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Semantic retrieval during overt picture description: Left anterior temporal or the parietal lobe?

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ABSTRACT

Retrieval of semantic representations is a central process during overt speech production. There is an increasing consensus that an amodal semantic 'hub' must exist that draws together modality-specific representations of concepts. Based on the distribution of atrophy and the behavioral deficit of patients with the semantic variant of fronto-temporal lobar degeneration, it has been proposed that this hub is localized within both anterior temporal lobes (ATL), and is functionally connected with verbal 'output' systems via the left ATL. An alternative view, dating from Geschwind's proposal in 1965, is that the angular gyrus (AG) is central to object-based semantic representations. In this fMRI study we examined the connectivity of the left ATL and parietal lobe (PL) with whole brain networks known to be activated during overt picture description. We decomposed each of these two brain volumes into 15 regions of interest (ROIs), using independent component analysis. A dual regression analysis was used to establish the connectivity of each ROI with whole brain-networks. An ROI within the left anterior superior temporal sulcus (antSTS) was functionally connected to other parts of the left ATL, including anterior ventromedial left temporal cortex (partially attenuated by signal loss due to susceptibility artifact), a large left dorsolateral prefrontal region (including 'classic' Broca's area), extensive bilateral sensory-motor cortices, and the length of both superior temporal gyri. The time-course of this functionally connected network was associated with picture description but not with non-semantic baseline tasks. This system has the distribution expected for the production of overt speech with appropriate semantic content, and the auditory monitoring of the overt speech output. In contrast, the only left PL ROI that showed connectivity with brain systems most strongly activated by the picture-description task, was in the superior parietal lobe (supPL). This region showed connectivity with predominantly posterior cortical regions required for the visual processing of the pictorial stimuli, with additional connectivity to the dorsal left AG and a small component of the left inferior frontal gyrus. None of the other PL ROIs that included part of the left AG were activated by Speech alone. The best interpretation of these results is that the left antSTS connects the proposed semantic hub (specifically localized to ventral anterior temporal cortex based on clinical neuropsychological studies) to posterior frontal regions and sensory-motor cortices responsible for the overt production of speech.

1. Introduction

Spoken language comprehension and production are dependent on widely distributed sensory, motor and linguistic systems comprising functionally specialized components (Indefrey and Levelt, 2004; Price, 2012). However, language is nothing without access to semantic representations. Geschwind (1965a, 1965b) proposed that the expansion of the human parietal lobe relative to that of other primates and mammalian species, its polysensory connections, its independence from the limbic system, and its anatomical connections with Wernicke's area in the posterior temporal lobe made it the most likely region that linked object words with their multiple perceptual semantic representations. This hypothesis still has its strong proponents in an era of imaging white matter tracts in the living human brain by the use of diffusion tensor imaging (Catani and ffytche, 2005). These two authors resurrected the Broca–Wernicke–Lichtheim model, one never abandoned by neurologists. Although Lichtheim had linked speech input (Wernicke's area) to output (Broca's area) via a third region that stored concepts (that is, semantic memories), this was never localized by him to a specific cortical area. Hence, the two eponymous areas of Broca and Wernicke were not accompanied by a third, 'Lichtheim's area'. Based on Geschwind's hypotheses, Catani and ffytche (2005) placed access to semantic

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representations, during both speech comprehension and production, in the left inferior parietal cortex, which they labeled as ‘Geschwind's region’.

This role for left inferior parietal cortex has been widely accepted by the clinical neurological community, but based on little direct evidence. The ‘gold standard’ when determining the role of a brain region in cognitive processing is to examine the behavioral consequences of focal lesions, usually infarcts. Strokes confined to the left parietal lobe are rare. For example, Borovsky et al. (2007) performed behavioral analyses on 50 patients with aphasic strokes, but none had lesions confined to the parietal lobe alone.

It was patients with the semantic variant of fronto-temporal lobar degeneration (svFTD) that drew attention to the possibility that it is anterior temporal cortex that provides an amodal route through which semantic representations are accessed (Acosta-Cabronero et al., 2011; Hodges et al., 1992; McClelland and Rogers, 2003; Patterson et al., 2007; Snowden et al., 1989; Warrington, 1975). These patients have a striking and progressive loss of semantic knowledge, irrespective of the modality of stimulus presentation (verbal, environmental sounds, pictures, etc.) (Bozeat et al., 2000). The maximum area of atrophy in these patients is the anterior temporal lobes (ATL), usually with greater atrophy on the left (Acosta-Cabronero et al., 2011). Based on the behavioural sequelae in patients with asymmetrical atrophy, that can manifest as more prominent loss of semantic knowledge in a specific modality (e.g. verbal vs. visual), some have suggested that verbal semantics is more dependent on the left ATL while non-verbal semantics is more dependent on the right ATL (Gainotti, 2012; Mesulam et al., 2013). Others have argued that these findings reflect differences in the strength of connectivity from a bilaterally distributed semantic hub to modality-specific input/output systems. The latter systems for speech production are lateralized to the left hemisphere (Lambon Ralph et al., 2001; Mion et al., 2010). Based on this assertion, it is reasonable to expect that a semantic hub would show functional connectivity with speech ‘output’ systems during retrieval of semantic knowledge while speaking.

