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The structural basis of semantic control: Evidence from individual differences in cortical thickness

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ABSTRACT

Semantic control allows us to shape our conceptual retrieval to suit the circumstances in a flexible way. Tasks requiring semantic control activate a large-scale network including left inferior prefrontal gyrus (IFG) and posterior middle temporal gyrus (pMTG) - this network responds when retrieval is focussed on weak as opposed to dominant associations. However, little is known about the biological basis of individual differences in this cognitive capacity: regions that are commonly activated in task-based fMRI may not relate to variation in controlled retrieval. The current study combined analyses of MRI-based cortical thickness with resting-state fMRI connectivity to identify structural markers of individual differences in semantic control. We found that participants who performed relatively well on tests of controlled semantic retrieval showed increased structural covariance between left pMTG and left anterior middle frontal gyrus (aMFG). This pattern of structural covariance was specific to semantic control and did not predict performance when harder non-semantic judgements were contrasted with easier semantic judgements. The intrinsic functional connectivity of these two regions forming a structural covariance network overlapped with previously-described semantic control regions, including bilateral IFG and intraparietal sulcus, and left posterior temporal cortex. These results add to our knowledge of the neural basis of semantic control in three ways: (i) Semantic control performance was predicted by the structural covariance network of left pMTG, a site that is less consistently activated than left IFG across studies. (ii) Our results provide further evidence that semantic control is at least partially separable from domain-general executive control. (iii) More flexible patterns of memory retrieval occurred when pMTG co-varied with distant regions in aMFG, as opposed to nearby visual, temporal or parietal lobe regions, providing further evidence that left prefrontal and posterior temporal areas form a distributed network for semantic control.

1. Introduction

Our ability to use semantic knowledge to drive appropriate thoughts and behaviour is fundamental to our mental lives. Semantic cognition is thought to involve at least two interacting components: *conceptual representations* encompass stored knowledge about the meanings of objects, words, sounds and people; while *semantic control* processes shape retrieval to suit our goals and the context (Jefferies, 2013; Lambon Ralph et al., 2017). These components are thought to draw on distinct large-scale networks in the brain (Corbett et al., 2011; Davey et al., 2016; Diez et al., 2017; Gold and Buckner, 2002; Gold et al., 2005; Hallam et al., 2018; Humphreys and Lambon Ralph, 2017; Jefferies, 2013; Jefferies and Lambon Ralph, 2006; Patterson et al., 2007; Snowden et al., 2017; Vatansever et al., 2017; Wei et al., 2012). However, little is known about individual differences in these abilities – i.e., what are the structural and functional markers of efficient semantic cognition in healthy participants?

If the capacity to control semantic retrieval is separable from how knowledge is represented, individual differences in task performance should reflect this multi-component structure. Semantic tests will not always measure *what* people know: since concepts have diverse features and associations, the capacity to shape retrieval to suit the circumstances will also have a major impact on performance. Semantic control processes are thought to be required when we have to retrieve non-dominant

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aspects of knowledge or promote specific aspects of knowledge in the face of strong competition, in order to suit the requirements of the current task or context (Badre et al., 2005; Jefferies, 2013; Lambon Ralph et al., 2017; Thompson-Schill et al., 1997). Semantic control demands are consequently higher when processing the meanings of ambiguous vs. unambiguous words (Rodd et al., 2005; Humphreys and Lambon Ralph, 2017; Whitney et al., 2011), matching items on the basis of a single feature such as colour rather than their global relatedness (Chiou et al., 2018; Davey et al., 2016), retrieving a specific semantic relationship in the face of strong competition, or retrieving weak associations (e.g., SAUCER and ASHTRAY) as opposed to strong associations (e.g., SAUCER and CUP) (Badre and Wagner, 2002; Badre et al., 2005; Davey et al., 2015; Wagner et al., 2001; Whitney et al., 2012). All of these manipulations have in common the need to promote a particular pattern of semantic retrieval which is not typical for that item, and all of these tasks activate a common semantic control network: a meta-analysis of neuroimaging studies including this range of tasks identified a distributed semantic control network that consisted of left inferior frontal gyrus (IFG), posterior middle temporal gyrus (pMTG), dorsal angular gyrus (dAG) bordering intraparietal sulcus (Noonan et al., 2013; see Fig. 1). Left IFG is the most reliably activated site across participants and tasks, while pMTG shows more variation (Vitello et al., 2014), suggesting that pMTG might be especially critical to individual differences in the efficiency of semantic control processes.

