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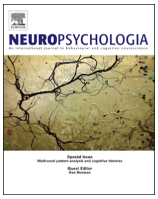

Visual object agnosia is associated with a breakdown of object-selective responses in the lateral occipital cortex

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ABSTRACT

Patients with visual object agnosia fail to recognize the identity of visually presented objects despite preserved semantic knowledge. Object agnosia may result from damage to visual cortex lying close to or overlapping with the lateral occipital complex (LOC), a brain region that exhibits selectivity to the shape of visually presented objects. Despite this anatomical overlap the relationship between shape processing in the LOC and shape representations in object agnosia is unknown. We studied a patient with object agnosia following isolated damage to the left occipito-temporal cortex overlapping with the LOC. The patient showed intact processing of object structure, yet often made identification errors that were mainly based on the global visual similarity between objects. Using functional Magnetic Resonance Imaging (fMRI) we found that the damaged as well as the contralateral, structurally intact right LOC failed to show any object-selective fMRI activity, though the latter retained selectivity for faces. Thus, unilateral damage to the left LOC led to a bilateral breakdown of neural responses to a specific stimulus class (objects and artefacts) while preserving the response to a different stimulus class (faces). These findings indicate that representations of structure necessary for the identification of objects crucially rely on bilateral, distributed coding of shape features.

1. Introduction

Visual object identification seems puzzlingly easy considering that the retinal image varies in almost infinite ways according to size, viewpoint, illumination or position (Connor, 2004; Logothetis & Sheinberg, 1996; Ullman, 1996). How the visual system computes invariant representations from varying inputs and how these representations affect object identification has been a major issue for theories of visual perception. Object identification depends on the representation of multiple 2D-views of the object (Riesenhuber & Poggio, 1999; Tarr, Williams, Hayward, & Gauthier, 1998) or on the transformation of local shape elements into a viewpoint-invariant description of geometrical object structure (Biederman, 1985; Edelman, 1997; Kourtzi & Connor, 2011; Riddoch & Humphreys, 2001). The primary candidate for this transformation is the lateral occipital complex (LOC). In fMRI studies this region is activated when subjects passively view pictures of common objects compared to textures or scrambled images (Denys et al., 2004; Grill-Spector et al., 1999; Grill-Spector & Malach, 2004; Kourtzi & Kanwisher, 2001; Malach et al., 1995). LOC activity is modulated by object shape irrespective of familiarity (Malach et al., 1995), semantics (Kim, Biederman, Lescroart, & Hayworth, 2009), or local image contours (Kourtzi & Kanwisher, 2001). In addition, the LOC response to intact objects varies with changes of viewpoint, but not with changes in object size or position (Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector et al., 1999). These findings place LOC at a hierarchically intermediate level of shape processing: after the computation of shape primitives, contours, size and position, but before a view-invariant representation is achieved.

However, the finding of LOC activation by object shape does not in itself prove that it is *necessary* for object recognition. It might be recruited because subjects engage additional processes that are irrelevant for recognition, or may perform computations related to the analysis of object category rather than shape (Kourtzi & Connor, 2011; Kriegeskorte et al., 2008). The study of patients with visual agnosia following occipito-temporal damage may provide causal evidence about the kind of object representations that are elaborated in this area. Object agnosia is not a clearly defined clinical entity, but rather a collection of deficits that result

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from impairments at different levels of perceptual analysis. Extensive bilateral occipito-temporal damage may lead to the complete breakdown of simple shape processing, a condition known as visual 'apperceptive' agnosia or form agnosia (Benson & Greenberg, 1969; Karnath, Ruter, Mandler, & Himmelbach, 2009; Milner et al., 1991). Other patients show deficits of perceptual organization and integration (Behrmann & Kimchi, 2003; Riddoch & Humphreys, 1987) or more subtle impairments suggesting impaired access to semantic knowledge through the visual modality (Anaki, Kaufman, Freedman, & Moscovitch, 2007; Farah, 2004; Schnider, Benson, & Scharre, 1994). The latter form of object agnosia has also been termed 'associative' because of a supposed disconnection between purely perceptual shape representations and their respective semantic associations (Farah, 2004; Rubens & Benson, 1971; Teuber, 1968). However, the precise functional relationship between shape processing in the LOC and impaired shape representations in object agnosia is unknown. Assuming that the LOC mediates visual representations at a specific stage in a hierarchical processing structure, damage to or dysfunction of this region should have an impact on later processing stages, while leaving representations elaborated at earlier stages intact. Functional imaging of patients with circumscribed brain lesions and object agnosia provides an important complement to behavioural studies, as it may help to identify the type of processing that depends on the LOC and to provide information about representations that are accessible beyond this brain area. Several previous studies have examined brain activations in patient DF, who has visual form agnosia following bilateral damage centred on the LOC (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al., 1991). These studies have revealed relatively intact activations in areas outside the damaged occipito-temporal cortex for colour and texture, but no activity to intact shapes in the areas of damage (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; James et al., 2003). These findings fit well to the impairments of DF, who fails to identify objects by sight and exhibits severe impairments in discriminating basic shape, size or orientation, but retains the capacity to make colour and texture discriminations. While these findings suggest a predominant role of the LOC in visual form processing it is unclear to what extent they bear to the occurrence of associative object agnosia, which generally results from unilateral occipito-temporal damage and in which basic form processing is preserved. One study has used fMRI in a patient who had associative agnosia due to a small lesion to the right posterior fusiform gyrus (Konen, Behrmann, Nishimura, & Kastner, 2011). When tested with stimuli that typically activate the LOC (objects vs. scrambled objects) this patient showed intact activations of the occipital cortex in the damaged hemisphere, but a significant reduction of activated temporal cortex. Moreover, he also exhibited decreased object-selectivity in the LOC of his intact *left* hemisphere, suggesting that visual object agnosia might be the result of a distant (possibly inhibitory) effect of the right on the left LOC. However, the interpretation of these findings is complicated by the fact that following his closed head injury the patient had shearing injuries to the corpus callosum, which might have affected interhemispheric interactions between the right and left LOC. In addition, occipito-temporal activity was only examined with objects and 2D or 3D nonsense shapes, leaving it open whether the seemingly dysfunctional cortex is activated by other visual categories.

Here, we studied a patient who became object agnosic following stroke to left lateral and inferior occipito-temporal cortex. Using behavioural experiments and fMRI we sought to determine the precise contribution of the LOC to the representation of shape in our patient. In addition, we sought for the reasons why his intact (right) LOC was not sufficient to support object recognition. We found that object agnosia in this patient is associated with a complete, bilateral breakdown of object-specific responses in the occipito-temporal cortex.

2. Material and methods

2.1. Subjects

The visual agnosic patient AL and seven age-matched healthy subjects (3 male; mean age, 73.9 ± 13.2 years) participated in the behavioural study. In addition, four healthy subjects (2 male; mean age, 75.2 ± 5.3 years) participated as controls in the fMRI study. All participants gave written informed consent and the study was approved by the Ethical committee of the University Hospital Geneva.

