CORTEX 103 (2018) 329–349

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Dynamic semantic cognition: Characterising coherent and controlled conceptual retrieval through time using magnetoencephalography and chronometric transcranial magnetic stimulation

Catarina Teige [a], *Giovanna Mollo* [a], *Rebecca Millman* [b], *Nicola Savill* [a,d], *Jonathan Smallwood* [a], *Piers L. Cornelissen* [c,**] and *Elizabeth Jefferies* [a,*]

[a] *Department of Psychology and York Neuroimaging Centre, University of York, UK*
[b] *Manchester Centre for Audiology and Deafness, Division of Human Communication, Development and Hearing, School of Health Sciences, Faculty of Biology, Medicine and Health, University of Manchester, UK*
[c] *Department of Psychology, Northumbria University, UK*
[d] *School of Psychology and Social Science, York St John University, York, UK*

ARTICLE INFO

Article history:
Received 19 July 2017
Reviewed 16 November 2017
Revised 24 January 2018
Accepted 20 March 2018
Action editor Peter Turkeltaub
Published online 30 March 2018

Keywords:
Comprehension
Beamforming
Semantic memory
Anterior temporal
Posterior middle temporal gyrus

ABSTRACT

Distinct neural processes are thought to support the retrieval of semantic information that is (i) coherent with strongly-encoded aspects of knowledge, and (ii) non-dominant yet relevant for the current task or context. While the brain regions that support readily coherent and more controlled patterns of semantic retrieval are relatively well-characterised, the temporal dynamics of these processes are not well-understood. This study used magnetoencephalography (MEG) and dual-pulse chronometric transcranial magnetic stimulation (cTMS) in two separate experiments to examine temporal dynamics during the retrieval of strong and weak associations. MEG results revealed a dissociation within left temporal cortex: anterior temporal lobe (ATL) showed greater oscillatory response for strong than weak associations, while posterior middle temporal gyrus (pMTG) showed the reverse pattern. Left inferior frontal gyrus (IFG), a site associated with semantic control and retrieval, showed both patterns at different time points. In the cTMS experiment, stimulation of ATL at ~150 msec disrupted the efficient retrieval of strong associations, indicating a necessary role for ATL in coherent conceptual activations. Stimulation of pMTG at the onset of the second word disrupted the retrieval of weak associations, suggesting this site may maintain information about semantic context from the first word, allowing efficient engagement of semantic control. Together these studies provide converging evidence for a functional dissociation within the temporal lobe, across both tasks and time.

* *Corresponding author*. Department of Psychology, University of York, York, YO10 5DD, UK.
** *Corresponding author*. Psychology Department, Faculty of Health and Life Sciences, Northumbria University, Newcastle upon Tyne, NE1 8ST, UK.
E-mail address: beth.jefferies@york.ac.uk (E. Jefferies).

https://doi.org/10.1016/j.cortex.2018.03.024

Semantic cognition allows us to understand the meaning of our environment to drive appropriate thoughts and behaviour. It comprises several distinct yet interacting components (Jefferies, 2013; Jefferies & Lambon Ralph, 2006; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017). Semantic representations capture the meanings of words and objects across contexts, supporting coherent conceptual retrieval from fragmentary inputs and generalisation across situations. However, the retrieval of specific aspects of knowledge in a context-dependent fashion requires control mechanisms that shape evolving retrieval towards currently-pertinent semantic features, and away from dominant yet irrelevant associations. While patterns of activation within the semantic store may be sufficient to uncover links between items that are highly coherent with long-term knowledge (i.e., items that share multiple features or are frequently associated, such as *pear-apple* or *tree-apple*), additional control processes may be required to recover non-dominant aspects of knowledge, such as *worm-apple*, since strong but currently-irrelevant associations (e.g., *worm-soil*) must be disregarded (Lambon Ralph et al., 2017; Gold et al., 2006).

