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Research report

Shared processes resolve competition within and between episodic and semantic memory: Evidence from patients with LIFG lesions



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ABSTRACT

Semantic cognition is supported by two interactive components: semantic representations and mechanisms that regulate retrieval (cf. 'semantic control'). Neuropsychological studies have revealed a clear dissociation between semantic and episodic memory. This study explores if the same dissociation holds for control processes that act on episodic and semantic memory, or whether both types of long-term memory are supported by the same executive mechanisms. We addressed this question in a case-series of semantic aphasic patients who had difficulty retrieving both verbal and non-verbal conceptual information in an appropriate fashion following infarcts to left inferior frontal gyrus (LIFG). We observed parallel deficits in semantic and episodic memory: (i) the patients' difficulties extended beyond verbal materials to include picture tasks in both domains; (ii) both types of retrieval benefitted from cues designed to reduce the need for internal constraint; (iii) there was little impairment of both semantic and episodic tasks when control demands were minimised; (iv) there were similar effects of distractors across tasks. Episodic retrieval was highly susceptible to false memories elicited by semanticallyrelated distractors, and confidence was inappropriately high in these circumstances. Semantic judgements were also prone to contamination from recent events. These findings demonstrate that patients with deregulated semantic cognition have comparable deficits in episodic retrieval. The results are consistent with a role for LIFG in resolving competition within both episodic and semantic memory, and also in biasing cognition towards task-relevant memory stores when episodic and semantic representations do not promote the same response.

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1. Introduction

Neuropsychological studies provide compelling evidence for the existence of separable episodic and semantic memory stores. Patients with semantic dementia have progressive yet selective degeneration of conceptual knowledge across all tasks and input modalities, which correlates with the degree of atrophy in the anterior ventrolateral temporal lobes (Butler, Brambati, Miller, & Gorno-Tempini, 2009; Mummery et al., 2000), yet their memory for recent episodic events is largely intact (Graham & Hodges, 1997; Graham, Becker, & Hodges, 1997; Graham, Kropelnicki, Goldman, & Hodges, 2003; Graham, Simons, Pratt, Patterson, & Hodges, 2000). In contrast, anterograde amnesia is characterised by poor encoding and retrieval of specific events as opposed to factual information, following damage to the hippocampus and associated structures in the medial temporal lobes (Nadel & Moscovitch, 1997; Nestor, Fryer, & Hodges, 2006; Vargha-Khadem et al., 1997). These findings suggest that anterior ventrolateral temporal cortex supports conceptual generalisation across experiences, while hippocampus promotes pattern separation for recently-encoded episodes (Kumaran & McClelland, 2012; McClelland, McNaughton, & O'Reilly, 1995).

Studies also point to the existence of contrastive types of semantic deficit. The term "semantic aphasia" was first coined by Head (1926) to describe patients showing difficulties in shaping and manipulating knowledge to serve symbolic processing - in the presence of heterogenous language impairments – rather than loss of semantic knowledge per se. In line with Head's clinical description, studies have shown that, unlike the degraded knowledge in semantic dementia, patients with semantic aphasia (SA) show deregulated semantic cognition across different tasks and input modalities following left frontoparietal stroke (Jefferies & Lambon Ralph, 2006; Jefferies, Patterson, & Lambon Ralph, 2008; Rogers, Patterson, Jefferies, & Lambon Ralph, 2015). SA patients show inconsistent semantic performance when the same concepts are tested under different control demands, as well as sensitivity to cues and miscues that constrain retrieval or increase the availability of irrelevant knowledge (Corbett et al. 2011; Jefferies et al., 2008; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010). They have difficulty retrieving nondominant aspects of knowledge and dealing with competition from strong yet irrelevant semantic distractors during semantic retrieval (Almaghyuli, Thompson, Lambon Ralph, & Jefferies, 2012; Noonan et al., 2010). These problems extend beyond language, to affect sound, picture and action understanding (Corbett et al., 2009a; Corbett, Jefferies, & Lambon Ralph, 2009b; Corbett, Jefferies, & Lambon Ralph, 2011; Gardner et al., 2012; Thompson, Robson, Lambon Ralph, & Jefferies, 2015). Collectively this evidence shows that SA patients have multimodal deficits of semantic control, i.e., they find it difficult to flexibly retrieve and shape semantic knowledge to suit the task or circumstances and show impairment when there is a need to resolve competition between different meanings or features of concepts. The distinction between semantic dementia and patients with SA supports a component process account, in which semantic cognition emerges from interactions between transmodal

conceptual representations and control processes (Controlled Semantic Cognition Framework; Jefferies, 2013; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017).

This proposal is also pertinent to understanding differences in episodic memory deficits in amnesia (see Blumenfeld & Ranganath, 2007 for a review). In contrast to patients with circumscribed medial temporal lobe injury (such as HM, Scoville & Milner, 1957), patients with additional prefrontal involvement show better cued than free recall (Mangels, Gershberg, Shimamura, & Knight, 1996; Incisa della Rocchetta & Milner, 1993) and disproportionate difficulty in retrieving word-pairs previously associated with other targets, reflecting a failure to overcome proactive interference (Shimamura, Jurica, Mangels, Gershberg, & Knight, 1995). In both semantic and episodic tasks, bringing to mind unusual associations, or task-relevant knowledge in the face of strong competition, might involve promoting specific aspects representations and suppressing irrelevant dominant information (Anderson, 1988; Badre & Wagner, 2007; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). The similarity of these theoretical accounts fuels interest in whether they have a shared or distinct neural

Functional neuroimaging studies suggest that overlapping networks are important for the control of episodic and semantic memory (see Fig. 1A). Left inferior frontal gyrus (LIFG) has a well-established role in the control of episodic memory: it shows a stronger response in the retrieval of weakly vs. strongly-encoded memories (Barredo, Öztekin, & Badre, 2015; Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011) and is engaged by interference resolution (Badre & Wagner, 2005; Wimber, Rutschmann, Greenlee, & Bäuml, 2009). Likewise, this region shows increased activation in semantic retrieval for ambiguous words, weak associations or strong distracters (for a meta-analysis, see Noonan, Jefferies, Visser, & Lambon Ralph, 2013; also Badre & Wagner, 2005, 2007; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Controlled retrieval from episodic and semantic memory partially overlaps with "multiple-demand regions" that are engaged for difficult tasks across multiple domains; however, anterior LIFG lies outside this network and appears to specifically support the control of memory (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Davey et al., 2016; Nelson, Reuter-Lorenz, Persson, Sylvester, & Jonides, 2009). In line with this proposal, inhibitory transcranial magnetic stimulation to LIFG disrupts controldemanding semantic judgements but not more automatic aspects of semantic retrieval or demanding non-semantic judgements (Gough, Nobre, & Devlin, 2005; Hallam, Whitney, Hymers, Gouws, & Jefferies, 2016; Hoffman, Jefferies, & Lambon Ralph, 2010; Krieger-Redwood & Jefferies, 2014; Whitney et al., 2011).

Despite these similarities, few studies have directly compared manipulations of difficulty across episodic and semantic judgements. It is unclear whether LIFG contributes to episodic memory indirectly by regulating conceptual retrieval or whether LIFG is crucial for regulating retrieval from both memory stores. Neuropsychology can help to resolve this theoretical uncertainty by establishing if damage to LIFG gives rise to symmetrical deficits of episodic and semantic memory. Semantic and episodic representations often mutually support retrieval: to understand the semantic link between items like

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