2.2. Case description

AL is a highly educated, 75 year-old right-handed man who suffered a left occipito-temporal stroke at the age of 72. Structural MRI revealed damage affecting the left lateral occipital cortex, extending medially into the fusiform and lingual gyri, and dorsally into the middle occipital gyrus (Fig. 1). The primary visual cortex, cuneus and anterior temporal lobe were spared. AL has right superior quadrantanopia and severely impaired visual identification of words (pure alexia) and objects (visual object agnosia), in the absence of elementary visual, language or semantic impairment (verbal IQ: 117). Details of the neuropsychological examination of AL were provided in a previous study, which focused on AL's alexia (Di Pietro, Ptak, &

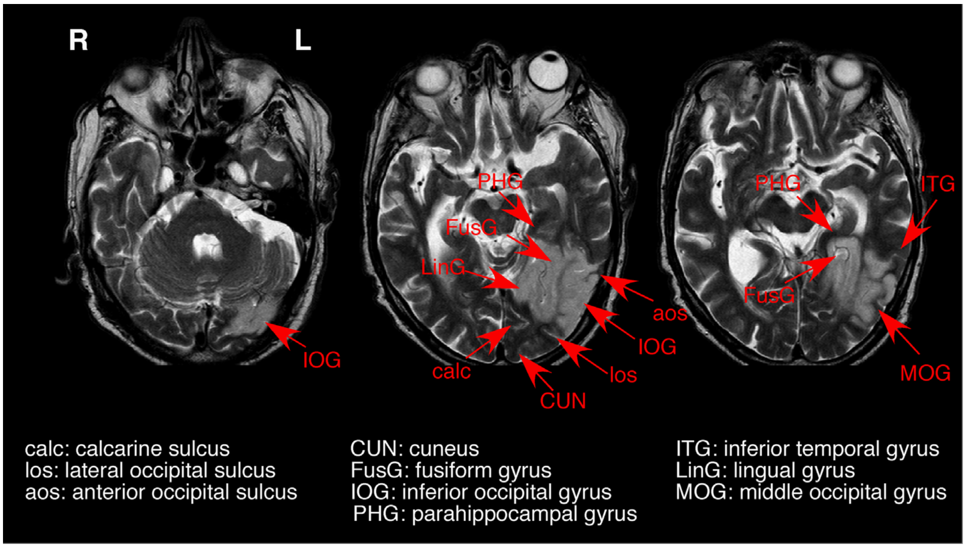

Fig. 1. T2-weighted structural MRI showing the extent of AL's vascular lesion (left hemisphere shown on the right side).

Table 1
Performance scores of AL in neuropsychological tests of visual and visuo-spatial processing.

Test	Task	AL	Control mean	Below cut-off
Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993)	Length match	27	26.9	
	Size match	27	27.3	
	Orientation match	25	24.8	
	Position of gap match	34	35.1	
	Minimal feature view	21	23.3	
	Foreshortened view	18	21.6	
	Object decision	87	114.7	X
	Item match	24	30	X
	Associative match	17	27.5	X
Visual Object and Space Perception Battery (Warrington & James, 1991)	Screening	20	19.9	
	Incomplete letters	14	18.8	X
	Silhouettes	1	22.2	X
	Object decision	16	17.7	
	Progressive silhouettes	20	10.8	X
	Dot counting	10	9.9	
	Position discrimination	20	19.6	
	Number location	8	9.4	
	Cube analysis	8	9.2	
LEXIS (Bilocq et al., 1999)	Pointing to target	64	78.8	X
	Semantic matching	108	156.3	X
Pyramids and Palm Trees Test (Howard & Patterson, 1992)	visual	37	50	X
	verbal	51	50	
Chimeric objects (Barbarotto et al., 2002)	Score	74.6	83.6	X
Benton faces (Benton et al., 1983)	Score	39		
Face processing (Bruyer & Schweich, 1991)	Facial decision	24	22.2	
	Face parts	9	8.9	
	Independent of expression	20	22.6	
	Independent of pose	4	9.7	X
	Identification of gender	19	19.6	
	Identification of age	29	29.4	
	Facial expression	12	11.2	
	Familiarity decision	38	42.8	

Schnider, 2012). Table 1 presents AL's scores on standard neuropsychological tests of visual and visuo-spatial function. AL's object agnosia is evidenced by impaired naming and gestural description of visually presented objects, while tactile naming and naming to verbal description is intact. He is severely impaired when making semantic associations between objects (Howard & Patterson, 1992) or when judging which of three objects belong to the same category (Bilocq, de Partz, De Wilde, Pillon, & Seron, 1999). He also scores below control cut-off when making decisions on chimeric objects (Barbarotto, Laiacona, Macchi, & Capitani, 2002). Despite these deficits he accurately copies line drawings that he fails to identify in a fluid, non-slavish manner (Fig. 2). In a local–global task with hierarchical letters AL shows robust interference effects from the local to the global level (i.e., he is 140 ms faster when the global and local letter are coherent than when they are incoherent, $p > .001$) and from the global to the local level (he is 56 ms faster for coherent than incoherent letters, $p < .01$). This finding indicates that AL does not have 'integrative' agnosia (Riddoch & Humphreys, 1987), as he can adequately integrate local parts into a perceptual whole. The patient also easily detects local shape variations of objects shown in the same (24/24 correct) or a mirrored presentation (23/24 correct; Op de Beeck & Wagemans, 2001), matches objects across viewpoints (38/40 correct) and identifies violations in 3D-structure (78/80 correct with Escher-like forms; Williams & Tarr, 1997). Perception of faces is comparatively less impaired than the perception of objects, as he has a borderline performance in the Benton face recognition test (Benton, Hamsher, Varney, & Spreen, 1983) and a performance within the lower range of healthy participants in a battery testing the configural aspects of face processing (Bruyer & Schweich, 1991; see Table 1).

2.3. *Behavioural study*

Naming of pictures and naming to verbal description was examined with 260 stimuli (Snodgrass & Vanderwart, 1980) presented as line drawings or in the form of a verbal description (e.g.,: 'a piece of furniture used for sleeping'—bed). Artefact naming was examined by asking subjects to identify 35 real objects and four digitized versions of the same objects: colour photographs, black & white photographs, line drawings and silhouettes. Tactile naming was tested with participants blindfolded and free to manipulate the artefacts with both hands. In order to avoid carry-over effects between different naming conditions controls were only tested in three conditions (colour photographs, line drawings and tactile naming). The effect of colour on naming accuracy was tested with 70 drawings of objects known to have prototypical colours (Rossion & Pourtois, 2004), presented once in the familiar and once in an unfamiliar colour. 40 common objects (courtesy of Michael Tarr Lab, Department of Cognitive and Linguistic Sciences, Brown University, RI) were used to test the dependence of object identification on viewpoint. Each object was shown once in canonical and once in a foreshortened representation. For the shape-modulation task 60 coloured line drawings (Rossion & Pourtois, 2004) were presented in their natural form or in a distorted form that was created by applying a square-shaped envelope to the original image. Stimuli were shown on a PC-screen at a distance of 60 cm and subtended 5–8°. In all experiments the order of presentation was counterbalanced, with half of the stimuli presented first in their familiar, then in their unfamiliar form, and vice versa.

