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The perirhinal cortex and conceptual processing: Effects of feature-based statistics following damage to the anterior temporal lobes

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ABSTRACT

The anterior temporal lobe (ATL) plays a prominent role in models of semantic knowledge, although it remains unclear how the specific subregions within the ATL contribute to semantic memory. Patients with neurodegenerative diseases, like semantic dementia, have widespread damage to the ATL thus making inferences about the relationship between anatomy and cognition problematic. Here we take a detailed anatomical approach to ask which substructures within the ATL contribute to conceptual processing, with the prediction that the perirhinal cortex (PRc) will play a critical role for concepts that are more semantically confusable. We tested two patient groups, those with and without damage to the PRc, across two behavioural experiments – picture naming and word–picture matching. For both tasks, we manipulated the degree of semantic confusability of the concepts. By contrasting the performance of the two groups, along with healthy controls, we show that damage to the PRc results in worse performance in processing concepts with higher semantic confusability across both experiments. Further by correlating the degree of damage across anatomically defined regions of interest with performance, we find that PRc damage is related to performance for concepts with increased semantic confusability. Our results show that the PRc supports a necessary and crucial neurocognitve function that enables fine-grained conceptual processes to take place through the resolution of semantic confusability.

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1. Introduction

It is widely acknowledged that conceptual knowledge – our knowledge of people, places and entities – is subserved by a distributed neural system which includes the anterior temporal lobes (ATL). These regions feature in a number of neurobiological models of semantic knowledge, and are central to the hub and spoke model (Patterson et al., 2007; Rogers and Patterson, 2007) which is based primarily on data from patients suffering from the neurodegenerative disease Semantic Dementia (SD). SD is characterised by a progressive deterioration of conceptual knowledge in the context of well-preserved cognition. Patients with SD typically have semantic deficits in all modalities, and for all kinds of concepts, leading to the claim that the ATL is an amodal semantic hub in which different types of information relevant to semantic representations – e.g. sensory, motor and linguistic – converge (Patterson et al., 2007).

However, since the pathology in SD involves widespread damage to the ATL (amoungst other regions, Brambati et al., 2009; Mion et al., 2010; Noppeney et al., 2007) as the disease progresses (Bright et al., 2008), it has not been entirely clear which specific regions within the ATL contribute to the patients' semantic memory deficits. Acknowledging this lack of clarity, Binney et al. (2010) carried out a study in which they differentiated between a series of regions in the ATL. They defined ROIs which covered the lateral to medial extent of the ATL – including the temporal pole, superior temporal gyrus, middle temporal gyrus, inferior temporal gyrus, fusiform gyrus and the parahippocampal gyrus - and reported that the anterior ventral and inferolateral temporal lobe regions were essential for performance on semantic tasks.

In contrast to reports of a ventral and lateral anterior temporal focus for semantic effects in the ATL, the anteromedial regions of the ATL are also claimed to be critically involved in semantic computation, as revealed in the reports of category-specific semantic deficits in patients with anteromedial temporal lobe damage (Warrington and Shallice, 1984) and in a variety of subsequent behavioural and neuroimaging studies with healthy participants (Barense et al., 2010; Clarke and Tyler, 2014; Kivisaari et al., 2012; Moss et al., 2005; Taylor et al., 2006, 2009; Tyler et al.,

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2013, 2004; Wang et al., 2010). Patients who have category-specific semantic deficits know the category of an object, but they are exceptionally poor at differentiating between similar objects within a category. Moreover, this pattern is most pronounced for living things, especially animals (Moss et al., 2005, 1998, 1997; Warrington and Shallice, 1984).

Moss et al. (2005) linked these findings to a hierarchical neurobiological system of increasing feature complexity along the ventral stream (Ungerleider and Mishkin, 1982) in which simple visual features are processed in more posterior sites, with increasingly complex conjunctions of features more anteriorly, culminating in the apex of the stream – the perirhinal cortex (PRc) – which performs the most complex feature conjunctions (Barense et al., 2012; Cowell et al., 2010; Murray and Bussey, 1999; Murray et al., 2007). Moss et al. (2005) argued that these neural properties of the PRc provided the basis for the fine-grained analysis required for differentiating between highly similar concepts. Related research has found that when the PRc is damaged, patients have a category-specific deficit for living things, whereas patients with antero-lateral temporal lobe damage have a generalised semantic impairment and no category-specific impairment (Moss et al., 2005; Noppeney et al., 2007; Rogers and Patterson, 2007) (also see Bruffaerts et al., 2014 for a case with a living things deficit and spared PRc). The relationship between antero-medial temporal lobe structures and semantic processing has been further supported by neuroimaging studies with healthy volunteers that show living things preferentially engage the antero-medial temporal lobes (Moss et al., 2005; Taylor et al., 2006).

