An individual differences analysis of the neurocognitive architecture of the semantic system at rest

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ABSTRACT

Efficient semantic cognition depends on accessing and selecting conceptual knowledge relevant to the current task or context. This study explored the neurocognitive architecture that supports this function by examining how individual variation in functional brain organisation predicts comprehension and semantic generation. Participants underwent resting state functional magnetic resonance imaging (fMRI) and, on separate days, performed written synonym judgement, and letter and category fluency tasks. We found that better synonym judgement for high frequency items was linked to greater functional coupling between posterior fusiform and anterior superior temporal cortex (aSTG), which might index orthographic-to-semantic access. However, stronger coupling between aSTG and ventromedial prefrontal cortex was associated with poor performance on the same trials, potentially reflecting greater difficulty in focussing retrieval on relevant features for high frequency items that appear in a greater range of contexts. Fluency performance was instead linked to variations in the functional coupling of the inferior frontal gyrus (IFG); anterior IFG was more coupled to regions of primary visual cortex for individuals who were good at category fluency, while poor letter fluency was predicted by stronger coupling between posterior IFG and retrosplenial cortex. These results show that individual differences in functional connectivity at rest predict semantic performance and are consistent with a component process account of semantic cognition in which representational information is shaped by control processes to fit the current requirements, in both comprehension and fluency tasks.

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1. Introduction

Semantic cognition has a central role in behaviour since it allows us to understand the meanings of words and objects around us and to use this conceptual knowledge to perform complex goal-orientated acts. Theories of semantic cognition emphasise that this capacity depends on multiple interacting components, supported by different neural processes (Jefferies, 2013; Jefferies & Lambon Ralph, 2006; Lambon Ralph, 2014). Although the extent to which visual, auditory and motor regions support semantic knowledge is still a matter of debate (Hauk & Tschentscher, 2013; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012), a wealth of studies provide evidence that these brain regions contribute to our knowledge of what things look and sound like, and how we hold and use objects (Martin & Chao, 2001; Pulvermuller, 2001; Pulvermuller & Fadiga, 2010; Thompson-Schill, 2003). Anterior regions of the temporal

lobe are thought to bring these different aspects of knowledge together to form amodal conceptual representations, allowing us to understand that items such as 'kiwi' and 'pineapple' are members of the same category even though they are different colours, sizes, shapes, have different textures, and are associated with different actions (Lambon Ralph, Pobric, & Jefferies, 2009; Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004). Finally, left ventral and lateral prefrontal regions, as well as posterior middle and inferior temporal cortex, are important when conceptual information must be retrieved in the absence of strong contextual support, when there is strong competition from competing meanings, or when non-dominant aspects of meaning must be brought to the fore: for example, understanding that "kiwi" can refer to a bird as well as fruit (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Jefferies, 2013; Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011).

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Semantic cognition, therefore, reflects our ability to use conceptual information in a flexible way to serve different purposes. We retrieve semantic information to make sense of the environment around us, and also to generate thoughts and actions. Consequently, we need to be able to differentially engage different components of semantic cognition that support the current task demands (Badre et al., 2005; Jefferies & Lambon Ralph, 2006). First, in order to understand the significance of words and objects that we encounter in the external world, we need to be able to access relevant semantic representations from our sensory systems: for example, the comprehension of written words is thought to utilise mappings between visual responses in posterior fusiform cortex (encompassing the so-called 'visual word form area') and conceptual representations in anterior temporal cortex (Carreiras, Armstrong, Perea, & Frost, 2014; Dehaene et al., 2010; Moore & Price, 1999). The nature of the stimulus can affect the efficiency of this visual-to-semantic transformation. For instance, highly imageable words, that rapidly arouse mental images associated with their meaning, enjoy a processing advantage compared to words that are less imageable. This advantage occurs because highly imageable words benefit from richer semantic associations (Plaut & Shallice, 1993; Wiemer-Hastings & Xu, 2005). Similarly, high frequency words that are often encountered benefit from a stronger mapping between orthography and meaning that is reflected in faster reading times (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Chen, Davis, Pulvermuller, & Hauk, 2015). However, this type of semantic "access" may not be sufficient for good performance on tasks such as synonym judgement. This is because for any given concept, we have a multitude of knowledge and only a subset of this information is relevant for any given context. In order to correctly match words on the basis of their shared features (e.g., kiwi with tomato), semantic retrieval must be channelled to focus on relevant elements and away from strong functional associations (tomato goes with cheese sandwich). High frequency words are thought to require this type of control to a greater extent since they occur in multiple contexts and thus have a higher 'contextual diversity' (Almaghyuli, Thompson, Lambon Ralph, & Jefferies, 2012; Hoffman, Lambon Ralph, & Rogers, 2013; Hoffman, Rogers, & Ralph, 2011).