For the object-matching task 20 pairs of line drawings (Snodgrass & Vanderwart, 1980) were selected that shared similar outline shape. In addition to the complete image, two alternative versions of each image were created: one by erasing inner features and preserving only the shape envelope, and one by erasing the shape envelope and preserving only inner features. On each trial ($n=80$) the target (e.g., a suitcase) or the visual distracter (e.g., a book) were shown together with a semantic (e.g., a basket) and a neutral distracter (e.g., a telescope), and subjects were asked to point to the target if they thought that it was present.

2.4. *fMRI study*

We used blocked-design fMRI adaptation (fMRIa) to study neural responses of AL and four controls to human faces, objects and scrambled versions of both types of stimuli. Stimuli were 62 grey-scale photographs (472×472 pixel) of unknown faces (half men, half women; courtesy of the Laboratoire de Psychologie et Neurocognition, Grenoble, France) and 62 objects. Scrambled pictures had the same horizontal and vertical dimensions as the original pictures and were created by dividing the latter into small rectangular parts using a matrix of 30×30 cells and rearranging these parts randomly. Given that scrambled pictures only differed from the originals regarding object shape, any difference in brain activity generated by these stimuli could not be attributed to differences in luminance or colour. Objects used for the study were diverse tools and artefacts similar to those used in the naming study. In order to check whether AL had the same degree of impairment with these two image sets we asked him to identify the objects outside the scanner. He named 32 out of the 62 objects correctly (51.6%), which was

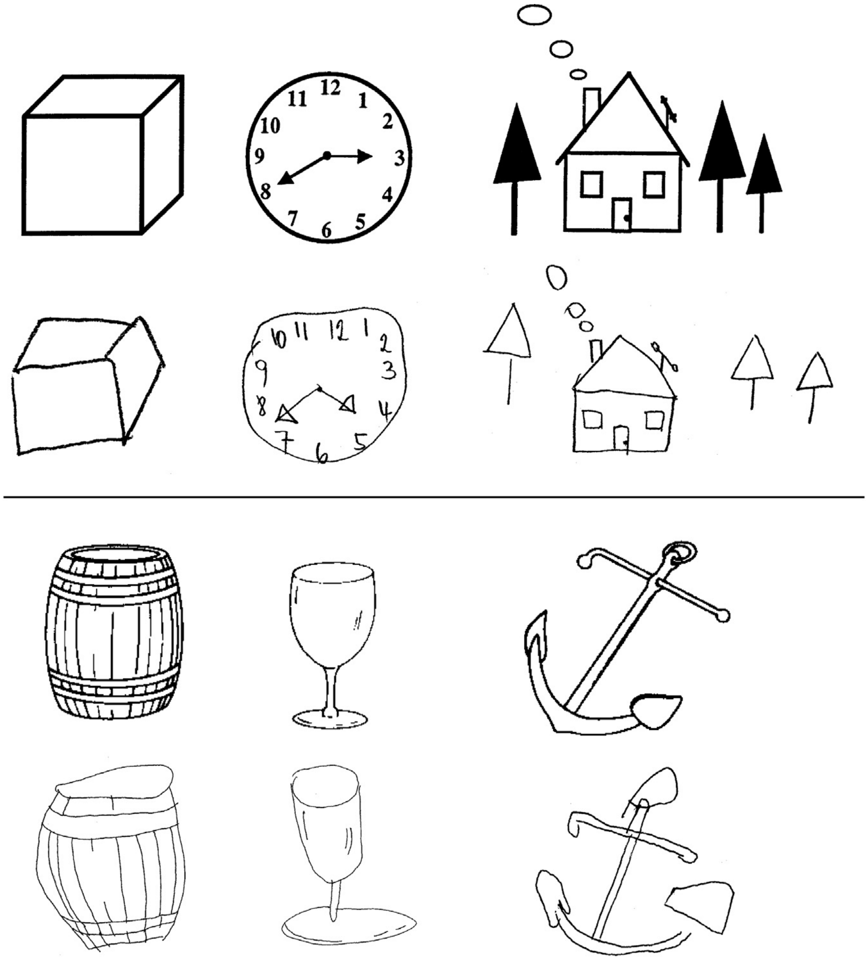

Fig. 2. Examples of AL's copying of various objects. The upper row shows pictures from the Birmingham Object Recognition Battery. The lower row shows line drawings from the Snodgrass & Vanderwart set that AL copied adequately, but misidentified.

almost identical to his performance with greyscale pictures in the behavioural study (54.3%; $X^2 = .06$).

Participants underwent three scans each of which contained 20 epochs of 9 stimuli, for a total of 180 stimuli. The duration of each epoch was 24 s and stimuli were presented for 2000 ms separated by 666 ms blank periods. Stimulus epochs differed according to stimulus type (face, object or scrambled image) and the number of different within-epoch items presented (nine different stimuli, each presented once; three stimuli, each presented three times; one stimulus presented nine times). In addition, a further condition was added in which three visually similar objects (e.g., a needle, a toothpick and a pencil) were presented three times. Thus, there were 10 types of stimulus epochs, and each was presented twice, arranged in random order within each scan. The different stimulus conditions were used for the assessment of brain activity related to the encoding of stimulus shape (by comparing activations of faces or objects with scrambled pictures), category-specificity (by comparing activations of faces with objects) and adaptation effects (by comparing epochs containing nine different stimuli with epochs containing one repeated stimulus). Activity related to the processing of shape similarity was examined by comparing epochs with three similar objects to epochs with three dissimilar objects.

Stimuli were projected centrally on a translucent screen located at the end of the scanner bore, and participants viewed them through a mirror mounted on the head coil. The screen was 15° wide and stimuli subtended between 3.9° and 6.6° of visual angle horizontally and between 2.5° and 4.5° vertically. A central fixation cross (0.25°) was presented in the blank periods between two stimuli. In order to control for attention effects subjects were asked to press a response button upon appearance of a red dot at fixation, which was presented at intervals of 5–8 images.

2.5. *fMRI data acquisition*

Structural and functional images were acquired on a 3T Siemens scanner (Siemens Medical Solutions, Erlangen, Germany) with a 12-channel head coil. T2*-weighted GRE echo planar imaging (EPI) was used to obtain blood oxygenation dependent contrast (BOLD) responses in 3 series of 270 volumes each. Each volume contained 30 slices and covered the whole brain, with a slice thickness of 4 mm (repetition time/TR: 2000 ms; echo time/TE: 30 ms; flip angle: 85°; matrix: 128 × 108; in-plane resolution: 2 mm × 1.7 mm). The acquisition of functional images was preceded by three dummy scans that were later discarded to ensure tissue steady-state magnetization. A high-resolution 3D MPRAGE T1-weighted sequence (TR: 2500 ms; TE: 2.97 ms; flip angle: 9°; matrix: 256 × 224; resolution: 1.1 mm^3) was also acquired for subsequent cortical surface alignment.

