area known to be involved in the planning and execution of saccades as well as covert shifts of attention; for review see Culham and Kanwisher 2001) to see if there was evidence for differences in the numbers of eye movements or differences in shifts of attention across conditions. As it turns out, this was not the case (see "Discussion" for more detail). We also used a conservative conjunction analysis to thoroughly investigate the response properties of ventral-stream cortical regions (see "Materials and methods" and "Results" for more details). This analysis allowed us to determine whether a given region (e.g. area LO) preferentially processes only a single attribute of an object (e.g. form) or instead processes multiple object attributes (e.g. form, texture, and colour). Taken together, we believe the methodological control over stimulus presentation afforded by fMRA and the computational power afforded by the conjunction analysis provide another powerful way to study ventral-stream stimulus selectivity. We used these two approaches in the present study to complement and extend upon our previous neuroimaging results (Cant and Goodale 2007).

Based on the results of previous neuroimaging studies of form and surface-property perception (Cant and Goodale 2007; Peuskens et al. 2004) and from the relevant neuropsychological literature (Duvelleroy-Hommet et al. 1997; Goodale and Milner 2004; Heywood et al. 1995; Heywood and Kentridge 2003; Humphrey et al. 1994; James et al. 2003; Milner et al. 1991; Steeves et al. 2004), we expected area LO, and perhaps the posterior fusiform gyrus (an area that demonstrates strong shape selectivity, see Hayworth and Biederman 2006), to show a release from adaptation when only the form of the objects was varied, and expected the CoS to show a release from adaptation when only the texture of the objects was varied. Because no colour-specific cortical regions were found in our previous study, we were unsure what to expect when only colour varied. The absence of any evidence for a colour-specific region is surprising, as it is believed that a ventral-stream region devoted to processing colour *does* exist, even if researchers

cannot agree where it is located (i.e. either in area V8, which is the putative human homologue of the macaque area TEO/TE: Hadjikhani et al. 1998; Tootell et al. 2003; or in area V4, as was first described in the monkey: Zeki 1973). It is worth emphasizing, however, that few of these studies have explored the sensitivity of these regions to visual texture. In any case, we hoped that by using the fMRA paradigm we could address the question as to whether or not there are any higher-order ventral-stream regions that are specialized for processing the colour of objects independent of their texture.

Materials and methods

Participants

Seventeen healthy participants (8 males, 9 females) took part in this experiment. All participants (mean age = 26.88, range = 21–39 years) were right-handed, reported normal or corrected-to-normal visual acuity, gave their informed consent to participate in the study in accordance with the Declaration of Helsinki, and had no history of neurological disorder. The participants were selected from undergraduate students, graduate students, research assistants, and postdoctoral fellows studying psychology, neuroscience, or biomedical physics at the University of Western Ontario. The procedures and protocols for both experiments were approved by Review Board for Health Sciences Research Involving Human Participants for the University of Western Ontario and the Robarts Research Institute.

Stimuli

Stimuli used in this experiment consisted of a series of unfamiliar 'nonsense' objects (Fig. 1), all of which were bilaterally symmetrical (i.e. each object had an arbitrarily assigned top, bottom, front, and back). These objects were rendered using computer software (Discreet 3DS Max, Montreal, Quebec, Canada) at 640 × 480 pixels (for a more detailed description of the creation of these stimuli, see Cant and Goodale 2007). Once rendered, different textures and colours could be applied to the object's surface. Four different object shapes were used, each of which were rendered in four different textures (metallic paint, laminated oak, marble, and tin foil), and four different colours (red, blue, yellow, and green). The orientation of all objects was the same and did not vary across trials. A fixation cross was placed at the centre of each object to ensure participants maintained fixation during the experimental runs (see below). While we tried to keep changes in the stimuli across visual dimensions as similar as possible, psychophysical testing was not conducted to ensure that differences in

Fig. 1 Examples of the stimuli used in the experiment. Each of the four shapes (only one shape is depicted here) was rendered in four different textures, and in four different colours

Fig. 2 Schematic of the protocol used in the experiment. Stimulus blocks were interleaved with periods of fixation. In each of the stimulus blocks, 16 trials were presented to the participant. Each trial consisted of the presentation of a single stimulus, and the participant's task was to fixate the cross on the centre of the display throughout the presentation of the 16 trials in a given stimulus block. Participants passively viewed four different stimulus blocks. In the form-change condition, the form of the stimuli varied, while the texture and colour remained constant. In the texture-change condition, only the texture of the stimuli varied. In the colour-change condition, only the colour of the stimuli varied. Finally, in the no-change condition (baseline-adaptation condition), no stimulus attribute varied

shape, for example, were perceived as similar as differences in texture. As such, it is possible that some of the activation observed in the shape, texture, and colour conditions may be due to differences in the magnitude of shape, texture, and colour changes presented to participants across conditions.
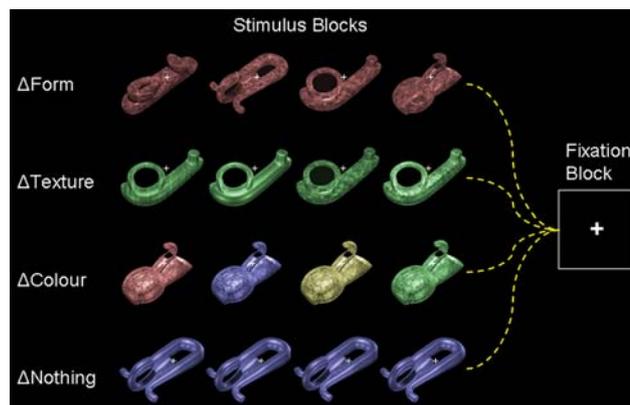
Apparatus

Stimulus presentation was controlled by Superlab Pro version 2.0.4 (Cedrus Corporation, San Pedro, California, USA). Each image was projected via an LCD projector (NEC VT540, Japan, screen resolution of 800×600) onto a screen mounted above the participant's waist as he or she lay in the bore of the magnet. The participant viewed the image through a mirror angled $45°$ from the brow-line, directly above the eyes. Distance from the participant's eyes, via the mirror, to the screen was ~60 cm.

Experimental procedure

Participants were shown an example of each form, texture, and colour prior to entering the magnet. Each texture was made explicit via verbal instruction from the experimenters (i.e. "this is metallic paint, this is laminated oak", etc.).

In each run, participants were presented with various blocks of trials where the form, texture, and colour of the stimuli were manipulated (Fig. 2). These experimental blocks lasted 16 s in duration, and were interleaved with 16 s periods of fixation (where no stimuli were presented, and participants were required to fixate the cross that remained on the centre of the screen) to allow the BOLD

response to return to baseline levels. In the four experimental blocks, participants passively viewed blocks where only one dimension varied (blocks where only form varied, blocks where only texture varied, and blocks where only colour varied) and blocks where no dimensions varied (baseline adaptation block), while fixating a cross in the centre of the display. Thus, throughout the experiment the participants' only task was to maintain fixation, whether stimuli were present (experimental blocks) or not (fixation blocks). It should be noted that the majority of participants were well-practiced in perceptual neuroimaging experiments, but nevertheless, since passive fixation is not extremely attentionally demanding, we communicated with participants via headphones between each experimental run to ensure that they remained alert throughout the experimental session.

A single trial in each experimental block consisted of the presentation of an image for 800 ms, which was followed by the presentation of a blank screen for 200 ms. Thus, each trial lasted for a duration of 1 s, and there were 16 trials in total, yielding 16 images presented in a 16-s long experimental block. In the blocks where only one stimulus attribute varied, there were no instances where the same exemplar of that attribute was repeated across successive trials. Each of the four block types (form change, texture change, colour change, no change) were randomly presented three times throughout each run, and there were a total of four unique run orders (one run order for each functional scan undertaken; each run lasted 6:40 min).