There may be some differences in the neurocognitive components that are engaged when semantic information must be generated internally, as opposed to accessed from an external input (although both situations are thought to recruit conceptual representations in the anterior temporal lobes) (Adlam, Patterson, Bozeat, & Hodges, 2010; Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000). In fluency tasks, conceptual information must be generated from a cue such as a letter or category name; here, the capacity to search for and select relevant knowledge is paramount. It is hypothesised that this process depends on the co-operation of the representational and control systems and draws heavily on left inferior frontal gyrus (Heim, Eickhoff, & Amunts, 2008; Wagner, Sebastian, Lieb, Tüscher, & Tadić, 2014). Moreover, the type of cue influences the extent to which control is required. Letter fluency, in which participants attempt to generate words starting with a particular letter, is particularly demanding of generation and selection mechanisms, while generating items from a category name such as "animals" requires less control, since a process of spreading activation between concepts will elicit high frequency and/or prototypical animals (Costafreda et al., 2006; Katzev, Tuscher, Hennig, Weiller, & Kaller, 2013). Recent work has shown that category fluency is more impaired in patients with degradation of conceptual representations following anterior temporal atrophy, while letter fluency is more vulnerable to poor semantic control (Rogers, Patterson, Jefferies, & Lambon Ralph, 2015). Moreover, category fluency appears to activate a broader range of sites implicated in internally-focussed memory retrieval,

particularly retrosplenial cortex, while letter fluency has a clear prefrontal focus (Davies, Graham, Xuereb, Williams, & Hodges, 2004; Perani et al., 2003; Ryan, Cox, Hayes, & Nadel, 2008; Shapira-Lichter, Oren, Jacob, Gruberger, & Hendler, 2013).

Since comprehension and generation tasks require the components of semantic cognition to be brought together differently, we might anticipate that individual differences in these capacities should depend on different patterns of neural coupling that emerge at rest. This individual difference approach has been used successfully to understand the neural basis of various features of higher order cognition including meta-cognition, binocular rivalry, intelligence, reading comprehension and spontaneous thought (Baird, Smallwood, Gorgolewski, & Margulies, 2013; Baker, Karapanagiotidis, Coggan, Wailes-Newson, & Smallwood, 2015; Gorgolewski et al., 2014; Smallwood & Andrews-Hanna, 2013; Smallwood et al., 2016; Xu et al., 2015). Few studies have attempted to link individual differences in semantic performance to the strength of resting state connectivity patterns. The most relevant study is by Wei et al. (2012), who found that stronger connectivity between posterior middle temporal gyrus and other parts of the semantic network, such as anterior temporal lobes and inferior frontal gyrus, predicted good performance on picture and sound naming and association judgements in a sample of 34 participants.

In the current study, we recorded resting state fMRI in a cohort of 48 participants who performed a series of tasks tapping different aspects of semantic performance on a subsequent day. This second experimental phase included a synonym judgement task to index the capacity to understand the meaning of an external stimulus (Jefferies, Patterson, Jones, & Lambon Ralph, 2009) and semantic and letter fluency tasks that required participants to internally generate representations. We explored how variation in participants' performance on these tasks was related to resting state connectivity between regions previously implicated in written comprehension and fluency. This allows us to test the diagnostic value of resting state fMRI in the domain of individual differences in semantic cognition.

1.1. Regions of interest

Reflecting the component process account of semantic cognition above, we selected regions for our analysis that are implicated in (i) semantic representation (in the anterior temporal lobes), (ii) access to semantics from orthographic input (in left posterior fusiform), and (iii) lexical selection and semantic control (in inferior frontal gyrus). Previous fMRI studies of verbal semantic tasks have observed two distinct peaks in left anterior temporal lobe (ATL), in anterior superior temporal gyrus (aSTG) and in ventral ATL respectively (Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Hoffman, Binney, & Lambon Ralph, 2015; Schwartz et al., 2011; Visser, Jefferies, Embleton, & Lambon Ralph, 2012; Visser & Lambon Ralph, 2011). Ventral ATL might provide a multimodal semantic hub anticipated by Patterson et al. (2007), since it responds across tasks and modalities (e.g., to pictures, environmental sounds, spoken and written words; Binney et al., 2010; Visser & Lambon Ralph, 2011; Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Rice, Lambon Ralph, & Hoffman, 2015; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015). Ventral ATL is functionally connected with semantic and default mode regions (Binney et al., 2010; Hoffman et al., 2015; Jackson, Hoffman, Pobric, & Lambon Ralph, 2016; Pascual et al., 2015; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006). However, magnetic susceptibility artefacts produce signal loss and distortion in this region in standard EPI sequences, which mean it is consequently under-represented in the fMRI literature (compared with studies employing PET; Visser, Jefferies, & Lambon Ralph, 2010). In contrast, aSTG is less