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Research report

From percept to concept in the ventral temporal lobes: Graded hemispheric specialisation based on stimulus and task

Paul Hoffman [a,b,*] *and Matthew A. Lambon Ralph* [b]

[a] *Centre for Cognitive Ageing and Cognitive Epidemiology (CCACE), Department of Psychology, University of Edinburgh, UK*

[b] *Neuroscience and Aphasia Research Unit (NARU), Division of Neuroscience & Experimental Psychology, School of Biological Sciences, University of Manchester, UK*

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ABSTRACT

The left and right ventral anterior temporal lobes (vATL) have been implicated as key regions for the representation of conceptual knowledge. However, the nature and degree of hemispheric specialisation in their function is unclear. To address this issue, we investigated hemispheric specialisation in the ventral temporal lobes using a distortion-corrected spin-echo fMRI protocol that enhanced signal in vATL. We employed an orthogonal manipulation of stimulus (written words *vs* pictured objects) and task (naming *vs* recognition). Words elicited left-lateralised vATL activation while objects elicited bilateral activation with no hemispheric bias. In contrast, posterior ventral temporal cortex exhibited a rightward bias for objects as well as a leftward bias for words. Naming tasks produced left-lateralised activation in vATL while activity for recognition was equal in left and right vATLs. These findings are incompatible with proposals that left and right ATLs are strongly modular in function, since these predict rightward as well as leftward biases. Instead, they support an alternative model in which (a) left and right ATL together form a bilateral, integrated system for the representation of concepts and (b) within this system, graded hemispheric specialisation emerges as a consequence of differential connectivity with other neural systems. On this view, greater left vATL activation for written word processing develops as a consequence of the inputs this region receives from left-lateralised visual word processing system in posterior temporal cortex. Greater left vATL activation during naming tasks is most likely due to connectivity with left-lateralised speech output systems in prefrontal and motor cortices.

* *Corresponding author*. Centre for Cognitive Ageing and Cognitive Epidemiology, Department of Psychology, University of Edinburgh, 7 George Square, Edinburgh, EH8 9JZ, UK.
E-mail address: p.hoffman@ed.ac.uk (P. Hoffman).

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1. Introduction

One key function of the ventral temporal cortices (VTC) is to act as a “ventral visual stream” that is critically involved in visual object recognition (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). In non-human primates, for example, posterior-to-anterior regions of the ventral occipitotemporal cortex are implicated in increasingly complex aspects of visual perception, at the apex of which are neurons in anterior temporal cortex that code for object categories independent of view or other low-level characteristics (Albright, 2012; Booth & Rolls, 1998; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). In humans, however, the role of the anterior portion of VTC (which we will refer to as the ventral anterior temporal lobe, or vATL) extends far beyond the visual domain. Convergent evidence indicates that the vATLs are involved in semantic processing of visual objects and faces, but also names, concrete and abstract words, auditory speech and non-verbal sounds (Mion et al., 2010; Nobre, Allison, & McCarthy, 1994; Pobric, Lambon Ralph, & Jefferies, 2009; Rice, Hoffman, & Lambon Ralph, 2015; Shimotake et al., 2015; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006; Visser, Jefferies, Embleton, & Lambon Ralph, 2012). These data have led us and others to propose a model of the functional anatomy of the temporal lobes, in which the vATLs act as an integrative “hub” for the development of transmodal conceptual representations (Binney, Parker, & Lambon Ralph, 2012; Guo et al., 2013; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Patterson, Nestor, & Rogers, 2007; Rice, Hoffman, & Lambon Ralph, 2015). On this view, high-level visual perceptual (in posterior VTC), auditory perceptual (in superior temporal cortex) and social and emotional processing streams (in orbitofrontal and temporopolar cortex) converge on vATL, which generates supramodal representations of concepts that bind these information sources together.