As with the inferior parietal lobe, due to vascular anatomy it is rare for the anterior temporal lobe alone to be the location of a stroke. Consequently, lesion-deficit analyses on aphasic stroke patients alone had not identified a role for this region in semantic processing. Furthermore, patients with anterior temporal lobectomy, an operation commonly performed to treat temporal lobe epilepsy, show, at most, only a limited impairment on semantic tasks, the most prominent being anomia (Alpherts et al., 2004; Davies et al., 1995, 2005). This may be because chronic pre-surgical focal epileptic discharges reorganize the normal functional neuroanatomy of the semantic system. An alternative view is that bilateral pathology may be necessary for major impairments of semantic memory (Schapiro et al., 2013); and bilateral temporal lobe surgery for epilepsy has been avoided since lessons from the effects on declarative memory of the consecutive, bilateral medial temporal lobe resections on patient H.M. were revealed. Thus, the argument is that right anterior temporal atrophy contributes to the progressive impairment in svFTD even when the left anterior temporal atrophy is more prominent. However, it could be (and has been) argued that other cortical regions, including parietal cortex, will also have pathological changes, and it may be that diffuse mild atrophy is at least contributing to the semantic deficit. Nevertheless, the same argument would apply to patients with posterior cortical atrophy, a variant of Alzheimer's disease, in whom bilateral occipital, parietal and posterior temporal atrophy is most evident. In addition to their prominent visuo-spatial deficits, these patients develop a progressive linguistic rather than semantic impairment, the reverse of what is observed in patients with svFTD (Crutch et al., 2012, 2013).

Therefore, there are good arguments for a major role for the anterior temporal lobe, or lobes, in semantic processing. Initially, it was hoped that functional neuroimaging results from normal subjects might resolve the debates arising from clinical studies. This has not been realized. Meta-analyses have demonstrated widely distributed cortical regions involved in semantic processing (Binder et al., 2009; Vigneau et al., 2006). Nevertheless, functional magnetic resonance imaging (fMRI) has probably underestimated any contribution from ventral anterior temporal cortex to semantic processing, as signal from this region is lost with conventional fMRI using gradient-echo echo-planar imaging, the consequence of local magnetic field inhomogeneity (susceptibility artifact) (Devlin et al., 2000). Different techniques have been adopted to minimize this effect (Embleton et al., 2010; Halai et al., 2014; Poser and Norris, 2009), with some success. In contrast, functional neuroimaging performed with positron emission tomography (PET), although a more cumbersome and limited technique, can recover signal from this region (Devlin et al., 2000); and PET studies of narrative language comprehension (spoken and written) and narrative speech production, have clearly demonstrated activity in anterior temporal cortex (Awad et al., 2007; Spitsyna et al., 2006). Nevertheless, the ventral AG was also activated in response to narrative language in both these studies, and any differences in function of anterior temporal and inferior parietal cortices could not be determined from the design of these studies.

One possibility is that a component of inferior parietal cortex is part of a system exerting task-dependent control over access to semantic representations, and that activity in this region observed in functional imaging studies of semantic processing reflects this control rather than activation of the semantic system itself (Lambon Ralph, 2014). These proposals have been based on lesion studies, in both stroke patients with ‘semantic aphasia’ (Jefferies, 2006), who have difficulty accessing largely intact semantic representations, and after the induction of temporary partial lesions in normal participants using transcranial magnetic stimulation (Whitney et al., 2011, 2012). It is also a conclusion from the reinterpretation of published functional neuroimaging studies (Noonan et al., 2013). This evidence is further backed up by demonstrations of functional connectivity between left inferior parietal, posterior temporal and posterior frontal cortices during spoken language production (Geranmayeh et al., 2012, 2014), connectivity that is also captured by analyses of ‘rest state’ functional neuroimaging data (Smith et al., 2009).

A further factor that has to be considered is the role of inferior parietal cortex in episodic memory. A review of functional imaging studies that investigated episodic memory retrieval discussed the activity of lateral parietal cortex and the medial retrosplenial and posterior cingulate cortices and the precuneus (Wagner et al., 2005). Studies of narrative speech comprehension and production have consistently demonstrated bilateral AG activity, although often rather more prominent on the left. The narrative tasks depended on retrieval of episodic memories, either personal autobiographic memories or stories that had been illustrated by picture cards prior to scanning that had to be recalled during scanning to elicit narrative speech production (AbdulSabur et al., 2014; Awad et al., 2007; Braun et al., 2001). Listening to narratives results in both encoding and retrieval of episodic information, as the comprehension of an unfolding story only makes sense if later passages can be related to information conveyed earlier in the course of the narrative. In contrast, it can be envisaged that naming or briefly describing a picture weights the task towards semantic memory retrieval and incidental episodic memory encoding, but not on retrieval. Therefore, the dependency on the two forms of declarative memory will be influenced by the specific task used to elicit speech from a participant.

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