Although difficult semantic decisions activate domain-general executive control regions along with other tasks, left pMTG and anterior portions of IFG fall outside the multiple-demand system; they are specifically activated by semantic (or memory) tasks (Humphreys and Lambon Ralph, 2017; Noonan et al., 2013). Left anterior IFG and pMTG show similar functional connectivity in line with the view that they form a network for semantic control (Davey et al., 2016; Humphreys and Lambon Ralph, 2017): interestingly, they show connections with both default mode and multiple-demand regions, which are typically anti-correlated across tasks and resting states (Davey et al., 2016). This distinctive pattern of connectivity might be critical for semantic control, which involves the coordination of brain regions allied to the default mode network that support heteromodal conceptual representations (e.g., Murphy et al., 2018), with control regions that support demanding tasks. By this view, individual differences in semantic control may occur somewhat independently of performance on difficult non-semantic tasks.

A causal role for left IFG and pMTG in semantic control has been established through neuropsychology and brain stimulation. Patients with multimodal semantic deficits in the context of stroke aphasia (i.e. semantic aphasia) have poor control over semantic retrieval, with largely intact conceptual knowledge, and this pattern is associated with damage to left IFG or temporoparietal regions including pMTG (Hallam et al., 2018; Jefferies and Lambon Ralph, 2006; Noonan et al., 2010;

Thompson-Schill et al., 1998). While neuropsychology lacks spatial specificity when drawing inferences about brain-behaviour relationships, inhibitory transcranial magnetic stimulation (TMS) delivered to left IFG and pMTG elicits equivalent disruption of control-demanding semantic judgements: for example, there is an inhibitory effect on the retrieval of weak associations, yet no effect on either strong semantic associations or control-demanding non-semantic decisions (Davey et al., 2015; Hoffman et al., 2010; Whitney et al., 2011). Moreover, damage to left IFG in semantic aphasia and inhibitory TMS to this region in healthy participants elicits an increased response in pMTG to semantic judgements with high control demands (Hallam et al., 2016, 2018), consistent with a pattern of functional compensation within the large-scale distributed semantic control network. The current study supplements these methods by establishing how structural covariation between brain distant regions predicts the efficiency of controlled semantic retrieval across individuals, even after accounting for performance on dominant associations and a non-semantic task.

Although most research in cognitive neuroscience focusses on commonalities across individuals, inter-individual differences can be exploited to understand the neural basis of human cognition (Kanai and Rees, 2011). Cognitive differences between people can be predicted from variation in the structure of specific brain regions (Choi et al., 2008; Schilling et al., 2012). For example, the grey matter density of pre-supplementary motor area (pre-SMA) can account for inter-individual variability in the ability to select the correct response in the presence of response conflict (van Gaal et al., 2011), while the cortical thickness of rostral medial temporal cortex correlates with verbal memory performance (Dickerson et al., 2008). However, cognitive variation is not only associated with the morphometry of individual brain regions but also with structural covariation between regions that form functional networks. For example, people with higher IQ have greater covariation in cortical thickness between IFG and other frontal and parietal brain areas (Lerch et al., 2006). For empathy and theory of mind tasks, structural covariance is more sensitive than regional differences between individuals (Bernhardt et al., 2013; Valk et al., 2017). Consequently, the current study links individual differences in performance on tests of semantic control to structural covariation between posterior temporal and prefrontal regions, as opposed to structural markers for individual sites in pMTG and IFG.

We used cortical thickness measures in around 200 individuals to characterise the structural covariance networks of left IFG and pMTG, two key sites for semantic control in previous group-level neuroimaging analyses (see Fig. 1). We examined how these structural covariance networks are modulated by individual differences in the efficiency of semantic control. Specifically, we assessed the identification of weak associations, after controlling for performance on strong associations. This paradigm has been used repeatedly to assess semantic control across



Fig. 1. A: Meta-analyses of (i) task contrasts manipulating semantic control demands from Noonan et al. (2013); (in red) and (ii) the term "semantic" from Neurosynth (in green). Semantic regions implicated in control are highlighted in yellow (showing the overlap of the two meta-analyses). B: Seeds for our analysis defined on the basis of these meta-analyses (Noonan et al., 2013). (L = Left hemisphere; R = hemisphere).

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