2.6. *fMRI data preprocessing*

Imaging data were analysed using SPM8 (www.fil.ion.ucl.ac.uk/spm) and Freesurfer (http://surfer.nmr.mgh.harvard.edu). Preprocessing involved head-motion correction through realignment to the image acquired closest in time to the anatomical scan (Ashburner & Friston, 2007), coregistration to the anatomical reference scan (Ashburner & Friston, 2005) and normalization to the segmented T1 image. Functional images were smoothed with a 4 mm FWHM Gaussian kernel and high-pass and low-pass filtered in order to remove scanner signal drift and physiological artefacts. Separate regressors of interest modelling the presentation conditions were convolved with the canonical hemodynamic response function (HRF). Using a general linear model approach (Friston et al., 1995) regressors of interest and six additional regressors derived from the motion corrections were entered in a multiple regression model. Statistical parametric maps (SPMs) were then generated for each participant from linear contrasts between HRF functions corresponding to different conditions of interest. All analyses were performed on the individual data of each subject. In a first step whole-brain analyses ($p < .001$, uncorrected; cluster-extent threshold: 10 voxels) were performed in order to identify voxels responding to faces and objects as compared to scrambled pictures. Voxels showing stimulus-specificity were identified by the contrast between face versus object presentation. Voxels showing adaptation effects were examined by contrasting epochs containing nine different stimuli with epochs containing one repeated stimulus. SPMs were then coregistered with the inflated cortical surface computed by FREESURFER.

In a second step we conducted region of interest (ROI) analyses in order to examine region-specific activity in occipito-temporal cortex. In fMRI experiments the lateral occipital complex (LOC) is typically defined by contrasting activity evoked by objects to scrambled images (Grill-Spector et al., 1999). However, given that AL did not show any detectable activity using this contrast we defined ROIs for all subjects anatomically rather than functionally, using the automatic cortical parcellation implemented in FREESURFER (Destrieux, Fischl, Dale, & Halgren, 2010). This procedure models anatomical labels by computing the probability of a given label at a specific position based on prior probabilities and current data as well as information about anatomical labels at neighbouring positions (Fischl et al., 2004). A high correspondence (~85%) has been reported between this method of automatic labelling and manual labelling by an experienced neuroradiologist (Destrieux et al., 2010). We restricted ROI analysis to four anatomical regions covering the dorsal extrastriate cortex (the middle occipital gyrus and the superior occipital gyrus, respectively) and the occipito-temporal cortex (the inferior occipital gyrus and the fusiform gyrus), which are known to exhibit activity related to face and object processing. The averaged grey-matter volume of each of these ROIs was comparable between AL and the control group (AL range, 2161–6413 mm^3; control range, 2229–6722 mm^3). ROI-specific activations related to contrasts of interest were compared with a *t*-statistic implemented in the MarsBaR toolbox for SPM (www.sourceforge.net/projects/marsbar). The *p*-values for this statistic were adjusted using Holms adaptation of the Bonferroni correction (Holm, 1979). The MarsBaR toolbox was subsequently used to compute the percent signal change averaged across voxels included in the ROI, normalized to the mean session signal across conditions.

3. Results

3.1. Behavioural results

A straightforward way to study object recognition is to present the target under different visual conditions and to measure how these conditions affect performance. However, this approach can be problematic because the target may activate implicit processes or explicit strategies that obscure the nature of the patient's object representations. In addition to this method of examination we here used an alternative approach, in that in some experiments we only presented distracters and studied the conditions under which false responses could be provoked. This allowed us to analyse the relationship between visual characteristics of a stimulus and the patient's visual representation of that stimulus.

We tested AL's object identification of 260 visually presented line drawings as compared to verbal descriptions of the same items (Fig. 3a). He identified significantly fewer items in the visual (46%) than the verbal condition (95%; $X^2 = 144.7$, $p < .0001$). The results of AL were compared to the average of the control group using a Bayesian approach for the comparison of a single case to a small control sample (Crawford & Garthwaite, 2007). Compared to controls AL scored worse in the visual condition ($p < .0001$), but significantly better in the verbal condition ($p < .05$), testifying for his excellent object knowledge. Many of AL's errors were either mixed visual-semantic (e.g., *dog* for donkey; 33%) or purely visual (e.g., *hat* for lamp; 12%). In order to examine systematically the impact of visual information present in different types of illustrations of objects we tested AL's visual recognition with tools and artefacts presented in five different visual formats (Fig. 3a). Controls scored at ceiling and significantly better than the patient

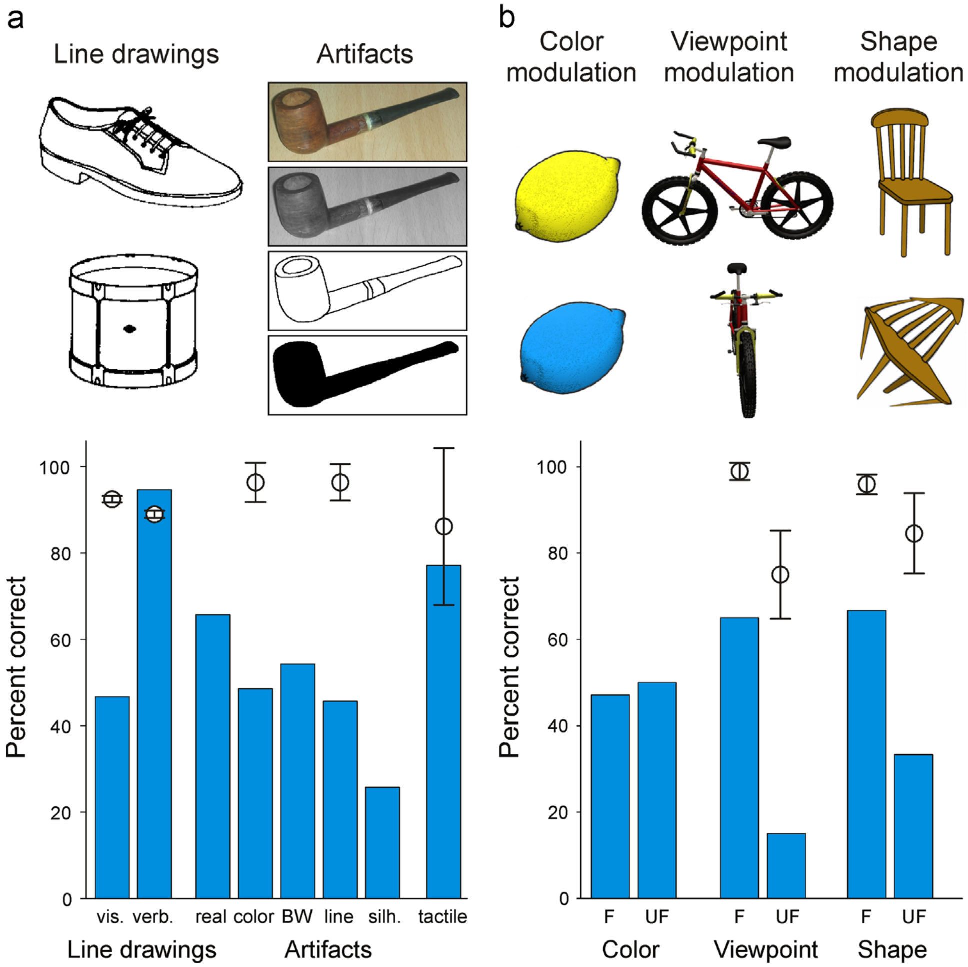

Fig. 3. Examples of items and naming performance of AL in the object identification tasks. (a) Items presented in the form of a line drawing were also tested using verbal descriptions. Artefact naming was additionally tested with the real object under visual and tactile presentation. (b) Pictures used to test identification of colour-, viewpoint- or shape-modulated objects. Familiar versions (F) of each object are shown in the upper row and unfamiliar versions (UF) in the lower row. The graphs show naming performance of AL (bars) and controls (circles, mean ± SD) for the different conditions shown above. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with colour photographs and line drawings (both $p<.0001$). In agreement with previous observations (Humphrey, Goodale, Jakobson, & Servos, 1994) AL's performance declined across visual conditions ($X^4=12.0$, $p<.05$), indicating that the lack of surface cues such as depth, shading and internal edge elements is detrimental for his object identification. In contrast, AL scored within the range of controls when asked to identify the same objects by touch ($p=.33$).