Although the brain regions that support semantic cognition are relatively well-described, the temporal dynamics are not. Neuroimaging studies have highlighted the importance of a distributed left-dominant network underpinning semantic cognition, including anterior temporal lobe (ATL), posterior middle temporal gyrus (pMTG) and inferior frontal gyrus (IFG) (Binder, Desai, Graves, & Conant, 2009; Jefferies, 2013; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Xu, Qixiang, Zaizhu, Yong, & Yanchao, 2016; Lambon Ralph et al., 2017). These brain regions make dissociable contributions to semantic cognition, although their specific roles remain controversial. The ventral ATL is proposed to support heteromodal concepts that are extracted from multiple inputs (e.g., vision, audition, smell; Patterson, Nestor, & Rogers, 2007; Lambon Ralph et al., 2017). Patients with semantic dementia (SD), show progressive degradation of knowledge across modalities following atrophy and hypometabolism in ATL (Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Mion et al., 2010; Rogers et al., 2006). Convergent evidence for a role of ATL in multimodal conceptual processing is provided by positron emission tomography (e.g., Bright, Moss, & Tyler, 2004; Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Devlin et al., 2000; Noppeney & Price, 2002; Rogers et al., 2006; Scott, Blank, Rosen, & Wise, 2000), functional magnetic resonance imaging (fMRI) – particularly when magnetic susceptibility artefacts within ATL are minimised (Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Murphy et al., 2017; Visser, Jefferies, Embleton, & Lambon Ralph, 2012; Visser, Jefferies, & Lambon Ralph, 2010), magnetoencephalography (MEG) (Clarke, Taylor, & Tyler, 2011; Marinkovic et al., 2003; Fujimaki et al., 2009; Lau, Gramfort, Hämäläinen, & Kuperberg, 2013; Mollo, Cornelissen, Millman, Ellis, & Jefferies, 2017), intracranial electrode arrays (Chan et al., 2011; Chen et al., 2016) and transcranial magnetic stimulation (TMS) (Lambon Ralph, Pobric, & Jefferies, 2009; Pobric, Jefferies, & Lambon Ralph, 2007; 2009; 2010). The ATL is allied to the default mode network (DMN) in terms of connectivity and function (Binder et al., 2003; Davey et al., 2016, 2015; Wirth et al., 2011), although the maximal semantic response in ATL is not identical to the site of peak DMN connectivity (Jackson, Hoffman, Pobric, & Lambon Ralph, 2016). In common with DMN regions, ATL shows a larger response to easy or more automatic aspects of semantic retrieval, such as identifying dominant aspects of knowledge (e.g., linking DOG with CAT; Davey et al., 2016), and when coherent meaning emerges from conceptual combinations (Bemis & Pylkkänen, 2013; Hoffman, Binney, & Lambon Ralph, 2015). ATL is also implicated in semantic retrieval during mind-wandering (Binder et al., 1999; Smallwood et al., 2016). Collectively, these findings suggest that ATL responds most strongly when ongoing semantic retrieval is highly coherent with long-term knowledge – although *causal* evidence is currently lacking.

Brain regions distinct from ATL are implicated in the *control* of semantic cognition. The contribution of left IFG to executive-semantic processes has been documented by many fMRI studies (e.g., Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Noppeney, Phillips, & Price, 2004; Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Bedny, McGill, & Thompson-Schill, 2008). Convergent evidence for a causal contribution of this region has been provided by transcranial magnetic stimulation (TMS, Hoffman, Jefferies, & Lambon Ralph, 2010; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011) and neuropsychology: patients with damage to left IFG have difficulty flexibly tailoring their semantic retrieval to suit the circumstances (Thompson-Schill et al., 1998; Jefferies & Lambon Ralph, 2006; Corbett, Jefferies, & Lambon Ralph, 2009; Thompson, Robson, Lambon Ralph, & Jefferies, 2015). While the contributions of ATL and IFG align with recent component process views of semantic cognition (e.g., the Controlled Semantic Cognition framework, which suggests semantic cognition reflects an interaction of conceptual representations and control processes, Lambon Ralph et al., 2017), the contribution of pMTG remains controversial. Some accounts have proposed that posterior temporal areas provide an important store of conceptual representations (Martin, 2007), with pMTG specifically implicated in knowledge of actions and events (Chao, Haxby, & Martin, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Alternatively, a growing literature supports the view that pMTG is part of a distributed network with IFG and other regions underpinning semantic control (Davey et al., 2016; Gold et al., 2006; Jefferies, 2013; Noonan et al., 2013; Vitello, Warren, Devlin, & Rodd, 2014). A meta-analysis showed that a widely distributed set of cortical regions is reliably activated across diverse manipulations of semantic control demands, with left pMTG showing the second most consistent response after left IFG (Noonan et al., 2013). Semantic control deficits can follow from either left prefrontal or posterior temporal lesions (Jefferies & Lambon Ralph, 2006; Noonan, Jefferies, Corbett, & Lambon Ralph, 2010); moreover, inhibitory TMS to left pMTG and IFG produces equivalent disruption of semantic judgements that require controlled but not automatic retrieval (Davey et al., 2015; Whitney et al., 2011), and inhibitory stimulation of IFG elicits a compensatory increase in pMTG (Hallam et al., 2016). These regions also show a strong pattern of both structural and functional connectivity (Davey et al., 2016; Hallam et al., 2016; JeYoung & Lambon Ralph, 2016), consistent with the view that they form a large-scale distributed network