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Review

The neural basis of semantic cognition: Converging evidence from neuropsychology, neuroimaging and TMS

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ABSTRACT

Recent studies suggest that a complex, distributed neural network underpins semantic cognition. This article reviews our contribution to this emerging picture and traces the putative roles of each region within this network. Neuropsychological studies indicate that semantic cognition draws on at least two interacting components: semantic representations [degraded in semantic dementia (SD)] and control processes [deficient in patients with multimodal semantic impairment following stroke aphasia (SA)]. To explore the first component, we employed distortion-corrected functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) in healthy volunteers: these studies convergently indicated that the anterior temporal lobes (ATLs; atrophied in SD) combine information from different modalities within an amodal semantic "hub". Regions of cortex that code specific semantic features ("spokes") also make a critical contribution to knowledge within particular categories. This network of brain regions interacts with semantic control processes reliant on left inferior frontal gyrus (LIFG), posterior middle temporal gyrus (pMTG) and inferior parietal cortices. SA patients with damage to these regions have difficulty focussing on aspects of knowledge that are relevant to the current goal or context, in both verbal and non-verbal tasks. SA patients with LIFG and temporoparietal lesions show similar deficits of semantic control, suggesting that a large-scale distributed cortical network underpins semantic control. Convergent evidence is again provided by fMRI and TMS. We separately manipulated the representational and control demands of a semantic task in fMRI, and found a dissociation within the temporal lobe: ATL was sensitive to the number of meanings retrieved, while pMTG and LIFG showed effects of semantic selection. Moreover, TMS to LIFG and pMTG produced equal disruption of tasks tapping semantic control. The next challenges are to delineate the specific roles of each region within the semantic control network and to specify the way in which control processes interact with semantic representations to focus processing on relevant features of concepts.

Semantic cognition is a fundamental component of mind and behaviour: it brings meaning to our ongoing verbal and non-verbal experiences and memories and allows us to use this knowledge to drive context- and time-appropriate behaviour (Lambon Ralph and Patterson, 2008; Corbett et al., 2009a). As such, it is at the core of language and communication as well

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as non-verbal, everyday skilled behaviours (e.g., using objects and sequencing actions to achieve a goal). Our semantic knowledge is multimodal: it allows us to determine the meanings of items encountered via any of our senses. We can recognise and understand pictures, faces, smells, environmental sounds, words and sentences and events, and establish the identity of objects through touch. However, multimodal semantic representations are not sufficient for successful semantic cognition because we store a wealth of information about the meanings of words/objects and typically only a subset of this knowledge is required for a task – other aspects of knowledge may actually be inappropriate and unhelpful. For example, thinking about “coins” and “loans” is probably not helpful when trying to understand the sentence “The bank was slippery” (since in this context, the word “bank” is likely to refer to a river). Similarly, playing the piano requires information about fine movements of the fingers to be retrieved, yet if your task is to move a piano across the room, it is necessary to retrieve very different actions (Saffran, 2000). Control processes therefore play an essential role in shaping the activation within the semantic system, such that context- and task-relevant aspects of meaning are brought to the fore. Although in some circumstances, it may be sufficient to retrieve dominant aspects of meaning relatively automatically, in many other situations, we need to retrieve distant semantic associations or weakly activated features in a more controlled way, and/or select pertinent aspects of knowledge whilst inhibiting irrelevant semantic features. We may also need to configure the components of the semantic network in line with our current goals or expectations and to monitor our semantic retrieval so that control processes can be adjusted if necessary.

Semantic representation and control are not encapsulated in single, modular brain areas but reflect the joint action of a widely distributed set of cortical regions (in common with other higher brain functions; see Fig. 1). To make progress in understanding this network of brain regions, we have conducted neuropsychological studies comparing the nature of semantic deficits that arise from different aetiologies and areas of brain injury. (1) Patients can show deficits in comprehension that are specific to a particular modality: for example, patients with ‘pure word deafness’ have difficulty accessing semantic knowledge from spoken words, while those with visual agnosia have difficulty assessing knowledge from vision (e.g., Farah, 2004; Franklin et al., 1996). The fact that comprehension from other modalities is intact in such patients indicates that the central store of conceptual knowledge is preserved. (2) Individuals with semantic dementia (SD) show progressive degradation of central conceptual representations, while other aspects of language and cognition remain largely intact (e.g., Hodges et al., 1992; Snowden et al., 1989; Warrington, 1975). This erosion of semantic knowledge gives rise to poor comprehension across all input and output modalities (Bozeat et al., 2000; Patterson et al., 2007). (3) Multimodal semantic deficits can also occur in patients with stroke aphasia (SA), although they are associated with different areas of brain damage that do not overlap with the regions in SD (see below; Jefferies and Lambon Ralph, 2006). These patients *inconsistently* access the meanings of items: in particular, they have difficulty in semantic tasks with greater executive demands. This suggests that SA patients have an intact store of conceptual knowledge but damage to semantic control processes.

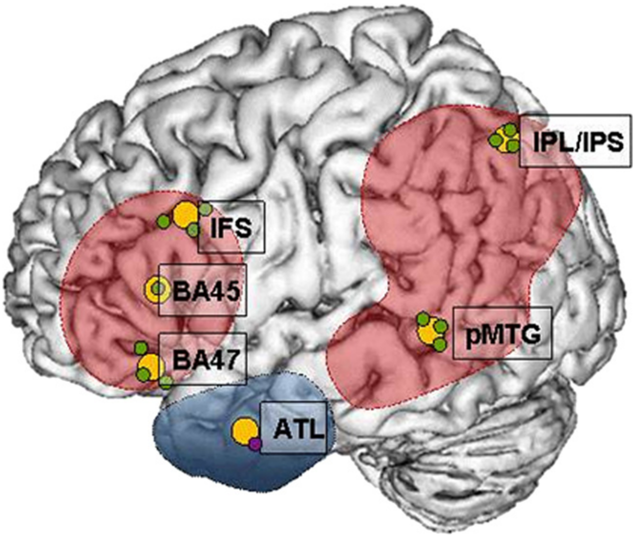

Fig. 1 – Convergent evidence for the distributed neural network underpinning semantic cognition (adapted from Whitney et al., 2011b, with permission).
Footnote: figure shows patient lesions (SD in *blue* and semantic aphasia in *pink*, from Jefferies and Lambon Ralph, 2006); activation peak in ATL identified using distortion-corrected fMRI (purple circle, from Binney et al., 2012); fMRI peaks produced by manipulations of semantic control (*green* circles, Thompson-Schill et al., 1997; Wagner et al., 2001; Badre et al., 2005), and sites used in our TMS studies (*yellow* circles, e.g., Whitney et al., 2011b; Pobric et al., 2007).

Following these case-series comparisons of patients with SD and SA, which have highlighted the effects of impairment to amodal semantic representations and control processes respectively, we have used complementary neuroscientific methods – functional neuroimaging and transcranial magnetic stimulation (TMS) – to seek converging evidence for our hypotheses about the neural basis of these two key components of semantic cognition in healthy volunteers.

1. Neural basis of semantic representation

Where is semantic knowledge represented in the brain? Many researchers propose an ‘embodied’ view in which semantic information draws on a distributed network of sensory and motor representations (e.g., Pulvermuller, 2005; Martin, 2007; Barsalou, 1999). According to this view, the meaning of an item like “scissors” is derived from links between neural assemblies that represent this object’s distinctive shape, the “snip” sound that it makes, information about how you hold and use scissors, linguistic properties of the word “scissors” and so on. These links allow all of the information you have about an object to be activated from a single modality – so that, on hearing the word “scissors”, you can easily imagine