Presentation of all four run orders was counterbalanced across participants.

Imaging parameters

This experiment was carried out with a 4.0 T Siemens-Varian (Erlangen, Germany; Palo Alto, California, USA) whole body imaging MRI system at the Robarts Research Institute (London, Ontario, Canada), using a radio-frequency (RF) head coil to collect BOLD weighted images (Ogawa et al. 1992). A series of sagittal T1-weighted test images were collected for each participant to select 17 contiguous, 5-mm thick functional slices of axial orientation, sampling all of occipital and temporal cortices (excluding the temporal poles), and a large extent of parietal cortex. Functional volumes were collected using a T2*-weighted, navigator echo-corrected, slice-interleaved multi-shot (2 shots) spiral imaging pulse sequence [volume acquisition time = 2 s, 200 volumes collected/imaging run, repetition time (TR) = 1,000 ms, 64×64 matrix size, flip angle (FA) = 40°, echo time (TE) = 15 ms, field of view (FOV) = 22 cm, $3.4 \text{ mm} \times 3.4 \text{ mm} \times 5 \text{ mm}$ voxel size]. After all the functional scans were completed, T1-weighted anatomical images were collected with axial slice orientation [3-D spiral acquisition with inversion time (TI) = 1,300 ms, TE = 3 ms, TR = 50 ms, 256×256 matrix $\times 128$ slices, $0.86 \text{ mm} \times 0.86 \text{ mm} \times 1.25 \text{ mm}$ voxel size].

Data analysis

Data analyses were carried out using the Brain Voyager QX software packages (Brain Innovation, Maastricht, The Netherlands). Imaging data were preprocessed by applying a linear trend removal and a temporal high-pass filter (removing frequencies in the data below 3 cycles per run), and the resulting functional data was superimposed onto anatomical brain images which had been transformed into a common stereotaxic space using the Talairach procedure (Talairach and Tournoux 1988). The functional data was not subjected to spatial smoothing, and a slice scan time correction was not performed because we used multi-shot imaging. To ensure that head motion or scanner artifacts did not contaminate the functional data we collected, we viewed timecourse movies of each functional run from each participant before any pre-processing was conducted. We also evaluated head motion and scanner artifacts by applying Brain Voyager's motion–correction algorithm. Based on the agreement between the output from the timecourse movies and the motion–correction algorithm, we eliminated any functional runs where we observed head motion in excess of 1 mm in translation and/or 1° of rotation, and we also eliminated runs where there was evidence of paradigm-correlated motion. We should note that we used this motion–correction algorithm for evaluation and exclusion purposes only. Similar to the logic outlined by Kroliczak et al. (2007), we report only non-motion corrected data because it has been suggested that motion correction may actually reduce data quality (Freire and Mangin 2001; Culham 2006).

To examine the patterns of form, texture, and colour processing in the brain, we conducted a voxelwise random-effects GLM analysis across the entire group of 17 participants, accounting for hemodynamic lag (Friston et al. 1995). Predictor variables were created for all four conditions in the experiment (form change, texture change, colour change, and no change). To uncover brain regions selective for processing a particular stimulus attribute (form, texture, or colour), we carried out stringent conjunction analyses where a voxel was labelled as being active only if it satisfied the criteria from three separate contrasts. Using the conjunction analysis for form as an example, a voxel was considered form-selective if (1) the activation observed when only the form of the images varied was greater than the activation observed when nothing varied (F+NC−), (2) the activation observed when only form varied was greater than the activation observed when only texture varied (F+T−), and (3) the activation observed when only form varied was greater than the activation observed when only colour varied (F+C−). Note that in addition to uncovering form-selective regions of cortex, this conjunction analysis allows for unbiased comparisons between the activations observed in these regions for the three other experimental conditions (texture-change, colour-change, and no-change conditions). Using the same logic, we used conjunction analyses to uncover regions of the brain that were selective for processing texture (T+NC−; T+F−; T+C−) and colour (C+NC−; C+F−; C+T−). To address the multiple-comparison problem inherent in imaging data, we calculated significance levels by taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster of activation (Alphasim, by B. Douglas Ward, a software module in Cox 1996). Through a series of Monte Carlo simulations, Alphasim outputs information regarding how large a particular cluster must be to be considered significantly active at a particular threshold value (i.e. Alphasim calculates the probability of a false detection). Clusters of cortex identified by t tests contrasting the predictors in the regression equation (contrasts in the conjunction analyses described above) satisfied the criteria for significance ranging from the level of $P < .01$, corrected, to $P < .006$, corrected. Event-related averages were then extracted from each significantly active region of cortex. The activation levels for each condition were measured as % BOLD signal change from a baseline, which was defined as the activation in a 4-s window that extended from 8 to 4 s before onset of the experimental block. This 4-s window corresponded to

the activity that was present in the previous fixation block. The event-related averages for each experimental condition were subjected to a one-way repeated measures analysis of variance (ANOVA), performed separately on each hemisphere on a region-by-region basis (SPSS software package, Chicago, Illinois, USA). The significant main effect of condition (form change, texture change, colour change, and no change) was investigated using post hoc *t* tests, employing Tukey's HSD procedure to correct for multiple comparisons.

Results

The voxelwise random-effects GLM analysis examined the BOLD activity (measured in % signal change) averaged

across 17 participants using separate conjunction analyses to investigate form-, texture-, and colour-selective cortical regions in occipito-temporal cortex (baselined against the activity from the fixation blocks). For illustrative purposes, the group data were mapped onto a single participant's anatomical brain scan. (This method of illustration, of course, does not account for the individual differences in the sulcal and gyral patterns across participants.) As Figs. 3 and 4 illustrate, form- and texture-selective cortical regions were confined to ventral occipito-temporal cortex. No colour-selective cortical regions were uncovered.

In total, seven regions of cortex met the Alphasim criteria for significance (based on a combination of the cluster size and probability threshold for false detection of each region). Of these seven regions, one region was found bilaterally, two regions were localized unilaterally in the left
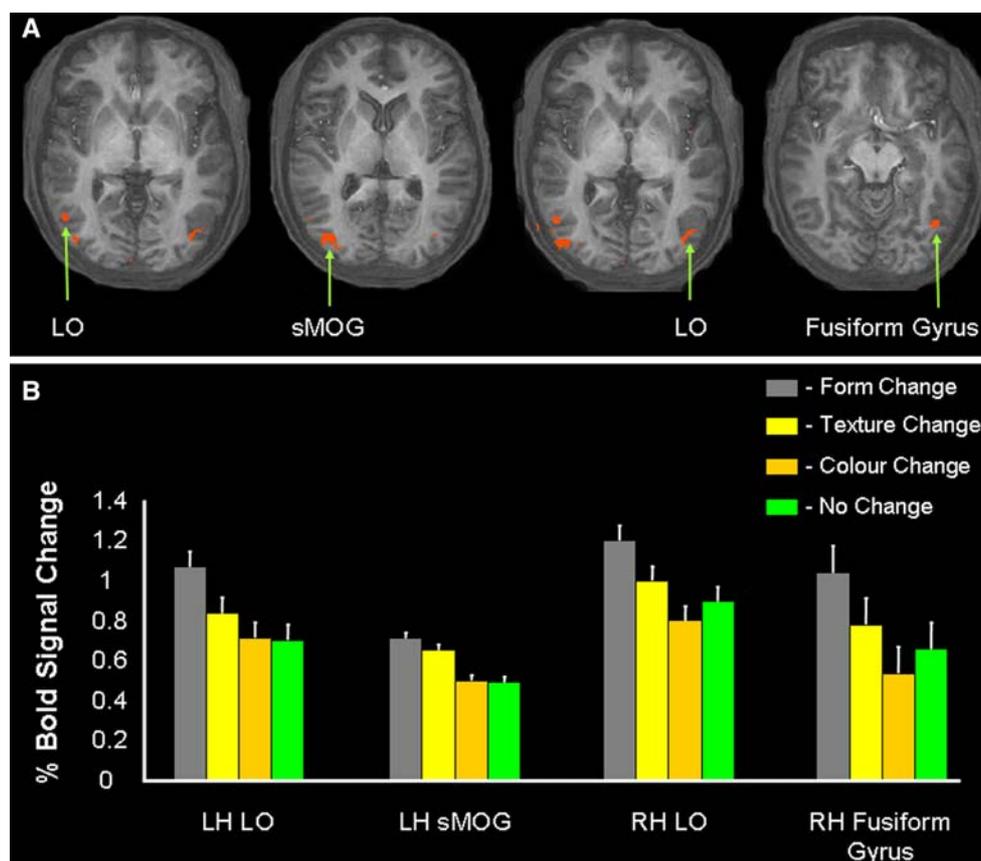
Fig. 3 Results of the voxelwise-conjunction analysis for form (F+NC−; F+T−; F+C−), averaged across all 17 participants. **a** Three regions of cortex were significantly active at the level of *P* < .006. Of these three regions, one was found bilaterally (LO), while the remaining two regions were localized to the left (sMOG) and right hemispheres (fusiform gyrus). All anatomical brain images (and all brain images presented in subsequent figures) follow neurological convention (left hemisphere is on the left, and right hemisphere is on the right). **b** Per cent BOLD signal changes in response to stimuli presented in the form-change, texture-change, colour-change and no-change conditions in each of the regions identified in the voxelwise-conjunction analysis for form. (See Supplementary Table 1 for a

