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Right fusiform response patterns reflect visual object identity rather than semantic similarity

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A B S T R A C T

We previously reported the neuropsychological consequences of a lesion confined to the middle and posterior part of the right fusiform gyrus (case JA) causing a partial loss of knowledge of visual attributes of concrete entities in the absence of category-selectivity (animate versus inanimate). We interpreted this in the context of a two-step model that distinguishes structural description knowledge from associative-semantic processing and implicated the lesioned area in the former process. To test this hypothesis in the intact brain, multi-voxel pattern analysis was used in a series of event-related fMRI studies in a total of 46 healthy subjects. We predicted that activity patterns in this region would be determined by the identity of rather than the conceptual similarity between concrete entities. In a prior behavioral experiment features were generated for each entity by more than 1000 subjects. Based on a hierarchical clustering analysis the entities were organised into 3 semantic clusters (musical instruments, vehicles, tools). Entities were presented as words or pictures. With foveal presentation of pictures, cosine similarity between fMRI response patterns in right fusiform cortex appeared to reflect both the identity of and the semantic similarity between the entities. No such effects were found for words in this region. The effect of object identity was invariant for location, scaling, orientation axis and color (grayscale versus color). It also persisted for different exemplars referring to a same concrete entity. The apparent semantic similarity effect however was not invariant. This study provides further support for a neurobiological distinction between structural description knowledge and processing of semantic relationships and confirms the role of right mid-posterior fusiform cortex in the former process, in accordance with previous lesion evidence.

Introduction

Elucidating the functional organisation of occipitotemporal cortex is crucial for understanding how visuoperceptual input is relayed to the semantic network (Farah, 2004; Humphreys and Riddoch, 2003; Logothetis and Sheinberg, 1996; Marr, 1982; Martin et al., 1999; Rogers and McClelland, 2004). Neuropsychology (Farah, 2004; Humphreys and Riddoch, 2003) and non-invasive mapping of the intact brain (e.g. Bright et al., 2005; Devlin et al., 2005; Huth et al., 2012; Lerner et al., 2001; Peelen and Caramazza, 2012; Price and Devlin, 2003) continue to play a prominent role in this endeavour, among other methods (Biederman, 1987; Chan et al., 2011; DiCarlo et al., 2012; Liu et al., 2009; Logothetis and Sheinberg, 1996; Marr, 1982; Nobre et al., 1994; Rogers and McClelland, 2004; Tyler and Moss, 2001). Theories differ in how basic-level identification of concrete entities relates to memory for semantic relationships between these entities. In healthy subjects object identification almost automatically provides access to the meaning of the object and activates to varying degrees the connections of the concrete entity within the semantic 'web'. Computational models propose that a concrete entity (such as e.g. 'cat') belongs to a semantic web consisting of a myriad of nodes (e.g. other concrete entities) which are connected with variable connection strengths (Dell, 1986; Rogers and McClelland, 2004). In the current paper, we will use object identification to refer to the 'nodal' level and semantic processing to the 'network' level, although we realise that the 'nodes' themselves, that correspond to entities at the basic level, are also constituted by combinations of different features (object parts, shape…) (Dell, 1986). From this it should be clear that, neurobiologically, to disentangle basic-level object identification from the automatic retrieval of semantic relationships and associations constitutes a difficult problem and that it requires converging evidence from multiple experimental sources.

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The distinction between object identification and associative-semantic processing may even be artificial: The 'embodied cognition' concept emphasises the intimate relationship between visuoperceptual identification and categorical processing (Barsalou, 2008; Martin et al., 1999). According to such models, category-specificity arises from the structure of the feature space as represented in occipitotemporal cortex (Martin and Chao, 2001). Functional imaging studies in healthy controls have indicated that ventral occipitotemporal cortex may be best viewed as a lumpy feature-space, representing stored information about features of object form shared by members of a category (Martin and Chao, 2001).

According to an alternative theory, the Hierarchical Interactive Theory (Forde et al., 1997; Humphreys and Riddoch, 2003), the structural description system mediates object identification and is neurobiologically distinct from the system mediating associative-semantic processing. According to this model, object recognition consists of at least two neurobiologically separable steps: one step permits the matching of the encoded representation of an object to the corresponding stored structural description, the other maps structural knowledge onto the 'semantic representations' (Hillis and Caramazza, 1995; Rumiati and Humphreys, 1997). Structural descriptions code for the long-term memory of perceptual features that are necessary for the identification of familiar objects, in particular shape and object parts (Forde et al., 1997; Humphreys and Riddoch, 2003). One of the principal sources of empirical evidence for these fundamental questions comes from focal lesions of the occipitotemporal processing stream in humans.