We further tested the impact of modulations of colour, viewpoint and shape on AL's identification of objects (Fig. 3b). His performance was equivalent for objects shown in their familiar colours as compared to when the same objects were atypically coloured ($X^2=0.1$). Object naming in the latter condition was independent of his capacity to identify prototypical object colours, which was highly accurate irrespective of whether he correctly identified the object (94.7%) or not (90.6%; $X^2=0.04$). In contrast, AL's object identification was strongly affected by the modulation of viewpoint ($X^2=20.8$, $p<.0001$) and distortions of shape ($X^2=13.3$, $p<.001$). Though controls also scored worse with unfamiliar views and distorted objects (both $p<.01$), the drop in performance due to viewpoint and shape modulation was significantly greater in AL (both $p<.05$).

These findings show that AL has intact access to object identity through the verbal and tactile, but not the visual modality. Surface characteristics and internal shape elements modulate AL's object identification, and he is particularly impaired with distorted objects or objects presented in unfamiliar views. We next used categorization tasks to study more precisely the role of shape characteristics necessary for AL's object recognition. When asked to point to a target picture (e.g., an orange) presented together with a visual (a ball), semantic (a banana), and neutral distracter (a violin) AL scored 87.5% correct. Similarly, he scored near ceiling when asked to point to the two visually similar objects in the array (orange and ball; 92.5%). However, when required to point to the two objects that were members of the same semantic category (orange and banana) he only made 12.5% correct decisions, selecting on the majority of trials (70%) the two visually similar objects. This could not be explained by a failure to understand the concept of semantic similarity, since AL performed much better when items were presented verbally (82.5% correct; $X^2=39.3$, $p<.0001$). We hypothesized that AL's tendency to categorize objects on the basis of their visual similarity rather than semantic category would lead to false recognitions when a visual distracter was present, but the target was absent. When asked to indicate whether an array of three objects contained a given item, he would indeed choose the visual distracter more often than a semantic ($X^2=26.7$, $p<.0001$) or neutral distracter ($X^2=40.6$, $p<.0001$; Fig. 4), though he knew that the target might not be present. A nearly identical pattern was obtained with stimuli that only preserved their outline shape envelope, with all inner features being eliminated (Fig. 4). In contrast, AL made significantly less visual errors with stimuli whose shape was only determined by their inner features ($X^2=5.1$, $p<.05$).

3.2. Functional imaging results

We used functional MRI to study brain responses of AL to faces, objects and scrambled pictures (Fig. 5a). In all four controls the contrast *face>scrambled* activated infero-lateral occipito-temporal cortex bilaterally (Table 2), centred on the occipito-temporal sulcus (OTS) and extending into the lateral fusiform gyrus (FG; Fig. 5b). AL's preserved right occipito-temporal cortex was activated at a threshold of $p<.001$ (uncorrected), with an activation peak (29 voxels, lying in the OTS) surviving correction for multiple comparisons (FWE: $t>4.66$, $p<.05$). The *object>scrambled* contrast yielded bilateral LOC activations in all four control subjects; in addition, three of four controls also showed clusters of activation in middle occipital cortex, the precuneus and

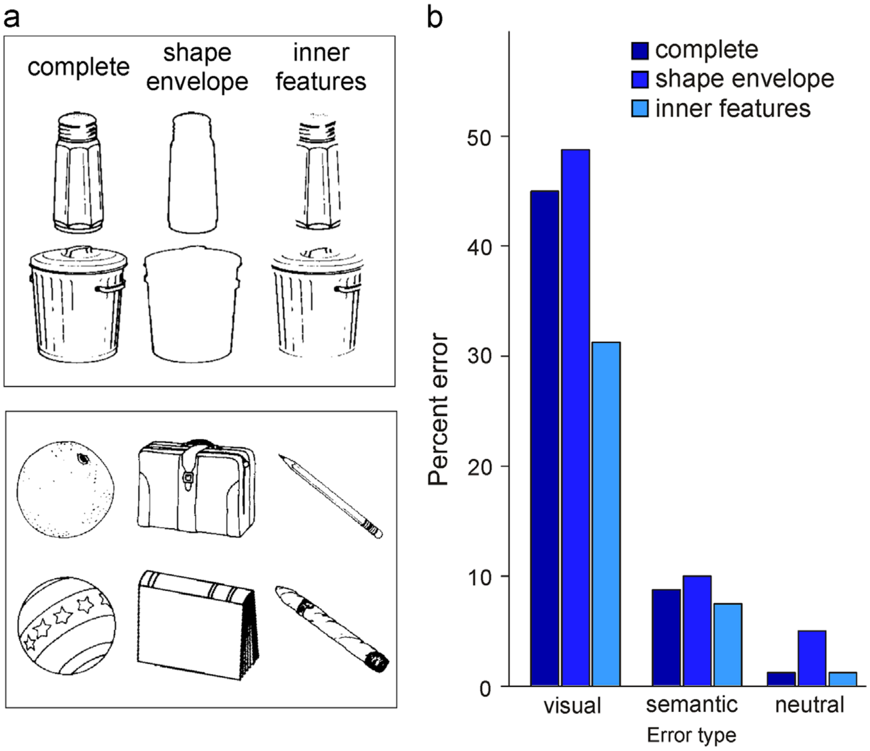

Fig. 4. Examples of items and performance in the object matching tasks. (a) Examples of line drawings showing a target and a distracter in each of the three matching conditions. The lower part shows examples of two visually similar items that AL would typically confuse (e.g., he would point to the ball when asked to point to the orange and vice versa). (b) Error distribution of AL in the three experimental conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