In this study, we investigated hemispheric specialisation in the function of the vATLs and compared this directly with visual processing specialisations in posterior VTC. There is already clear evidence from neuropsychological, neurostimulation and neuroimaging studies that both left and right vATLs make important contributions to concept representation (Butler, Brambati, Miller, & Gorno-Tempini, 2009; Gainotti, 2012; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Lambon Ralph, Ehsan, Baker, & Rogers, 2012; Mion et al., 2010; Shimotake et al., 2015). However, there is an ongoing debate over the degree to which the function of each vATL is specialised for particular sensory modalities, conceptual categories or tasks (Gainotti, 2011, 2012, 2014; Drane et al., 2013; Rice, Hoffman et al., 2015). In considering these possible specialisations, a useful starting point is to consider hemispheric specialisation in posterior VTC. Visual processing in posterior VTC is bilateral but exhibits hemispheric specialisations, most notably a left-hemisphere bias for word recognition and a right-hemisphere bias for face and object recognition (Cohen & Dehaene, 2004; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Thierry & Price, 2006). Importantly, these distinctions are graded rather than absolute. Patients with left posterior VTC lesions exhibit severe deficits in word recognition but are also impaired in face recognition. In patients with right posterior VTC damage, the situation is reversed: face recognition is most severely affected but word recognition deficits are also present (Behrmann & Plaut, 2014; Roberts et al., 2013).

There is some evidence and debate that this form of graded hemispheric specialisation might extend anteriorly into the ATL region, including vATL. To date, the principal source of data in this debate has been neuropsychological, with minimal information coming from fMRI studies of healthy participants (which is the core target of the present study). Patients with predominately left-hemisphere ATL damage have greater difficulty comprehending written words compared with pictures or faces, while the reverse is true of right ATL damage (Butler et al., 2009; Gainotti, 2007; Snowden, Thompson, & Neary, 2004). However, these dissociations are graded rather than absolute and both sets of patients have significant difficulty with both classes of stimuli. These findings have led some researchers to propose that left ATL is specialised for representation of verbal concepts and right ATL for non-verbal concepts (Gainotti, 2012, 2014; Snowden, Thompson, & Neary, 2012).

Another factor potentially driving specialisation is the retrieval of lexical labels based on semantic information. Patients with left ATL damage have greater difficulty naming pictures and faces than do patients with right ATL damage (Acres, Taylor, Moss, Stamatakis, & Tyler, 2009; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Drane et al., 2013; Lambon Ralph, McClelland, Patterson, Galton, & Hodges, 2001; Lambon Ralph et al., 2012), which may be a consequence of the greater connectivity between left ATL and left-lateralised speech output regions (Rice, Hoffman et al., 2015; Schapiro, McClelland, Welbourne, Rogers, & Lambon Ralph, 2013). A recent TMS study has also shown greater effects of left ATL disruption on picture naming tasks, relative to right ATL (Woollams, Lindley, Pobric, & Hoffman, 2017). In contrast, some studies suggest that damage to right ATL has a disproportionate effect on visual recognition tasks that do not require retrieval of a name (Damasio et al., 2004; Drane et al., 2013). These findings have led some researchers to claim that left ATL is specialised for lexical retrieval (i.e., naming) from visual information while the right ATL plays a greater role in visual discrimination tasks (Drane et al., 2013). It is not clear whether these laterality effects occur upstream in posterior VTC.

Although they have been influential in identifying potential sources of hemispheric specialisation, the patient studies described thus far are limited in terms of anatomical specificity. Most studies involve either patients with semantic dementia or patients with temporal lobe epilepsy undergoing ATL resection. The lesions in these conditions invariably encroach on the temporal pole and on the lateral and superior aspects of the ATL, as well as the vATL region that is the focus of the present study (Galton et al., 2001). This is important because there is emerging evidence for functional specialisation across the broader ATL region, with the superior temporal lobe in particular showing a markedly different pattern of functional and structural connectivity to the rest of the ATL, as well as greater specialisation for auditory-verbal semantic