detailed summary of all of the post hoc statistical results for this analysis.) Of course, one would expect the highest activation in the form-change condition (*grey bars*) compared to the three other conditions based on the conjunction analysis for form that we used. *Error bars* indicate 95% confidence intervals derived from the mean square error term from the repeated-measures analyses of variance. *F+NC−* contrast of form-change and no-change conditions, *F+T−* contrast of form-change and texture-change conditions, *F+C−* contrast of form-change and colour-change conditions, *LO* lateral occipital area, *sMOG* superior portion of the middle occipital gyrus, *LH* left hemisphere, *RH* right hemisphere
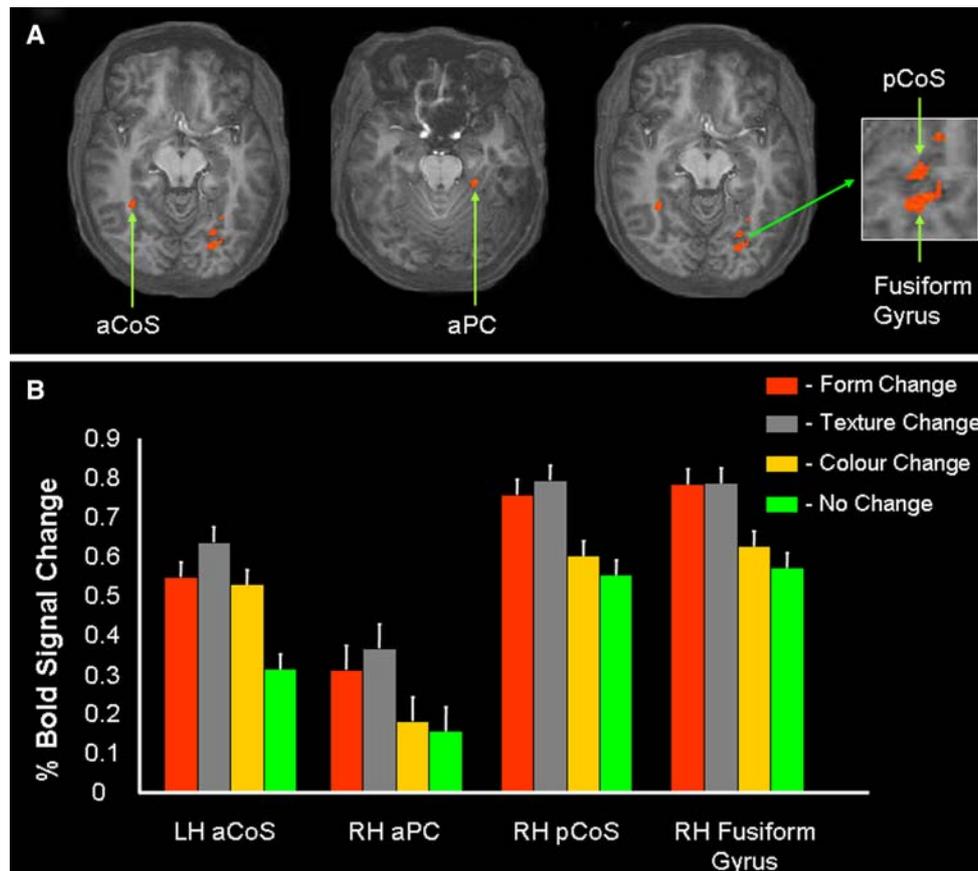
Fig. 4 Results of the voxelwise-conjunction analysis for texture (T+NC−; T+F−; T+C−), averaged across all 17 participants. **a** Four regions of cortex were significantly active at the levels of $P < .001$ (aCoS, pCoS, fusiform gyrus) and $P < .01$ (aPC). Of these four regions, one was localized unilaterally to the left hemisphere (aCoS), while the remaining three regions were localized unilaterally to the right hemisphere (aPC, pCoS, fusiform gyrus). **b** Per cent BOLD signal changes in response to stimuli presented in the form-change, texture-change, colour-change and no-change conditions in each of the regions identified in the voxelwise-conjunction analysis for texture. (See Supplementary Table 1 for a detailed summary of all of the post hoc

statistical results for this analysis.) Of course, one would expect the highest activation in the texture-change condition (*grey bars*) compared to the three other conditions based on the conjunction analysis for texture that we used. *Error bars* indicate 95% confidence intervals derived from the mean square error term from the repeated-measures analyses of variance. *T+NC−* contrast of texture-change and no-change conditions, *T+F−* contrast of texture-change and form-change conditions, *T+C−* contrast of texture-change and colour-change conditions, *aCoS* anterior aspect of the collateral sulcus, *aPC* anterior parahippocampal cortex, *pCoS* posterior aspect of the collateral sulcus, *LH* left hemisphere, *RH* right hemisphere

hemisphere, and the remaining four regions were localized unilaterally in the right hemisphere (Table 1). The conjunction analysis for form (i.e. F+NC−; F+T−; F+C−) yielded bilateral activity in a region of cortex that appears to correspond with area LO, $t(16) = 2.8$, $P < .006$ (Fig. 3a). Two additional form-selective regions were uncovered in this analysis and were localized to the left superior portion of the middle occipital gyrus (sMOG) and the right fusiform gyrus [both regions: $t(16) = 2.8$, $P < .006$]. The conjunction analysis for texture (T+NC−; T+F−; T+C−) yielded unilateral texture-selective activity in four brain regions (Fig. 4a). One of these regions was located along the anterior aspect of the left CoS (aCoS), $t(16) = 2.8$, $P < .001$. The remaining three texture-selective regions were confined to the right hemisphere, and were located in the anterior parahippocampal cortex (aPC), the posterior aspect

of the CoS (pCoS), and the fusiform gyrus [all regions: $t(16) = 2.8$, $P < .001$, except the aPC, where $P < .01$]. As mentioned above, no colour-selective regions were uncovered in the conjunction analysis for colour (C+NC−; C+F−; C+T−).