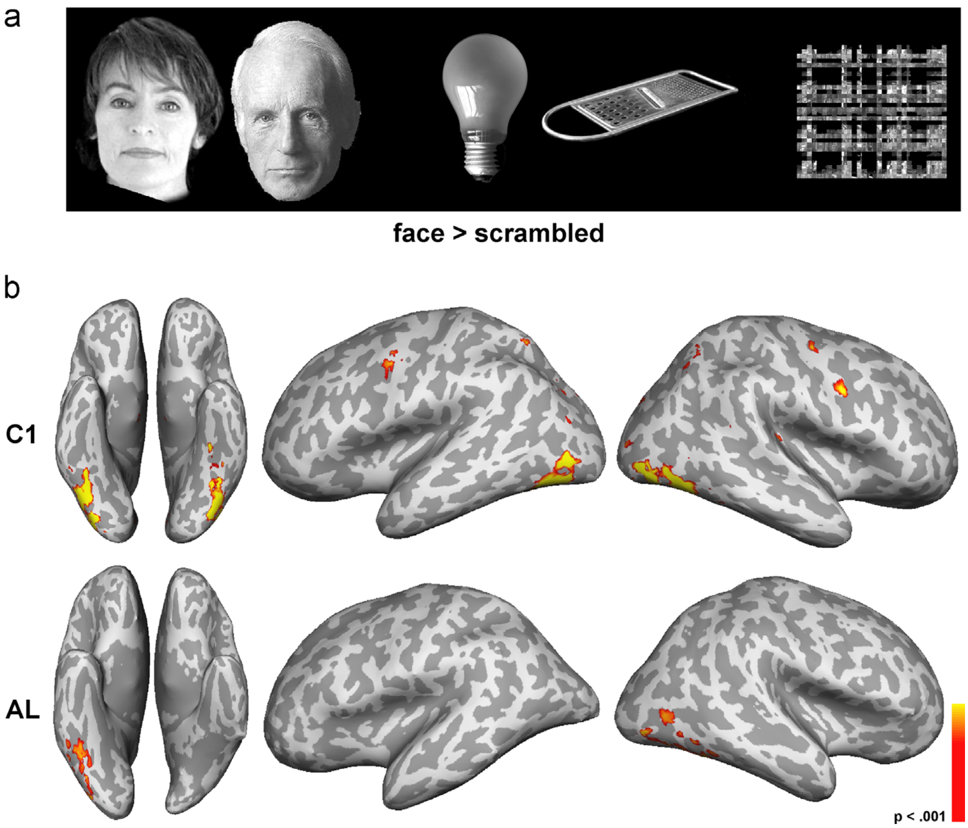

Fig. 5. Examples of items used in the fMRI study and brain activation evoked by faces. (a) Examples of faces, objects and scrambled pictures. (b) Statistical parametric maps (SPMs) of the *face* > *scrambled* contrast projected on the inflated brain of a representative control (C1) and patient AL.

the intraparietal sulcus (Fig. 6). In contrast, neither the left nor the structurally intact right visual cortex of AL was activated by objects as compared to scrambled pictures. We further explored differences in activation to faces and objects by contrasting both conditions directly. In the *face* > *object* contrast, the OTS and lateral FG were bilaterally activated in controls and on the right side in AL (Fig. 7). In AL this condition also activated the parietal and superior temporal cortex. In contrast, while *object* > *face* reliably activated the LOC bilaterally in controls this condition did not yield any activations in AL (Fig. 7).

In order to examine the selectivity of response of areas activated by faces and objects we used fMR-adaptation (fMR-A) paradigms (Krekelberg, Boynton, & van Wezel, 2006). Three of four controls showed moderate adaptation effects to faces in LOC and FG (Table 2), but all exhibited adaptation effects in the LOC to repeated presentation of objects. In contrast, while AL exhibited adaptation to faces in the right middle occipital and middle temporal cortex (Table 2), he had no adaptation to objects. We examined the adaptation response closer in four anatomical ROIs covering inferior occipito-temporal, lateral and superior occipital cortex (Fig. 8a). Healthy controls showed significant decreases of activation to repeated objects in all four ROIs of the left hemisphere ($F_{1,9}=17.8$, $p<.01$). In the right hemisphere, though adaptation interacted with the factor ROI ($F_{3,27}=4.9$, $p<.01$), post-hoc tests revealed robust adaptation effects in all four ROIs ($t>3.1$, $p<.02$; Fig. 8b). Because of AL's left occipito-temporal damage, anatomical ROIs could only be determined in his right hemisphere. In contrast to controls AL exhibited negative signal changes in all four right-hemispheric ROIs when shown pictures of objects, and none of these showed significant adaptation.

We finally searched for a functional correlate of AL's tendency to confuse visually similar objects by examining selectivity to shape similarity at the ROI level. Controls did not exhibit differential responses to visually similar and dissimilar objects in the left hemisphere. However, there was an ROI x similarity interaction in the right hemisphere ($F_{3,27}=3.67$, $p<.05$) reflecting the fact that the fusiform and inferior occipital gyrus exhibited stronger responses to similar than dissimilar objects ($t>2.2$, $p<.05$; Fig. 8c). In contrast, similar and dissimilar objects produced negative signal changes and no modulation by shape similarity in AL's intact right occipito-temporal cortex.

4. Discussion

By combining fMRI with comprehensive behavioural testing we identified functional changes in the LOC of a visual agnosic patient that mirror his deficient object identification. Our results reveal a possible neural mechanism that may underlie object agnosia: the selective breakdown of neural response to object shape despite the preservation of face-selectivity in structurally intact occipito-temporal cortex.

Following a left occipito-temporal stroke AL had lasting and remarkably pure visual recognition deficits affecting the identification of objects and words. He demonstrated intact object identification and easily accessed semantic knowledge when tested in the auditory or tactile modality. Though not perfect, he was also less impaired with faces, as he could discriminate and match faces across different views or illumination conditions. It is important to distinguish his visual impairments from visual form agnosia, which typically results from diffuse bilateral occipito-temporal damage and is characterized by severe deficits of elementary form and orientation processing, figure-ground assignment and perceptual grouping mechanisms (Benson & Greenberg, 1969; Campion & Latto, 1985; Karnath et al., 2009; Milner et al., 1991). AL's pattern of deficits conforms more to patients classified as 'associative' visual agnosics, as he was able to

Table 2
Activations to contrasts involving faces and objects ($p < .001$). Side refers to the hemisphere where any activation in a given contrast was observed.

Contrast	Subject	Side	Max. *T*-score	MNI-coordinates (in mm)			Volume (mm^3)
				x	*y*	*z*	
Face > scrambled	C1	L/R	17.68	-48	−76	−11	13149
	C2	L/R	14.76	51	−73	1	7308
	C3	L/R	12.96	45	−73	−11	2295
	C4	L/R	16.19	−36	−70	−17	5481
	AL	***R***	***6.87***	***42***	***−75***	***−9***	***1926***
Face > obj	C1	L/R	13.83	−51	−76	−11	33966
	C2	L/R	9.92	39	−49	−11	1503
	C3	R	8.85	45	−73	−11	1278
	C4	L/R	13.04	−36	−70	−17	9477
	AL	***L/R***	***6.70***	***48***	***−60***	***−12***	***20988***
Face9 > face1	C1	L/R	4.40	−45	−82	−11	1881
	C2	–	–	–	–	–	0
	C3	L/R	5.86	−27	−94	1	2646
	C4	L	3.83	−36	−82	−11	117
	AL	***L/R***	***3.80***	***45***	***−72***	***−6***	***1080***
Obj > scrambled	C1	L/R	13.91	−45	−76	−8	12834
	C2	L/R	12.33	−42	−76	−5	34605
	C3	L/R	10.17	48	−82	−5	3546
	C4	L/R	10.9	−36	−88	−5	7470
	AL	–	–	–	–	–	***0***
Obj > face	C1	L/R	8.30	−36	−82	16	5760
	C2	L/R	8.01	−6	−88	−14	16677
	C3	L/R	11.05	33	−82	4	37413
	C4	L/R	7.84	−36	−91	13	9126
	AL	–	–	–	–	–	***0***
Obj9 > obj1	C1	L/R	8.26	−39	−82	19	25839
	C2	L	4.26	−39	−70	−5	693
	C3	L/R	8.94	12	−79	−11	85212
	C4	L/R	5.81	18	68	−5	13329
	AL	–	–	–	–	–	***0***

