Varieties of semantic cognition revealed through simultaneous decomposition of intrinsic brain connectivity and behaviour

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ABSTRACT

Contemporary theories assume that semantic cognition emerges from a neural architecture in which different component processes are combined to produce aspects of conceptual thought and behaviour. In addition to the state-level, momentary variation in brain connectivity, individuals may also differ in their propensity to generate particular configurations of such components, and these trait-level differences may relate to individual differences in semantic cognition. We tested this view by exploring how variation in intrinsic brain functional connectivity between semantic nodes in fMRI was related to performance on a battery of semantic tasks in 154 healthy participants. Through simultaneous decomposition of brain functional connectivity and semantic task performance, we identified distinct components of semantic cognition at rest. In a subsequent validation step, these data-driven components demonstrated explanatory power for neural responses in an fMRI-based semantic localiser task and variation in self-generated thoughts during the resting-state scan. Our findings showed that good performance on harder semantic tasks was associated with relative segregation at rest between frontal brain regions implicated in controlled semantic retrieval and the default mode network. Poor performance on easier tasks was linked to greater coupling between the same frontal regions and the anterior temporal lobe; a pattern associated with deliberate, verbal thematic thoughts at rest. We also identified components that related to qualities of semantic cognition: relatively good performance on pictorial semantic tasks was associated with greater separation of angular gyrus from frontal control sites and greater integration with posterior cingulate and anterior temporal cortex. In contrast, good speech production was linked to the separation of angular gyrus, posterior cingulate and temporal lobe regions. Together these data show that quantitative and qualitative variation in semantic cognition across individuals emerges from variations in the interaction of nodes within distinct functional brain networks.

1. Introduction

Semantic cognition allows us to understand the meaning of words, objects, places and people, and guides our thoughts and actions in a manner that suits the circumstances (Jefferies, 2013; Lambon Ralph et al., 2017; Patterson et al., 2007). In addition, this type of cognition also plays a critical role in thoughts that are unconnected from the here and now, such as when we daydream about a future achievement or remember a past event (Binder et al., 2009; Smallwood et al., 2016). Contemporary accounts suggest that semantic cognition emerges from the interactions of multiple components, supported by distinct brain networks (Jefferies and Lambon Ralph, 2006; Lambon Ralph et al., 2017). Studies have recently begun to address how these between-network interactions might momentarily change, depending on task demands (Bianchi et al., 2013; Davey et al., 2016; Hallam et al., 2016; Jung and Lambon Ralph, 2016; Krieger-Redwood et al., 2016). However, relatively little is known about individual differences in semantic cognition i.e. aspects of brain connectivity that are associated with trait-level variability in semantic task performance.

From the component process perspective, semantic cognition is thought to involve the interaction of semantic representations and control processes that tailor retrieval to suit the behavioural circumstances (Jefferies, 2013; Lambon Ralph et al., 2017). Evidence suggests that the semantic representations in long-term memory draw on modality-
specific brain regions (supporting visual and verbal features, such as our knowledge that zebras have black and white stripes, and linguistic associations, such as “zebra crossing” (Buccino et al., 2016; Fernandino et al., 2016)), as well as heteromodal areas, including the anterior temporal lobe (Lambon Ralph et al., 2017; Patterson et al., 2007). Anterior temporal cortex is argued to provide a graded “hub” supporting the convergence of diverse unimodal semantic features. This permits the extraction of deep conceptual similarity incorporating both verbal and non-verbal knowledge. In addition, since we all know a diverse range of features and associations to any given concept, conceptual retrieval must be constrained in accordance with goals and environmental conditions (Badre et al., 2005; Jefferies and Lambon Ralph, 2006; Thompson-Schill et al., 1997). Hence, semantic control processes may play a vital role in focusing retrieval on currently relevant aspects of knowledge and suppressing strongly encoded but currently irrelevant information. This aspect of semantic cognition is thought to be supported by a distinct set of brain regions including domain-general executive areas (e.g. dorsal/posterior inferior frontal gyrus, pre-supplementary motor area) and areas more specifically implicated in semantic control (e.g. ventral/anterior inferior frontal gyrus, posterior middle temporal gyrus (Davey et al., 2016; Noonan et al., 2013)).

In line with this interactive view, cognitive neuroscience research has provided converging evidence for multiple, interrelated components within semantic cognition. Lesion studies have revealed that selective damage to the anterior temporal lobe, left inferior frontal gyrus and/or posterior middle temporal gyrus produce dissociable impairments, compromising the integrity of conceptual representations (Bozeat et al., 2000; Patterson et al., 2007), or their use in a goal-oriented manner, respectively (Jefferies and Lambon Ralph, 2006; Jefferies et al., 2008; Noonan et al., 2010; Rogers et al., 2015). The functional dissociation between these brain regions is also supported by neuroimaging (Hoffman et al., 2015; Humphreys et al., 2015; Noonan et al., 2013) and neurostimulation (Binney et al., 2010; Davey et al., 2015; Pobric et al., 2007; Whitney et al., 2011) investigations of semantic processing in healthy participants.

