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The anterior temporal lobes are critically involved in acquiring new conceptual knowledge: Evidence for impaired feature integration in semantic dementia %

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ABSTRACT

Recent evidence from multiple neuroscience techniques indicates that regions within the anterior temporal lobes (ATLs) are a critical node in the neural network for representing conceptual knowledge, yet their function remains elusive. The hub-and-spoke model holds that ATL regions act as a transmodal conceptual hub, distilling the various sensory-motor features of objects and words into integrated, coherent conceptual representations. Singlecell recordings in monkeys suggest that the ATLs are critically involved in visual associative learning; however, investigations of this region in humans have focused on existing knowledge rather than learning. We studied acquisition of new concepts in semantic dementia patients, who have cortical damage centred on the ventrolateral aspects of the ATLs. Patients learned to assign abstract visual stimuli to two categories. The categories conformed to a family resemblance structure in which no individual stimulus features were fully diagnostic; thus the task required participants to form representations that integrate multiple features into a single concept. Patients were unable to do this, instead responding only on the basis of individual features. The study reveals that integrating disparate sources of information into novel coherent concepts is a critical computational function of the ATLs. This explains the central role of this region in conceptual representation and the catastrophic breakdown of concepts in semantic dementia.

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1. Introduction

Conceptual knowledge for objects comprises a diverse set of information about their sensory qualities, motor plans and verbal associations. How are these disparate sources of information linked to form a concept? According to one influential view, originally proposed by Wernicke (Wernicke, 1900; as cited in Eggert, 1977), conceptual knowledge for objects arises from the co-activation of their sensory-motor properties within a network of modality-specific processing regions that are widely distributed throughout the cortex (Barsalou, 2008; Martin, 2007; Pulvermuller, 2001). This

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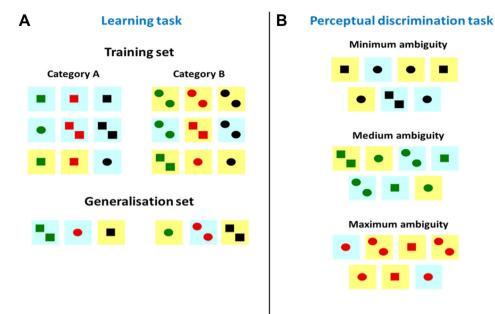


Fig. 1 — Experimental Stimuli. (A) Stimuli were divided into two categories according to a family resemblance structure. The top row of the training set comprises exemplars that possessed all three typical features of their respective category. The remaining exemplars possessed two typical features of the category and one feature associated with the opposing category. Stimuli in the generalisation set were not presented during training but retained for subsequent test. (B) Perceptual discrimination test. Each trial comprised three identical pairs of stimuli and a lone one odd-one-out. The three levels of ambiguity manipulated the number of features the odd-one-out shared with the pairs.

approach makes two key predictions concerning the breakdown of conceptual knowledge under brain damage. First, damage to a single, modality-specific region should give rise to knowledge deficits that disproportionately affect properties in that modality and, by extension, categories of objects for which the affected modality is particularly central (Capitani, Laiacona, Mahon, & Caramazza, 2003; Mahon & Caramazza, 2009; Warrington & Shallice, 1984). So, for example, damage to regions of inferior parietal cortex involved in representing skilled actions should impair knowledge of how objects are manipulated and lead to a disproportionate deficit for tools (Buxbaum & Saffran, 2002). The second prediction concerns global, pan-modal conceptual impairments. According to Wernicke and his modern counterparts, these should only occur as a result of global cortical damage, because only damage to all of the modality-specific regions would be sufficient to produce a global impairment. This prediction is challenged by the neurodegenerative syndrome of semantic dementia (SD). SD patients suffer from a global conceptual knowledge deficit that affects all categories of object and word (Hoffman & Lambon Ralph, 2011; Lambon Ralph, Lowe, & Rogers, 2007) and all sensory-motor modalities (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Bozeat, Lambon Ralph, Patterson, & Hodges, 2002; Luzzi et al., 2007; Piwnica-Worms, Omar, Hailstone, & Warren, 2010), yet the cerebral atrophy and hypometabolism that gives rise to this debilitating impairment is not global: it is focused bilaterally on the anterior ventrolateral and polar portions of the temporal lobes (Galton et al., 2001; Mion et al., 2010). Evidence from functional neuroimaging (Binney, Embleton, Jefferies,

Parker, & Lambon Ralph, 2010; Visser & Lambon Ralph, 2011) and transcranial magnetic stimulation (Pobric, Jefferies, & Lambon Ralph, 2007; Pobric, Jefferies, & Lambon Ralph, 2010) in neurologically-intact participants confirms that ventrolateral anterior temporal lobe (ATL) areas are involved in all forms of conceptual processing irrespective of the modality of the information or the category of object probed. The crucial role of this area in transmodal semantic representation also fits with recent *in vivo* tractography data demonstrating the convergence of multiple white-matter pathways into the ATL. Such results indicate that this region's structural connectivity is ideal for blending different sources of verbal and nonverbal information into integrated, coherent concepts (Binney, Parker, & Lambon Ralph, 2012).

To account for the global, pan-modal involvement of the ventrolateral ATLs in conceptual knowledge, we have developed an alternative framework for conceptual knowledge termed the "hub-and-spoke" model (Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson, Nestor, & Rogers, 2007; Pobric et al., 2010; Rogers et al., 2004). This model holds that in addition to modality-specific sources of information ("spokes") and their inter-connections, representation of conceptual knowledge requires an integrative "hub". The hub uses information from the modality-specific spoke regions to develop modality-invariant, conceptual representations that capture deeper patterns of conceptual similarity across all sensory-motor and verbal modalities. These integrated representations are necessary because similarity in any particular sensory-motor domain is, at best, only a partial guide to conceptual similarity (Dilkina & Lambon Ralph, 2013; Lambon

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