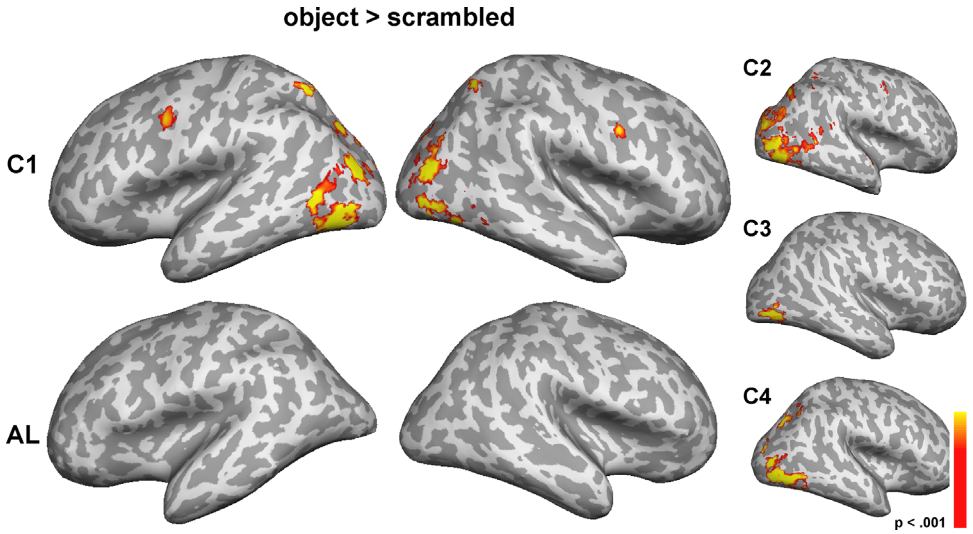

Fig. 6. Brain activation evoked by objects. SPMs of the *object > scrambled* contrast shown for the four controls and patient AL.

analyse global object structure and local details efficiently, yet failed to identify, to determine the semantic category of or to gesture the use of an object (Anaki et al., 2007; Behrmann & Kimchi, 2003; Delvenne, Seron, Coyette, & Rossion, 2004; Farah, 2004; Grüsser & Landis, 1991; Rubens & Benson, 1971). Nevertheless, AL did not have integrative visual agnosia, a subtype of associative agnosia characterized by slavish copying and a difficulty in integrating local shape elements into a perceptual whole (Riddoch & Humphreys, 1987). The patient did neither copy slavishly nor did he evidence abnormal effects when asked to identify local or global elements embedded in hierarchical stimuli. In contrast, modulations of object viewpoint and distortions of object shape significantly affected his performance. In addition, AL was strongly biased toward categorizing objects based on visual features, rather than category membership. Finally, he frequently indicated visually similar distracter objects when provided the verbal label of a target object. These findings suggest that AL had access to a viewpoint-dependent representation of crude object structure that was mainly based on global shape characteristics of objects. Furthermore, the fact that his object naming suffered with increasing disparity between the target and a canonical 2D-projection suggests that AL's deficit affects a processing stage at

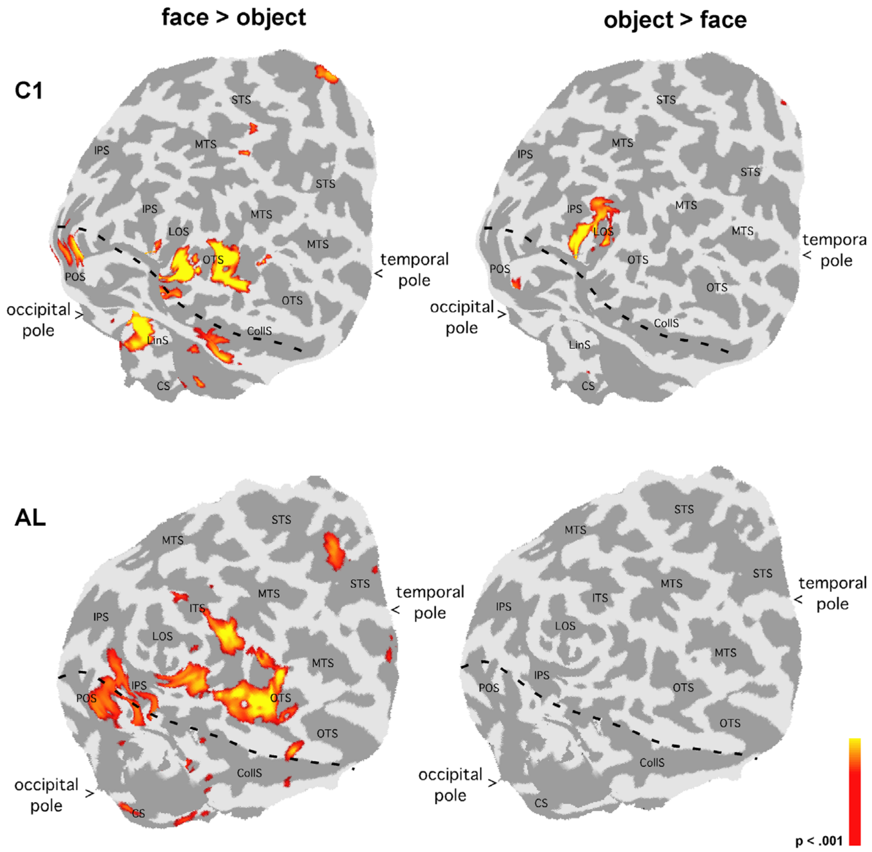

Fig. 7. Direct comparison of brain activations evoked by faces and objects. SPMs of the *face* > *object* and *object* > *face* contrast projected on a flattened map of the occipito-temporo-parietal cortex, shown for control subject C1 and patient AL (CS: calcarine sulcus; CollS: collateral sulcus; IPS: intraparietal sulcus; LinS: lingual sulcus; LOS: lateral occipital sulcus; MTS: middle temporal sulcus; OTS: occipito-temporal sulcus; PO: parietal–occipital sulcus; STS: superior temporal sulcus).