Lesion case studies have provided evidence for a role of right posterior/middle fusiform cortex in invariant visuoperceptual identification (Konen et al., 2011) as well as in mnemonic retrieval of visual features of concrete entities (Vandenbulcke et al., 2006). Case JA had a lesion confined to right posterior and middle fusiform gyrus (Fig. 1) (Vandenbulcke et al., 2006). JA was impaired on the object decision task, a task that requires subjects to discriminate drawings of real-life objects from chimaeric objects and that is classically regarded as diagnostic for a structural description deficit (Riddoch and Humphreys, 1993). Perceptual identification speed was decreased in JA (Vandenbulcke et al., 2006) while copying was preserved. Case JA was impaired on tasks probing explicit retrieval of visuoperceptual features through both verbal (feature generation, forced-choice naming to definition) and nonverbal means (drawing from memory). Despite a selective impairment of retrieval of visual features, JA did not demonstrate a semantic category effect, biological versus non-biological (Vandenbulcke et al., 2006) and was able to name pictures of objects from different categories, although JA needed longer stimulus presentation durations than controls. We interpreted the deficit in JA as a selective loss of knowledge of visual features of real-life concrete entities and situated the deficit at the structural description processing level. According to these lesion data, this structural description knowledge can be retrieved explicitly through verbal or nonverbal means (Vandenbulcke et al., 2006). A second relevant case, SM, had a traumatic lesion similar in location to JA's lesion. SM displayed integrative object agnosia (Behrmann and Kimchi, 2003a, b; Behrmann and Williams, 2007), characterised by impaired spatial integration of object parts (Behrmann et al., 2006). Recognition of a visual stimulus that represents a real-life entity entails identification of the stimulus as an instantiation of that entity in a way that tolerates variations in viewpoint, stimulus position, scaling etc. (DiCarlo et al., 2012; Rust and Dicarlo, 2010). Viewpoint invariance, a prerequisite for the processing of structural descriptions, was bilaterally reduced in the Lateral Occipital Complex (LO) in case SM (Konen et al., 2011). A third case, DHY (Hillis and Caramazza, 1995), who had optic aphasia, fundamentally differred from JA and SM. In DHY, access to structural description knowledge was preserved while processing of fine-grained semantic distinctions (e.g. sorting between cats and dogs, or edible versus non-edible animals) was impaired (Hillis and Caramazza, 1995). Taken together, these cases provide evidence for a neurobiological distinction between object identification and processing of fine-grained semantic relationships between objects.

In the current fMRI study, we tested the hypothesis that the region that was lesioned in JA, right mid-posterior fusiform cortex (Fig. 1), is involved in structural description processing which is necessary for invariant basic level object identification and that this process can

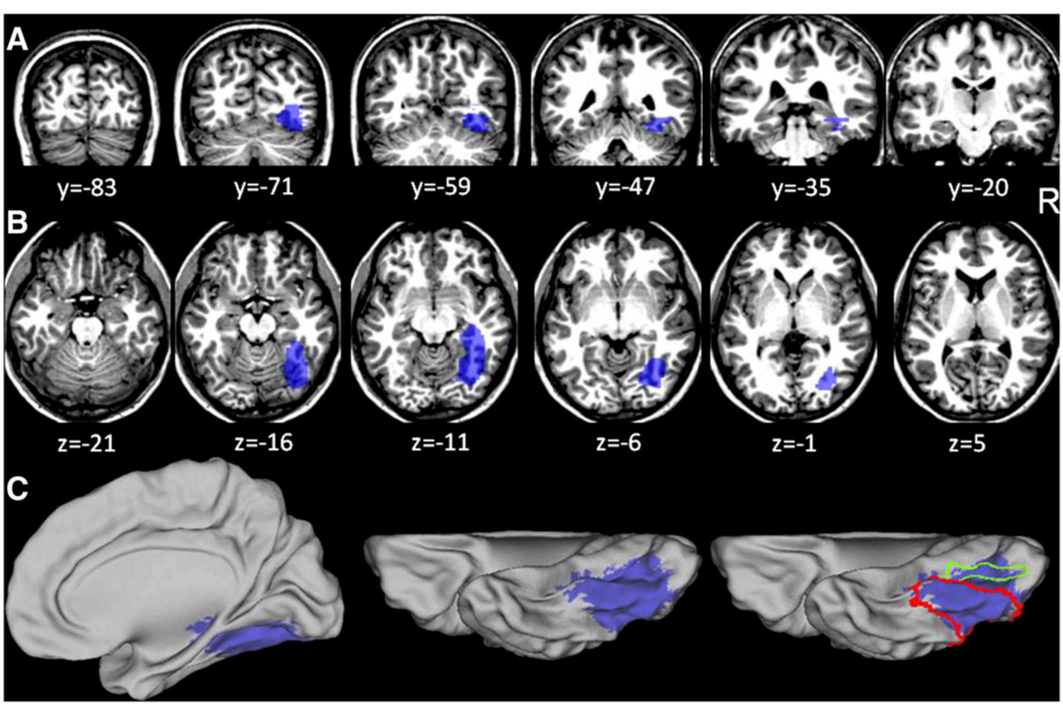

Fig. 1. Lesion map of case JA (blue). A. Coronal sections. B. Transverse sections. C. Projections onto a surface rendering of the brain (Caret v5.65 (Van Essen, 2005)). Green outline: area V4v (green, extracted from Caret v5.65 (Van Essen, 2005)). Red outline: area LO, defined by contrasting the picture stimuli of Kourtzi and Kanwisher (2001) with the scrambled pictures from that study (Vandenbulcke et al., 2006).