However, Tyler and colleagues argue that the association between living things deficits and increased activity for living things in the PRc is not due to category membership *per se* (Moss et al., 2005; Taylor et al., 2006; Tyler et al., 2013, 2004). Indeed, category effects in neuroimaging are not only observed in the PRc but also in more posterior regions (see Martin, 2007). Instead, they propose that effects for living things in the PRc are due to the extent to which members within a category are confusable. They assume a componential model of conceptual representations in which concepts are made up of smaller elements of meaning, referred to as features, properties or attributes (Cree and McRae, 2003; Gotts and Plaut, 2004; McRae et al., 1997; Mirman and Magnuson, 2008; Randall et al., 2004). In this type of model, features that are shared by many objects provide the basis for categorization (Smith and Medin, 1981), while those that are distinctive enable similar objects to be differentiated from each other (Cree and McRae, 2003; Taylor et al., 2012, 2008). According to property norm data, living things have more shared features and are therefore more highly confusable than members of other categories (Devereux et al., 2014; Keil, 1986; Malt and Smith, 1984; McRae et al., 1997; Randall et al., 2004), making them more dependent upon PRc function in order to differentiate one living thing from another, a prediction that has been supported by recent data from an fMRI study (Tyler et al., 2013). In contrast, category effects in the fusiform are claimed to be due to overlap in shared features, providing the basis of category structure (Tyler et al. 2013).

Conceptual structure measures derived from one feature-based model, the Conceptual Structure Account (CSA; Taylor et al., 2011; Tyler and Moss, 2001), which captures the statistical properties within and between concepts, have been widely used to probe the details of conceptual representation in behavioural, modelling and brain imaging studies (Clarke et al., 2013; Randall et al., 2004; Taylor et al., 2012, 2008; Tyler et al., 2013). Specifically, a feature statistic reflecting differentiation between highly similar objects, thus enabling object-specific representations, was associated with bilateral PRc activity in a recent fMRI study (Tyler et al., 2013). In the current paper, we manipulate semantic confusability to ask whether damage to the PRc impairs performance in the conceptual processing of concepts that require a high degree of within-category differentiation. To do this we developed two behavioural studies which measured different aspects of conceptual representation and were appropriate for brain-damaged patients – picture naming and word-picture matching. We tested patients who had a single lesion that was confined within the ventral temporal lobe, occipital lobe or temporal pole. These patients were divided into two groups depending on whether they had damage including the PRc, or whether the PRc was intact, and performance was compared in the different tasks to assess the impact of PRc damage on conceptual processing. As damage was not restricted to the PRc, but also effected other ventral anterior temporal lobe (vATL) structures, we also relate the degree of damage in anatomically defined vATL substructures (such as the PRc, fusiform etc.) to performance in order to test specific claims about the nature of semantic processing in specific vATL substructures.

Across the experiments we tested the impact of semantic confusability in three ways. First, we tested picture naming performance for different categories, with the prediction that damage to the vATL, and the PRc specifically, will result in impaired performance for living things which have a greater degree of within-category confusability than nonliving things. Second, we tested the relationship between key conceptual structure statistics and naming performance. Three measures were derived from our property norm data (Devereux et al., 2014) to capture the internal conceptual structure of the objects, (a) mean distinctiveness, (b) correlational strength and (c) the relationship between distinctiveness and correlational strength (‘correlation × distinctiveness’; see Taylor et al., 2012 for further details). Mean distinctiveness is calculated as the average distinctiveness of all the features in a concept. When a concept has many shared features, distinctiveness will be low and when it has many distinctive features, it will be high. The correlational strength of a concept is the average of all significant pairwise correlations between the shared features (i.e. those occurring in at least three concepts) of a concept. High correlational strength indicates that the features in a concept tend to co-occur and is a measure that is crucial to the formation of categories. The ‘correlation × distinctiveness’ measure aims to capture the relationship between correlational strength and a concept's distinctive and shared features. The measure is the unstandardised slope of the regression line describing the scattergraph of each concept's features with correlational strength and distinctiveness on the axes (see Taylor et al., 2012, pp. 366–367 for a full description of this measure). Following our previous studies, we predicted that objects which have many shared features and few weakly correlated features (e.g. the typical conceptual structure of living things and measured by the ‘correlation × distinctiveness’ measure) would be most affected by damage to the ventral anterior temporal lobe and in particular to the perirhinal cortex. Further, we predict that neither mean distinctiveness nor correlational strength would influence behaviour for patients with damage to the PRc, as mean distinctiveness (or sharedness, as its inverse) is associated with the posterior fusiform gyrus (Tyler et al., 2013) which is not damaged in these patients, and correlational strength is important for the representation of categories, an area where we do not expect this group to have any difficulty. Third, we manipulated the semantic confusability of concepts in a word-picture matching paradigm with the prediction that damage to the PRc will result in impaired performance in distinguishing between semantically close words and pictures.

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