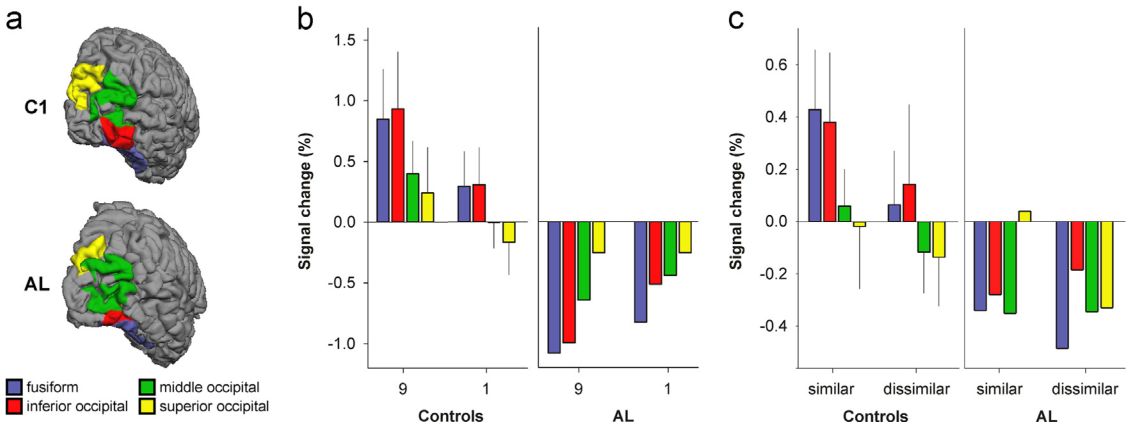

Fig. 8. Region of interest (ROI) analyses. (a) Posterior views of the right-hemisphere anatomical ROIs in which fMRI signal change was examined, shown for control subject C1 and AL. (b) Signal change measured in the four ROIs when subjects viewed nine different objects or one single object presented repeatedly. (c) Signal change measured in the four ROIs when subjects viewed visually similar objects as compared to dissimilar objects.

which pre-semantic and viewpoint-invariant representations are computed.

AL's visual processing deficits can be directly correlated to modifications of local brain activity revealed by fMRI. In none of the functional contrasts did we found activation of the damaged left occipito-temporal cortex in AL, indicating widespread dysfunction of damaged and perilesional left-hemispheric tissue. Similarly to healthy controls (Grill-Spector, 2003; Kanwisher, McDermott, & Chun, 1997) and an agnosic patient (Steeves et al., 2006) faces activated AL's right occipito-temporal face-selective cortex, and this area also showed normal adaptation to the repeated presentation of faces. This finding is coherent with AL's comparatively less impaired face processing capacities. In contrast to the results obtained with faces, objects did not evoke any functional activity in AL, whether they were contrasted to scrambled pictures or to faces. Thus, activity in AL's right occipito-temporal cortex retained its selectivity for a specific subclass of visual stimuli (faces), but lost its selectivity for another subclass (objects). A closer look at regional signal changes within the LOC revealed that viewing objects was associated with increased activity in controls, but decreased activity in AL. Additionally, ROI analyses revealed that while controls showed functional adaptation of object-selective responses in the LOC when objects were presented repeatedly, in AL the strength of the LOC response remained unchanged. Neural adaptation is considered a measure of the specialization of a brain region for the processing of particular stimulus features (such as colour or shape) or a subclass of stimuli that contain specific feature combinations (such as faces; Krekelberg et al., 2006). The absence of adaptation in AL's LOC (together with the absence of LOC response in the *object > scrambled* contrast) therefore suggests that this region had partially lost its functional specificity for the processing of object shape. In addition to this breakdown of stimulus-specificity, we observed that while controls' LOC activity reliably distinguished between similar and dissimilar objects, the responses in AL remained undifferentiated. Previous fMRI studies have shown that the occipito-temporal cortex is sensitive to perceived shape similarity, as expressed both locally in specific regions such as the LOC (Op de Beeck, Torfs, & Wagemans, 2008) and through more widespread activity (Haxby et al. 2001). Interestingly, the ventral and the lateral LOC appear to code for shape at different spatial scales, the former part being involved in coarse coding and the latter in more fine-grained coding of shape, suggesting that these LOC subregions respectively represent local features and global shapes (Drucker & Aguirre, 2009). Though we did not design our experiments with the aim to measure such a distinction, control participants exhibited similarity effects only in the posterior fusiform and inferior occipital cortex, which roughly correspond to the location of ventral LOC. The absence of a selective response to shape similarity in AL's ventral LOC may seem contradictory to his tendency to categorize objects based on their global shape similarity. However, these findings can be reconciled when we consider the possible functional significance of increased neural responses to similar as compared to dissimilar objects. The heightened response of ventral LOC to visual similarity may reflect an increased necessity for more precise processing in order to avoid visual errors in the presence of highly confusable objects. AL's behaviour fits well with this interpretation, as the absence of a selective response to shape similarity in his ventral LOC is associated with a tendency to confuse objects based on their outline shape. In addition, our data support the hypothesis that object shape may be coded at two distinct spatial scales (Drucker & Aguirre, 2009): coarse coding of global shape (which is independent of the LOC and largely intact in our patient) and fine coding of local shape elements. This segregation of global and local shape processing within the ventral occipito-temporal cortex may also underlie the puzzling observation that AL did not show any significant activity in the object-scrambled contrast, yet remained able to make shape discriminations. This finding suggests that AL's spared visual cortex mediated shape computations that are not adequately captured by the object-scrambled contrast. Given that the degree of high spatial frequency content is higher in scrambled pictures compared to intact pictures (Grill-Spector et al., 1999; James et al., 2003) any bias favouring either local or global processing likely influences brain responses evoked by these images, eventually resulting in an absence of difference in activity.

In conclusion, the present findings agree with previous fMRI studies of agnosic patients with bilateral (Cavina-Pratesi et al., 2010; James et al., 2003) or unilateral (Konen et al., 2011) occipito-temporal damage in suggesting a causal contribution of the LOC to the computation of object shape. In particular, the finding that AL's structurally intact right-hemisphere LOC lost object-selectivity complements a previous study, in which (conversely to our patient) damage of the *right* hemisphere was found to reduce object-selective responses in the intact *left* hemisphere (Konen et al., 2011). Our findings converge with these observations, suggesting that in the intact brain the perception of object structure may depend on a functional coupling between the left and right LOC (Farah, 1991). How would such a mechanism explain the absence of right LOC response in AL? One possibility is that his damaged left LOC inhibited activity of the contralateral homologous region. The finding of a negative signal change in the right LOC when AL viewed objects is compatible with this interhemispheric inhibition account. However, an intriguing alternative is that viewing objects automatically recruits widespread regions of occipito-temporal cortex and that representations of object shape emerge from such distributed activity. Under this assumption the computation of object shape is a result of cooperative activity within distributed interhemispheric neural circuits (Behrmann & Plaut, 2013). These findings are also relevant for the controversy whether object representations in occipito-temporal cortex are hierarchically organized based on object structure or according to semantic category (Kourtzi & Connor, 2011; Kriegeskorte et al., 2008). AL tended to categorize objects based on their visual characteristics, irrespective of their semantic relationship. This feature of his agnosia suggests that – at least at the level of the LOC – the representation of object shape dominates over category membership. An impairment of fine-grained processing of shape elements may give more weight to global visual similarity for the coding of object categories and thus lead to more 'fuzzy' categorical representations. Thus, the absence of object-selectivity in the LOC is accompanied by subtle deficits of shape processing which preclude a correct mapping between the current perception and stored representations of objects seen in the past.

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