The time-courses of the per cent BOLD-signal change (compared to baseline fixation epochs) for each condition (form change, texture change, colour change, and no change) were extracted from each significantly active region by means of event-related averaging in Brain Voyager. The integrated area under the curve of each of these time-courses for each region was calculated and the resulting measures were then subjected to a one-way repeated-measures ANOVA to detect overall differences in activation across the conditions (performed separately in each hemisphere and region). To account for hemodynamic lag

Table 1 Talaraich coordinates and cluster sizes of the regions identified in the voxelwise analysis

	x	y	z	t value	Cluster size (# vox/27 mm^3)
Form regions					
L LO	−51	−61	1	2.8	10.70
R LO	38	−77	0	2.8	8.11
L sMOG	−41	−77	7	2.8	25.93
R FG	43	−65	−9	2.8	6.89
Texture regions					
L aCoS	−33	−47	−10	2.9	9.30
R aPC	26	−32	−19	2.9	5.19
R pCoS	30	−68	−12	2.9	15.48
R FG	24	−78	−9	2.9	13.15

vox voxels, *mm* millimetres, *L* left, *R* right, *LO* lateral occipital, *sMOG* superior portion of the middle occipital gyrus, *FG* fusiform gyrus, *aCoS* anterior aspect of the collateral sulcus, *aPC* anterior parahippocampal cortex, *pCoS* posterior aspect of the collateral sulcus

(i.e. the delay between stimulus onset and the rise in the BOLD signal), the first two data points for each waveform were not included in the calculation of the area under the curve. If significant results were yielded, the four conditions were further contrasted by means of post hoc *t* tests, corrected for multiple comparisons ($P < .05$) using Tukey's HSD procedure. Of course, based on our criteria for identifying regions of cortex selectively involved in processing a given stimulus attribute (e.g. the conjunction analysis for form uncovers form-selective regions by performing three separate contrasts, F+NC−; F+T−; F+C−), we would certainly expect to find the same pattern of selectivity inherent in the results from the post hoc analyses. Note, however, that the conjunction analysis requires only that the activation for one stimulus condition be higher than the activation for the other three. Thus, it says nothing about whether or not the levels of activation for those three conditions are significantly different from each other. The conjunction analyses we selected are ideally suited for investigating this as they do not bias the comparisons made between the remaining three experimental conditions (see "Materials and methods"). Finally, it should be pointed out that it is possible that within a region revealed by the conjunction analysis, the activation for the defining stimulus condition might not always differ significantly from the other three conditions. (For a detailed summary of all the post hoc statistical results, see Supplementary Table 1. Any significant difference described below is significant at $P < .05$ or better.)

The main effect of condition was significant in each region investigated. As expected, post hoc analyses revealed that area LO (bilaterally) was most sensitive to processing form, as the activation when only the form of the stimuli varied was higher than the activation in the three other conditions where form did not vary (i.e. texture-change, colour-change, and no-change conditions; see Fig. 3b). In the left LO, the activation observed in these latter three conditions did not differ significantly from each other, whereas in the right LO the activation when only texture varied was significantly higher than the activation when only colour varied (note, however, that the activation in the texture-change condition was not significantly higher than the activation in the baseline adaptation condition where no stimulus dimension varied). This pattern of activation was also observed in the right fusiform gyrus: the highest activation was observed in the form-change condition compared to all other conditions, and the activation in the texture-change condition was significantly higher than the activation in the colour-change condition (but not significantly different from the activation in the no-change condition). A final region that was most sensitive to processing object form resided on the left sMOG. In this region, the activation in the form-change condition was significantly higher than the activations in the texture-change, colour-change, and no-change conditions. There was also evidence of texture-sensitivity in this region, as the activation when only texture varied was significantly higher than the activation when only colour varied, and was also significantly higher than the activation when no stimulus dimension varied (baseline adaptation condition).

One region of cortex was found to be most sensitive to processing texture, and this region resided in the left aCoS. The patterns of activity in this region revealed significantly higher activation when only texture varied compared to the three conditions when texture did not vary (i.e. form-change, colour-change, and no-change conditions; see Fig. 4b). Note, however, that this region also shows evidence of form and colour sensitivity, in that both the form-change and colour-change conditions had higher levels of activation compared to the baseline adaptation condition where no stimulus attribute changed. Interestingly, this is the first evidence we have found with this stimulus set for colour-sensitivity in more medial and anterior regions of the ventral stream. The aCoS was the only region we found that was most sensitive to processing variations in texture (i.e. no other regions showed the same pattern of activations as the aCoS, where the highest activation was observed when only texture varied, compared to the 3 conditions where texture did not vary). We did, however, find three additional regions that showed equivalent sensitivity to form and texture, in that the activation in the form-change and texture-change conditions did not differ significantly from each other, but the activations in both of these conditions were significantly higher than the activations in the colour-change and no-change conditions. These regions coincided with the right aPC, the right pCoS, and the right

fusiform gyrus. In both the right aPC and the right pCoS, the activations in the colour-change and no-change conditions did not differ significantly from each other. Interestingly, the activation in the right fusiform gyrus when only colour varied was significantly higher than the activation in the baseline adaptation condition where nothing varied, demonstrating evidence of colour-sensitivity in a medial-anterior aspect of the ventral stream. Recall that this result was also demonstrated in the aCoS in the left hemisphere. Taken together, these results are quite interesting in that they represent evidence of colour sensitivity in regions that were initially defined by a conjunction analysis for texture (it is worth repeating again that no colour-selective regions were found when we carried out a conjunction analysis for colour). It is certainly encouraging that these regions are in the vicinity of the known colour-sensitive V4/V8 complex.

Discussion

The results of this fMRA experiment demonstrate that the processing of form and the processing of surface properties engage functionally and anatomically distinct regions in the ventral stream. These results, which show that area LO is most sensitive to processing variations in form and the aCoS is most sensitive to processing variations in texture (whereas no regions were found that were most sensitive to processing variations in colour), convincingly replicate the results of our previous study, which used an attentional-modulation paradigm (Cant and Goodale 2007). Taken together, these two studies provide evidence for a gradient of processing in the ventral stream, where form is processed preferentially in more lateral regions and surface properties (particularly texture) in more medial and anterior regions. Importantly, the results from the present study also suggest some of these areas, particularly the more medial ones, process more than one attribute of an object. Finally, our results show that the differences we observed were unlikely to reflect differences in eye movements or the deployment of attention across stimulus blocks.

Processing of object form, texture, and colour

The finding that area LO is most sensitive to processing object form is not surprising, as numerous neuroimaging studies have reported that area LO is sensitive to processing the geometric structure of objects (e.g. Cant and Goodale 2007; Kanwisher et al. 1996; Kourtzi and Kanwisher 2000; Malach et al. 1995). Moreover, many researchers have suggested that the processing of form carried out by area LO is critical for object recognition (e.g. Bar et al. 2001; Grill-Spector et al. 2001; James et al. 2002). These suggestions, and the results from the present study, are certainly

consistent with findings from the visual form agnosic patient DF, who has bilateral lesions to area LO and cannot recognize objects on the basis of their form but can recognize their surface properties (Humphrey et al. 1994; James et al. 2003). But area LO was not the only region that was most sensitive to processing variations in form. Two regions, one in the left sMOG and one in the right fusiform gyrus showed more sensitivity to changes in form than to changes in other object attributes, although both these regions also showed some sensitivity to changes in texture. Although it is beyond the scope of this paper to give a detailed discussion of the specific contributions these regions might make to form processing and to object recognition, it is interesting to note that previous studies have demonstrated that both the middle occipital gyrus and parts of the fusiform gyrus seem to be preferentially activated by objects (MOG: Vandenberghe et al. 1996; posterior fusiform gyrus: Hasson et al. 2003).