Recent studies have also shown that although these brain regions act in concert to support semantic cognition (i.e., they co-activate during task fMRI), they form distinct large-scale brain networks at rest (Davey et al., 2016; Jackson et al., 2016), depicting functional integration when participants shift from rest to semantic tasks (Krieger-Redwood et al., 2016). For example, as an important hub of semantic processing (Patterson et al., 2007), anterior temporal lobe shows strong connectivity at rest to regions of the default mode network (DMN), including angular gyrus and posterior cingulate cortex (Jackson et al., 2016; Murphy et al., 2017). In contrast, semantic control regions such as left inferior frontal gyrus and posterior middle temporal gyrus show strong intrinsic connectivity to each other, and they connect to both default mode and fronto-parietal networks (Davey et al., 2016). Together these studies suggest that semantic cognition is an emergent property of variable interactions between not only particular brain regions, but also distributed large-scale brain networks, present at rest and in cognitive tasks (Cole et al., 2014).

Although this assumption is broadly accepted, it remains unclear how individual differences in the strength of specific connections within and between these networks might relate to trait-level differences in semantic abilities. For example, the strength of particular network interactions might give rise to global differences in the efficiency of semantic retrieval across tasks, linked to the tendency to stay on task. Studies have associated both task-based semantic behaviour and off-task mind-wandering to overlapping brain regions involved in semantic processing that are allied to the DMN (Binder et al., 2009; Smallwood et al., 2016). The strength of intrinsic connectivity between these default mode regions and areas linked to task engagement might therefore determine whether individuals are generally willing or able to focus semantic retrieval on an externally-imposed goal, as opposed to conceptual associations that might have greater personal relevance. In addition, since research has revealed network differences that relate to the modality of information being retrieved (i.e., words vs. pictures) and the extent to which semantic control processes are required to shape retrieval to suit the task, we might expect individual differences in patterns of intrinsic network connectivity to relate to relative strengths and weaknesses in these varieties of semantic cognition across participants.

To assess these hypotheses, we recorded task-based and resting state functional magnetic resonance imaging (fMRI) data in a large cohort of participants, who also described their thoughts while at rest inside the scanner. On a subsequent day, these participants performed a battery of semantic tasks, including relatedness, identity and feature judgements, picture naming and verbal fluency. The tasks used different types of stimuli including words and pictures, manipulated the requirement for controlled retrieval using strong and weak associations (Badre et al., 2005; Davey et al., 2016), and assessed both comprehension and production, allowing us to characterise diverse aspects of semantic cognition. We used advanced multivariate statistics (Smith et al., 2015; Tsvetanov et al., 2016) to simultaneously decompose individual variation in brain data (resting state connectivity) and behaviour (measured outside the scanner) to identify the neurocognitive components of semantic cognition. We confirmed the validity of these components by examining their association with independent measures: the neural response to meaningful over meaningless information in task-based fMRI and subjective descriptions of self-generated thoughts during the resting state scan (Gorgolewski et al., 2014). This allowed us to specify neurocognitive components that relate to the (i) average performance on semantic tasks and (ii) varieties of semantic cognition. Overall, these results help to elucidate the fundamental mechanisms underpinning variation in semantic cognition in healthy individuals.

2. Methods

2.1. Participant demographics

Ethical approval was obtained from the Department of Psychology and York Neuroimaging Centre, University of York ethics committees. A total of 165 right-handed, native English speaker, undergraduate or postgraduate students with normal to corrected vision were recruited for this study. Informed consent was sought prior to taking part in the fMRI as well as the behavioural assessments. The participants received either a monetary reward of £80 or 8 h of course credit.

As per the exclusion criteria, none of the participants had a history of psychiatric or neurological illness, severe claustrophobia, anticipated pregnancy or drug use that could alter cognitive functioning. In total, 11 participants were excluded from the analysis; eight due to incomplete behavioural assessment and three because of registration problems associated with the neuroimaging data. Consequently, the final group included 154 participants, who completed all the neuroimaging and behavioural assessments. The average age for this group was 20.20 years (range = 18–31, $SD = 2.43$) with 94 females.

2.2. Behavioural assessment

Following the imaging protocol, participants took part in a comprehensive set of behavioural assessments that captured different aspects of semantic cognition. The tasks were completed over three 2 h long sessions on different days, with the order of the sessions counterbalanced across participants. Full details about the semantic tasks are provided in the supplementary materials (Tables S1–S5). In total, there were 12 tasks that examined semantic cognition:

- Two 3-alternative forced choice (3AFC) tasks required participants to identify pictures at two levels of specificity. Superordinate-word/picture matching required participants to link a picture of a Dalmatian with the word “animal” (as opposed to distractors such as “vehicle; clothes”). Specific-level matching, however, involved the
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