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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, &

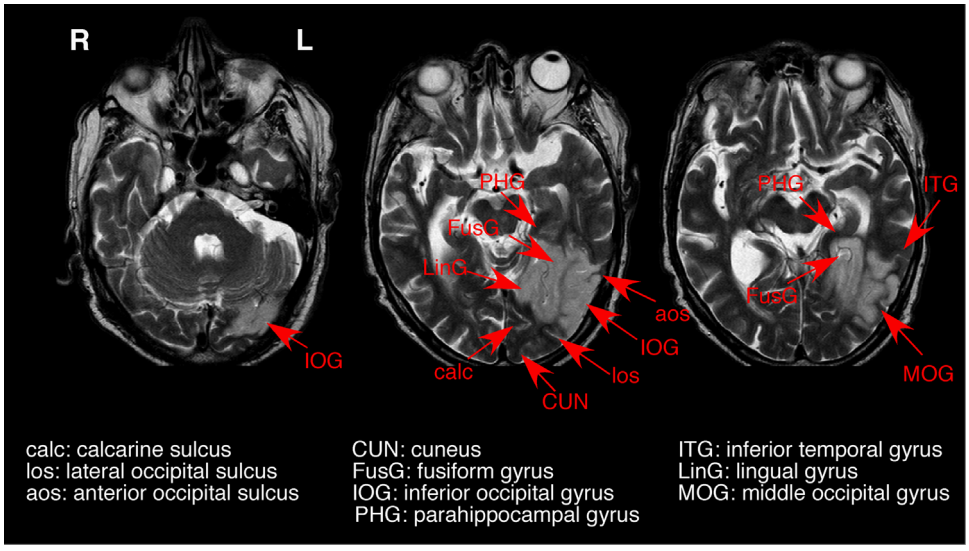

Fig. 1. T2-weighted structural MRI showing the extent of AL's vascular lesion (left hemisphere shown on the right side).