We found one region of cortex that was most sensitive to processing texture, and that region coincided with the left aCoS. This finding replicates the results of our previous study (Cant and Goodale 2007), and adds to the small but growing body of evidence, suggesting that the CoS plays a prominent role in the processing of surface texture (compared to 3-D shape and 3-D motion: Peuskens et al. 2004; compared to faces and letterstrings: Puce et al. 1996). Indeed, we have recently shown that proximal areas in this medial ventral stream region (i.e. the parahippocampal gyrus) also respond preferentially to material-property information conveyed through sound alone (Arnott et al. 2008). In addition, as we have shown before (Cant and Goodale 2007), this CoS area overlaps regions that have been shown to be specialized for the processing of scenes (e.g. Epstein and Kanwisher 1998), a finding that supports the idea that scene processing relies heavily on the analysis of surface properties, such as visual texture (for review, see Steeves et al. 2004). (Of course, this is not to deny the fact that scene processing can also rely on outline shape cues, which people can utilize to recognize line drawings of scenes.) This convergence of anatomy and function illustrates the importance of investigating not only category-specific processing in the ventral stream, but also the types of stimulus attributes that best support the processing of those categories.

No regions were found that were more sensitive to variations in colour than to variations in form or texture. We did, however, find evidence of colour sensitivity in the left aCoS and in the right fusiform gyrus, regions that were uncovered using a conjunction analysis for texture. This finding suggests that there may be shared mechanisms for processing colour and texture in the same pathway. In other words, this might be a pathway better characterized as one that is specialized for the processing of an object's surface

properties, where colour and texture are typically closely integrated. It is certainly encouraging that these same regions, which are located in more medial and anterior regions of the ventral stream, have been also been implicated in the processing of colour in studies of both neurologically intact individuals (Beauchamp et al. 1999; Corbetta et al. 1990, 1991; Hadjikhani et al. 1998; Lueck et al. 1989; Zeki et al. 1991) and cerebral achromatopsics (for review see Heywood and Kentridge 2003). It is not entirely clear why we found no evidence of colour sensitivity in medial and anterior regions of the ventral stream in our previous study (Cant and Goodale 2007), which utilized the same stimulus set as the one used here. We believe the discrepancy may be a consequence of the different experimental paradigms that were used. Our previous study used a conventional 1-back attentional task whereas the present study used a passive fMRA paradigm. Although the 1-back task ensures that participants are attending the relevant stimulus, the fMRA paradigm affords more experimental control since only one stimulus attribute varies at a time. Thus, the latter offers (potentially) greater spatial resolution in the detection of functional areas. Of course, these medial-anterior regions were more sensitive to texture (both aCoS and fusiform gyrus) and form (only fusiform gyrus) than they were to colour. This suggests that the interpretation of the patterns of response in ventral-stream regions that appear to be specialized for processing a given stimulus attribute may not be as straightforward as one might think. Indeed, findings from monkey electrophysiology suggest that the colour area V4 has separate populations of neurons that are tuned to multiple stimulus properties (form: Desimone and Schein 1987; colour and pattern: Heywood and Cowey 1987; texture: Hanazawa and Komatsu 2001). Thus, given the relatively small size of this region, the spatial resolution used in the present study may not have been sufficient to uncover all of the stimulus-specific subpopulations of the V4/V8 complex (we should note that while the fMRA paradigm can potentially increase spatial resolution, perhaps high-resolution imaging with voxel dimensions of less than 3 mm are necessary to disambiguate these neuronal subpopulations). But there may be a more methodological reason why we did not find any region that was most sensitive to processing colour in the ventral stream, particularly in the fusiform gyrus (i.e. in the vicinity of area V4/V8). Previous studies on colour selectivity in area V4 have identified this region by contrasting static, coloured Mondrian displays with isoluminant grey shaded versions of those coloured displays (Lueck et al. 1989; Zeki et al. 1991). The intermittent flashing of stimulus variations in the present study may have been sufficient to activate sub-regions of the fusiform gyrus that are sensitive to processing form and texture, but the same stimulus presentation may have made it nearly impossible to activate the colour-specific region of the fusiform gyrus when conducting the conjunction analysis for colour. Nevertheless, we find it encouraging that we found evidence of form, texture, and colour sensitivity in the fusiform gyrus, a finding that resonates with the findings from monkey electrophysiology described above.

Response properties of form and surface-property regions in the ventral stream

The goal of this study was to determine whether the activations associated with attention to non-preferred object attributes in a particular region that had been observed in our earlier study (Cant and Goodale 2007) reflected the processing of those attributes or were simply a consequence of obligatory processing of the preferred object attribute. By using an fMRA paradigm coupled with a conjunction analysis, we were able to address the question directly. Below is a description of what we believe the results of this study suggest about the response properties of form and surface-property regions in the ventral stream.

Three regions were found to be most sensitive to processing form: area LO (bilaterally), the left sMOG, and the right fusiform gyrus. In the left LO, there was activation present in the texture-change and colour-change conditions. Importantly, however, the activations associated with changes in texture or colour did not differ from the no-change baseline adaptation condition (or from each other), strongly suggesting that the left LO is insensitive to variations in these two attributes. Instead, the left LO appears to be a form-selective region. The non-preferred activations in the left LO probably reflect, therefore, the processing of object form even when that form is not changing from trial to trial. In contrast, in the left sMOG, the right LO, and the right fusiform gyrus, there was evidence for texture processing in these form-defined regions. In other words, the activations to changes in texture were significantly higher than the activations to changes in colour (which did not differ from the baseline condition). It is not immediately clear what is going on here. It could mean that these areas are indeed playing a role in extracting information about the visual texture of objects (as a surface property). But it is also possible that some sort of form or pattern processing is required to distinguish one texture from another. Finally, it is also possible that by extracting information about texture gradients, the processing of texture is contributing directly to the computation of object form, although this last possibility is less likely since the texture gradients did not change very much over trials in the texture-change condition. This discussion highlights once more the fact that the extraction of texture information is a complex operation—and that activation to changes in texture in different regions of the ventral stream could reflect different aspects of this process.

In the left aCoS, an area that we found to be most sensitive to changes in texture, the activations in the form-change and the colour-change conditions were significantly higher than the activation in the no-change condition. Again it is possible that the extraction of information about the visual texture of an object (as a clue to its material properties) also requires some processing of both form and even colour—but this is entirely speculative. It could also mean that these attributes are processed quite independently in this area. In any case, the fact that this area was sensitive to all three object attributes resonates with the results of earlier studies that have also demonstrated sensitivity in this area to these attributes (texture: Cant and Goodale 2007; Peuskens et al. 2004; Puce et al. 1996; colour and form: Corbetta et al. 1990, 1991).

The activation in the colour-change condition in the left aCoS (which was greater than the activation in the no-change condition, but no different from the activation in the form-change condition) represents evidence of colour sensitivity in the medial-anterior aspect of the ventral stream. This finding supports our claim for the existence of a pathway specialized for processing the surface properties of objects in the medial-anterior ventral stream. Moreover, the colour-sensitivity in the right fusiform gyrus (discovered using the conjunction analysis for texture) also supports this claim. In fact, two different contrasts (form and texture) activated the right fusiform gyrus, and the pattern of activations seen across these different contrasts showed evidence of sensitivity to form, texture, *and* colour. Granted, we were sampling two different regions within the right fusiform gyrus across the two contrasts, but these results suggest that this area is an intermediate region in the gradient of form and surface-property processing evident in the ventral stream. We suggest that along this gradient (which we have described elsewhere, see Cant and Goodale 2007), the processing of object form is more prominent laterally, whereas the processing of surface properties, particularly texture, becomes more prominent in medial-to-anterior regions of the ventral stream. As a consequence of this gradual shift from the prominence of form processing to the prominence of texture processing, there exist regions that process both form and surface-properties (i.e. texture and colour), and one such intermediate region may reside along the fusiform gyrus. Indeed other studies have found evidence of object form (Hasson et al. 2003), texture (Kastner et al. 2000), and colour processing (McKeefry and Zeki 1997; Miceli et al. 2001) in the fusiform gyrus. In this regard, it is interesting to note that one region along the fusiform gyrus that has received a great deal of attention in fMRI studies is the fusiform face area, or FFA (Kanwisher et al. 1997; Puce et al. 1996; for review, see Grill-Spector and Malach 2004). Pre-dating these fMRI studies are a number of positron emission tomography (PET) studies

which have also demonstrated face-sensitivity in the fusiform gyrus (Grady et al. 1994; Haxby et al. 1994; Sergent et al. 1992). The fact that current models of face processing suggest that both geometry (Wilson et al. 2002) and surface properties (Price and Humphreys 1989; Russell et al. 2006; Tarr et al. 2001, 2002) are important to face recognition fits quite nicely with the evidence of form, texture, and colour sensitivity in the fusiform gyrus described above. Moreover, when we localized the FFA in a previous study (using a face, place, object localizer), we found evidence of equivalent sensitivity in this area to both form and surface properties (Cant and Goodale 2007). Similar to the results with the processing of surface properties and scenes discussed above, these results highlight the importance of studying both the category to which a region responds most robustly (e.g. faces in the FFA), and the particular stimulus attributes that best support the processing of that category (e.g. form and surface properties). Taken together, these results suggest that the fusiform gyrus is an intermediate region in the gradient of form and surface-property processing in the ventral stream, where there is evidence of sensitivity to stimulus attributes that support the processing of faces (i.e. form, texture, and colour).

Eye movements, shifts of attention, and functional independence

In the version of the fMRA paradigm that we employed in the present study, the participants' only task was to maintain fixation. That is, there were no explicit manipulations of attention to object form, texture or colour throughout the study, as there were when we used an attentionally demanding 1-back task previously (Cant and Goodale 2007). We should note that even though we asked participants to maintain fixation, we did not record eye movements to ensure that they complied with this request. We do not feel, however, that the pattern of results observed here are due to differences in the number of saccades made across the four conditions, as we observed no differential activation in the human homologue of the macaque area LIP in any of the statistical contrasts performed, suggesting that participants were maintaining fixation throughout the entire session. [Area LIP is situated in the posterior parietal cortex and is known to be involved in the planning and execution of saccades (Anderson et al. 1992; Colby et al. 1996) and shows robust fMRI activation during saccades (for review, see Culham and Kanwisher 2001).] Moreover, even if there were occasional eye movements, which of course is entirely possible, the absence of differential activation in LIP suggests that these lapses in fixation were as likely to occur in one condition as another. It should be emphasized as well that the majority of participants had been in the scanner many times. In fact, because there was no

behavioural task other than fixation, it would seem rather unnecessary to employ different viewing strategies across conditions in the first place. But of course it is also possible that some stimulus conditions attracted attention more than others while participants were successfully maintaining fixation throughout the experiment. For example, it is possible that the conditions where one stimulus attribute varied (form-change, texture-change, and colour-change conditions) attracted attention more than the condition where no stimulus attribute varied (baseline adaptation condition). If this were the case, then these conditions should almost always yield higher BOLD signal changes compared to the condition where no stimulus attribute varied (owing to findings that attention has been shown to increase neural activity; see Murray and Wojciulik 2004). But this was not the case with our results, as in many regions the BOLD activation in at least one (and sometimes two or three) of the stimulus-change conditions did not differ significantly from the BOLD activation in the no-change condition. Moreover, as already discussed, there was no differential activation across stimulus conditions in area LIP, an area that has been implicated in covert shifts of attention (Culham and Kanwisher 2001). As such, we do not believe the activation patterns we report here are due to differences in how the participants attended to the stimuli across conditions. Finally, it is worth emphasizing that numerous other fMRA studies have reported robust results when using passive viewing as their primary experimental task (e.g. Kourtzi and Kanwisher 2000, 2001; Valyear et al. 2006). This, coupled with the discussions on attention and different viewing strategies discussed above, suggests to us that the pattern of activations seen here reflects stimulus-specific processing of form, texture, and colour, not differences in how participants attended to or viewed variations in each of these dimensions.

Despite the differences in attentional demands between the passive-adaptation paradigm used here and the 1-back task used previously, the results from these two paradigms are remarkably similar, especially in the form-sensitive area LO and the texture-sensitive CoS. We believe the similarity between these results validates our decision to use passive fixation as our primary experimental task, and suggests that these regions can respond in a stimulus-driven manner, independent of task demands. Indeed, a recent study which utilized the fMRA paradigm supports this notion. In an elegantly designed study, Xu et al. (2007) demonstrated that the patterns of repetition attenuation in the parahippocampal place area (PPA) were identical for two tasks that required different levels of processing (on the same visual stimuli). That is, identical repetition attenuation was observed in a scene task where responses were faster and more accurate when the images were very similar, compared to an image task where responses were faster and

more accurate when the images were less similar. This intriguing dissociation between repetition attenuation and performance suggests that the processing in ventral-stream perceptual regions reflects obligatory stimulus-specific processing independent of task demands. Of course, it has already been established that attention to a particular stimulus attribute can increase the neural response of cortical regions which process the attended attribute (Corbetta et al. 1990; Murray and Wojciulik 2004). But based on the results of the present study, we think it reasonable to assert that variations in a stimulus attribute in the absence of explicit deployments of attention is sufficient to activate the regions most responsible for processing that attribute. Furthermore, when attention is directed towards that attribute, the responses in those regions responsible for processing the attended attribute are facilitated, and may become higher than the responses that passive viewing elicit. To test this directly, it will be necessary to conduct a study using both an attentionally demanding task and a passive-fixation scheme. Such a direct comparison between tasks should uncover further information regarding the functional properties of ventral-stream perceptual regions. Nevertheless, we believe the replication of our previous results using an entirely different paradigm lends more evidence to the notion that form and surface properties (particularly texture) are processed in functionally and anatomically distinct regions of the ventral stream.

At this point it is worth emphasizing that the existence of separate brain regions that process form and surface properties does not necessarily imply that the processing carried out in these regions is functionally independent. For example, it may be the case that these separate anatomical regions are richly interconnected and thus share common processing resources. To demonstrate true functional independence, it is necessary to examine the behavioural performance when people attend to one dimension while the other varies. This is precisely what we did in a recent study which used the behavioural paradigm known as the Garner Speeded-Classification task (Cant et al. 2008; Garner 1974). In our experiments the results were clear: discriminating the form of objects was not disrupted by changes in surface properties, and discriminating the surface properties of objects was not disrupted by changes in form. Taken together, it would appear that the separate brain regions activated for form and surface properties in our neuroimaging studies do reflect some sort of parallel processing of visual input.

Organizing principles of the ventral stream

What implications do our findings have for current models of ventral-stream organization? The fact that some regions, such as the left LO, appeared to be remarkably selective to

a single attribute is consistent with the idea that there are categorical representations, such as an 'object recognition area' in the ventral stream (Reddy and Kanwisher 2006). Yet the fact that other regions, such as the fusiform gyrus, showed evidence of shared processing of attributes is more consistent with Haxby et al.'s (2001) notion of distributed representations of stimulus categories in the ventral stream. As we have discussed earlier (Cant and Goodale 2007), however, one need not appeal to a single theory of ventral-stream cortical organization to explain these apparently contradictory findings. Instead of either a distributed or a categorical representation, there may be a matrix of distributed representations, where high nodes in a network that are most responsible for processing a single stimulus category are maximally active when that category is presented. Along with these high nodes, however, there may exist other regions that display sub-maximal—but significant—activations to the same stimulus category. These nodes (both high and low), may arise because of the intersection between a particular stimulus category, and the stimulus attribute that best supports the processing of that category. This account may explain the distributed nature of form processing in the present study, as regions most sensitive to processing form intersected with categorical areas of cortex known to be maximally active to objects (area LO) and faces (the fusiform gyrus), respectively. Furthermore, the distribution of regions sensitive to processing form, texture, and colour may also be based on a quasi-retinotopic organizing principle (Hasson et al. 2003; Levy et al. 2001), where ventral stream regions that show a preference for processing particular biological categories are organized based on the typical location that those categories fall on the retina (e.g. 'face' areas have a centre-field bias and 'place' areas have a peripheral-field bias). In short, attempting to resolve the nature of the organizing principles of the ventral stream is a complex task. We believe some resolution to this issue may come from studying not only the particular stimulus category to which a region maximally responds, but also the stimulus attribute that best supports the processing of that category. By taking this approach, we have found that form is processed preferentially in object-sensitive areas, surface properties (particularly texture) in scene-sensitive areas, and the combination of form, texture, and colour in face-sensitive areas.

Future directions

Unlike the results seen with form and texture in the present study, no cortical regions were discovered that were *most* sensitive to processing variations in colour. This is somewhat surprising, as it is generally agreed that a cortical region devoted to processing colour *does* exist in the human brain, although there is vigorous debate surrounding

whether the colour centre resides in area V4 or in area V8 (Beauchamp et al. 1999; Hadjikhani et al. 1998; Heywood and Kentridge 2003; McKeefry and Zeki 1997; Tootell et al. 2003). Despite the controversy surrounding the location of this colour centre, the degree to which this area processes other surface properties (such as texture) is presently unknown and deserves direct investigation.

Another outstanding question is whether or not the brain areas responsible for the perception of objects contribute to the execution of actions directed towards those same objects. Shape processing in area LO appears not to play a major role in the control of manual grasping movements, which are known to depend on circuitry in the posterior parietal cortex (Cavina-Pratesi et al. 2007). But the contribution of other ventral-stream areas to the control of grasping, particularly those areas that process the surface properties of objects, is unknown. Surface properties, which provide important cues to the material properties of objects, such as their density, are clearly critical to the setting of the initial grip and lift forces necessary to heft objects (e.g. Gordon et al. 1993). Although it has been demonstrated that the anterior intraparietal sulcus (or area AIP) and the supplementary motor area contribute to the calibration of these forces (Bursztyn et al. 2006; Davare et al. 2007; Ehrsson et al. 2000, 2001; Imamizu et al. 2004; Kuhtz-Buschbeck et al. 2001), it is not clear where these areas derive the information about object density and mass that is necessary for this calibration. Because this information depends on making associations between the *perceived* surface properties of objects and their density and mass, it seems likely that ventral-stream areas will be involved. In short, it would be of interest to investigate whether or not ventral-stream regions such as the CoS are co-activated with posterior parietal and premotor regions when lifting objects of different material properties.

Summary and conclusions

The main finding of the present study was that the processing of form and the processing of surface properties engages functionally and anatomically distinct regions in the ventral stream. Using an fMRA paradigm, we showed that area LO, the left sMOG, and the right fusiform gyrus were most sensitive to processing variations in object form, while the left aCoS was most sensitive to processing variations in texture. Some regions appeared to be remarkably selective, whereas others responded to changes in a number of attributes. No cortical regions were found that were most sensitive to processing colour, although there was evidence of colour sensitivity in medial and anterior regions of the ventral stream such as the left aCoS and the right fusiform gyrus. These results, along with the results of our previous

neuroimaging study (Cant and Goodale 2007), demonstrate the existence of a gradient of processing for form and surface properties (i.e. texture and colour) in the ventral stream, where form is processed in more lateral regions and surface properties (particularly texture) are processed in more medial and anterior regions.

References

Anderson RA, Brotchie PR, Mazzoni P (1992) Evidence for the lateral intraparietal area as the parietal eye field. Curr Opin Neurobiol 2:840–846

Andrews TJ, Ewbank MP (2004) Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. Neuroimage 23:905–913

Arnott SR, Cant JS, Dutton GN, Goodale MA (2008) Crinkling and crumpling: an auditory fMRI study of material properties. Neuroimage (in press)

Bar M, Tootell RBH, Schacter DL, Greve DN, Fischl B, Mendola JD, Rosen BR, Dale AM (2001) Cortical mechanisms specific to explicit visual object recognition. Neuron 29:529–535

Beauchamp MS, Haxby JV, Jennings JE, DeYoe EA (1999) An fMRI version of the Farnsworth-Munsell 100-Hue test reveals multiple color-selective areas in human ventral occipitotemporal cortex. Cereb Cortex 9:257–263

Bursztyn LL, Ganesh G, Imamizu H, Kawato M, Flanagan JR (2006) Neural correlates of internal-model loading. Curr Biol 16:2440–2445

Cant JS, Goodale MA (2007) Attention to form or surface properties modulates different regions of human occipitotemporal cortex. Cereb Cortex 17:713–731

Cant JS, Large M-E, McCall L, Goodale MA (2008) Independent processing of form, colour, and texture in object perception. Perception 37:57–78

Cavina-Pratesi C, Goodale MA, Culham JC (2007) fMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. PLoS One 2:e424

Colby CL, Duhamel JR, Goldberg ME (1996) Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. J Neurophysiol 76:2841–2852

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE (1990) Attentional modulation of neural processing of shape, color, and velocity in humans. Science 248:1556–1559

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE (1991) Selected and divided attention during visual discrimination of shape, color, and speed: functional anatomy by positron emission tomography. J Neurosci 11:2383–2402

Cox RW (1996) AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Comput Biomed Res 29:162–173

Culham JC (2006) Functional neuroimaging: experimental design and analysis. In: Cabeza R, Kingstone A (eds) Handbook of functional neuroimaging of cognition, 2nd edn. MIT Press, Cambridge, pp 53–82

Culham JC, Kanwisher NG (2001) Neuroimaging of cognitive functions in human parietal cortex. Curr Opin Neurobiol 11:157–163

Davare M, Andres M, Clerget E, Thonnard J-L, Olivier E (2007) Temporal dissociation between hand shaping and grip force scaling in the anterior intraparietal area. J Neurosci 27:3974–3980

Desimone R, Schein SJ (1987) Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. J Neurophysiol 57:835–868

Duvelleroy-Hommet C, Gillet P, Cottier JP, de Toffol B, Saudeau D, Corcia P, Autret A (1997) Cerebral achromatopsia without prosopagnosia, alexia, object agnosia. Rev Neurol (Paris) 153:554–560

Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H (2000) Cortical activity in precision-versus power-grip tasks: an fMRI study. J Neurophysiol 83:528–536

Ehrsson HH, Fagergren A, Forssberg H (2001) Differential fronto-parietal activation depending on force used in a precision task: an fMRI study. J Neurophysiol 85:2613–2623

Epstein R, Kanwisher N (1998) A cortical representation of the local visual environment. Nature 392:598–601

Ewbank MP, Schluppeck D, Andrews TJ (2005) fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. Neuroimage 28:268–279

Freire L, Mangin JF (2001) Motion correction algorithms may create spurious brain activations in the absence of subject motion. Neuroimage 14:709–722

Friston KJ, Homes AP, Worsley KJ, Poline J-P, Frith CD, Frackwowiak RSJ (1995) Statistical parametric maps in functional imaging: a general linear model approach. Hum Brain Mapp 2:189–210

Garner WR (1974) The processing of information and structure. Erlbaum, Potomac

Grady CL, Maisog JM, Horwitz B, Ungerleider LG, Mentis MJ, Salerno JA, Pietrini P, Wagner E, Haxby JV (1994) Age-related changes in cortical blood flow activation during visual processing of faces and location. J Neurosci 14:1450–1462

Grill-Spector K, Henson R, Martin A (2006) Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn Sci 10:14–23

Grill-Spector K, Kourtzi Z, Kanwisher N (2001) The lateral occipital complex and its role in object recognition. Vision Res 41:1409–1422

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

Grill-Spector K, Kushnir T, Edelman S, Itzchak Y, Malach R (1998) Cue-invariant activation in object-related areas of the human occipital lobe. Neuron 21:191–202

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

Grill-Spector K, Malach R (2004) The human visual cortex. Annu Rev Neurosci 27:649–677

Goodale MA, Milner AD (2004) Sight unseen: an exploration of conscious and unconscious vision. Oxford University Press, Oxford

Gordon AM, Westling G, Cole KJ, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. J Neurophysiol 69:1789–1796

Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RBH (1998) Retinotopy and color sensitivity in human visual cortical area V8. Nat Neurosci 1:235–241

Hanazawa A, Komatsu H (2001) Influence of the direction of elemental luminance gradients on the responses of V4 cells to textured surfaces. J Neurosci 21:4490–4497

Hasson U, Harel M, Levy I, Malach R (2003) Large-scale mirror-symmetry organization of human occipito-temporal object areas. Neuron 37:1027–1041

Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P (2001) Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293:2425–2430

Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL (1994) The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J Neurosci 14:6336–6353

Hayworth K, Biederman I (2006) Neural evidence for intermediate representations in object recognition. Vision Res 46:4024–4031

Henson RN (2003) Neuroimaging studies of priming. Prog Neurobiol 70:53–81

Heywood CA, Cowey A (1987) On the role of cortical area V4 in the discrimination of hue and pattern in macaque monkeys. J Neurosci 7:2601–2617

Heywood CA, Gaffan D, Cowey A (1995) Cerebral achromatopsia in monkeys. Eur J NeuroSci 7:1064–1073

Heywood CA, Kentridge RW (2003) Achromatopsia, color vision, and cortex. Neurol Clin 21:483–500

Humphrey GK, Goodale MA, Jakobson LS, Servos P (1994) The role of surface information in object recognition: studies of a visual form agnosic and normal subjects. Perception 23:1457–1481

Imamizu H, Kuroda T, Yoshioka T, Kawato M (2004) Functional magnetic resonance imaging examination of two modular architectures for switching multiple internal models. J Neurosci 24:1173–1181

James TW, Culham J, Humphrey GK, Milner AD, Goodale MA (2003) Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain 126:2463–2475

James TW, Humphrey GK, Gati JS, Menon RS, Goodale MA (2002) Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. Neuron 35:793–801

Kanwisher NG, Chun MM, McDermott J, Ledden PJ (1996) Functional imaging of human visual recognition. Cogn Brain Res 5:55–67

Kanwisher N, McDermott J, Chun M (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311

Kastner S, De Weerd P, Ungerleider LG (2000) Texture segregation in the human visual cortex: a functional MRI study. J Neurophysiol 83:2453–2457

Kourtzi Z, Kanwisher N (2000) Cortical regions involved in perceiving object shape. J Neurosci 20:331–3318

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

Kroliczak G, Cavina-Pratesi C, Goodman DA, Culham JC (2007) What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. J Neurophysiol 97:2410–2422

Kuhtz-Buschbeck JP, Ehrsson HH, Forssberg H (2001) Human brain activity in the control of fine static precision grip forces: an fMRI study. Eur J Neurosci 14:382–390

Levy I, Hasson U, Avidan G, Hendler T, Malach R (2001) Center-periphery organization of human object areas. Nat Neurosci 4:533–539

Lueck CJ, Zeki S, Friston KJ, Deiber MP, Cope P, Cunningham VJ, Lammerstma AA, Kennard C, Frackowiak RSJ (1989) The colour centre in the cerebral cortex of man. Nature 340:386–388

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 92:8135–8139

McKeefry DJ, Zeki S (1997) The position and topography of the human colour centre as revealed by functional magnetic resonance imaging. Brain 120:2229–2242

Miceli G, Fouch E, Capasso R, Shelton JR, Tomaiuolo F, Caramazza A (2001) The dissociation of color from form and function knowledge. Nat Neurosci 4:662–667

Milner AD, Perrett DI, Johnston RS, Benson PJ, Jordan TR, Heeley DW, Bettucci D, Mortara F, Mutani R, Terazzi E (1991) Perception and action in 'visual form agnosia'. Brain 114:405–428

Murray SO, Wojciulik E (2004) Attention increases neural selectivity in the human lateral occipital complex. Nat Neurosci 7:70–74

Ogawa S, Tank DW, Menon R, Ellermann JM, Kim SG, Merkle H, Ugurbil K (1992) Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. Proc Natl Acad Sci USA 89:5951–5955

Peuskens H, Claeys KG, Todd JT, Norman JF, Van Hecke P, Orban GA (2004) Attention to 3-D shape, 3-D motion, and texture in 3-D structure from motion displays. J Cogn Neurosci 16:665–682

Price CJ, Humphreys GW (1989) The effects of surface detail on object categorization and naming. Q J Exp Psychol 41A:797–827

Puce A, Allison T, Asgari M, Gore JC, McCarthy G (1996) Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J Neurosci 16:5205–5215

Reddy L, Kanwisher N (2006) Coding of visual objects in the ventral stream. Curr Opin Neurobiol 16:408–414

Russell R, Sinha P, Biederman I, Nederhouser M (2006) Is pigmentation important for face recognition? Evidence from contrast negation. Perception 35:749–759

Schacter DL, Buckner RL (1998) Priming and the brain. Neuron 20:185–195

Sergent J, Ohta S, MacDonald B (1992) Functional neuroanatomy of face and object processing. Brain 115:15–36

Steeves JKE, Humphrey GK, Culham JC, Menon RS, Milner AD, Goodale MA (2004) Behavioral and neuroimaging evidence for a contribution of color and texture information to scene classification in a patient with visual form agnosia. J Cogn Neurosci 16:1–11

Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. Thieme Medical Publishers, New York

Tarr MJ, Kersten D, Cheng Y, Doerschner K, Rossion B (2002) Men are from mars, women are from venus: behavioral and neural correlates of face sexing using color. J Vision 2:598a

Tarr MJ, Kersten D, Cheng Y, Rossion B (2001) It's pat! Sexing faces using only red and green. J Vision 1:337a

Tootell RBH, Tsao D, Vanduffel W (2003) Neuroimaging weighs in: humans meet macaques in "primate" visual cortex. J Neurosci 23:3981–3989

Valyear KF, Culham JC, Sharif N, Westwood D, Goodale MA (2006) A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: a human fMRI study. Neurophysiology 44:218–228

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ (1996) Functional anatomy of a common semantic system for words and pictures. Nature 383:254–256

Wiggs CL, Martin A (1998) Properties and mechanisms of perceptual priming. Curr Opin Neurobiol 8:227–233

Wilson HR, Loffler G, Wilkinson F (2002) Synthetic faces, face cubes, and the geometry of face space. Vision Res 42:2909–2923

Xu Y, Turk-Browne NB, Chun MM (2007) Dissociating task performance from fMRI repetition attenuation in ventral visual cortex. J Neurosci 27:5981–5985

Zeki SM (1973) Colour coding in rhesus monkey prestriate cortex. Brain Res 53:422–427

Zeki S, Aglioti S, McKeefry D, Berlucchi G (1999) The neurological basis of conscious color perception in a blind patient. Proc Natl Acad Sci USA 96:14124–14129

Zeki S, Watson JDG, Lueck CJ, Friston KJ, Kennard C, Frackowiak RSJ (1991) A direct demonstration of functional specialization in human visual cortex. J Neurosci 11:641–649