Neuropsychologia 76 (2015) 92–107

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Conceptual control across modalities: graded specialisation for pictures and words in inferior frontal and posterior temporal cortex

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A R T I C L E I N F O

Article history:
Received 29 September 2014
Received in revised form
20 February 2015
Accepted 21 February 2015
Available online 26 February 2015

Keywords:
Cognitive control
Semantic
Executive
Conceptual
Modality
Verbal
Picture
fMRI

A B S T R A C T

Controlled semantic retrieval to words elicits co-activation of inferior frontal (IFG) and left posterior temporal cortex (pMTG), but research has not yet established (i) the distinct contributions of these regions or (ii) whether the same processes are recruited for non-verbal stimuli. Words have relatively flexible meanings – as a consequence, identifying the context that links two specific words is relatively demanding. In contrast, pictures are richer stimuli and their precise meaning is better specified by their visible features – however, not all of these features will be relevant to uncovering a given association, tapping selection/inhibition processes. To explore potential differences across modalities, we took a commonly-used manipulation of controlled retrieval demands, namely the identification of weak vs. strong associations, and compared word and picture versions. There were 4 key findings: (1) Regions of interest (ROIs) in posterior IFG (BA44) showed graded effects of modality (e.g., words > pictures in left BA44; pictures > words in right BA44). (2) An equivalent response was observed in left mid-IFG (BA45) *across* modalities, consistent with the multimodal semantic control deficits that typically follow LIFG lesions. (3) The anterior IFG (BA47) ROI showed a stronger response to verbal than pictorial associations, potentially reflecting a role for this region in establishing a meaningful context that can be used to direct semantic retrieval. (4) The left pMTG ROI also responded to difficulty across modalities yet showed a stronger response overall to verbal stimuli, helping to reconcile two distinct literatures that have implicated this site in semantic control and lexical-semantic access respectively. We propose that left anterior IFG and pMTG work together to maintain a meaningful context that shapes ongoing semantic processing, and that this process is more strongly taxed by word than picture associations.

1. Introduction

Semantic cognition is inherently multimodal, allowing us to assign meaning to things we encounter in different modalities (words, pictures, actions, smells, etc.) and to map between these modalities (Jefferies, 2013; Lambon Ralph et al., 2008; Patterson et al., 2007). For example, on encountering the word "piano", we can retrieve the full range of multimodal features for this concept, including visual properties (large size, black and white keys), actions (finger presses) and sounds (musical notes). Since only a subset of our semantic information is likely to be relevant for any given context, uncontrolled spreading activation within the conceptual store is insufficient for successful semantic cognition: we also need mechanisms that can focus processing on currently-relevant features or associations (Badre et al., 2005; Noonan et al., 2013b; Thompson-Schill et al., 1997). For instance, if you hear the question "how do you move a piano?" in the context of *moving house*, the dominant movements for the object (i.e., key presses) are irrelevant or even unhelpful (Saffran, 2000). Therefore, semantic cognition involves the interaction of (i) a store of multimodal semantic information, accessed by inputs in different modalities and (ii) control processes that shape semantic retrieval according to high-level goals established by the context or task (Jefferies and Lambon Ralph, 2006). However, the details of this interaction are still poorly understood. For example, there is next-to-no information in the literature about whether control processes vary across verbal and non-verbal tasks, because the vast majority of previous neuroimaging studies have presented written or spoken words (see Noonan et al., 2013b). Since concepts are multimodal, we might anticipate *identical* control processes for words and pictures; however, there are also differences in the information provided by these two types of inputs which might give rise to different executive demands, even when the task instructions are unchanged. Words have more flexible meanings and

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.02.030
0028-3932/

their interpretation is highly dependent on the context in which they appear. In contrast, pictures are more constrained by their visual features; however, not all of these features will be relevant in any given task, potentially increasing inhibitory requirements. In this study, we explored similarities and differences in the neural basis of controlled semantic retrieval from words and pictures.

Verbal and non-verbal semantic tasks elicit common activity in a large-scale cortical network that includes bilateral anterior lobes (ATL), left angular gyrus, bilateral inferior frontal gyrus (IFG), and left posterior temporal cortex with a peak for multimodal processing in posterior middle temporal gyrus (pMTG) (Adams and Janata, 2002; Binder et al., 2009; Bright et al., 2004; Chee et al., 2000; Vandenberghe et al., 1996; Visser et al., 2012; Visser and Lambon Ralph, 2011). However, neuropsychological, TMS and neuroimaging studies have revealed dissociations between brain regions implicated in (1) the representation of multimodal concepts (in ATL) and (2) the controlled retrieval of semantic information (in IFG and pMTG) (Jefferies and Lambon Ralph, 2006; Noonan et al., 2013b; Whitney et al., 2011a). Patients with semantic dementia following ATL atrophy show progressive *degradation* of conceptual knowledge: their deficits are highly consistent across different modalities (for example, across word, picture, sound and smell inputs) and performance is poorer for specific concepts and unique features (e.g., the camel's hump is forgotten before the camel's tail) (Bozeat et al., 2000; Lambon Ralph et al., 2010; Patterson et al., 2007; Rogers et al., 2004). In contrast, patients with semantic aphasia following left inferior frontal or temporoparietal stroke show *deregulated* semantic retrieval which is dominated by strong associations even when these are irrelevant to the task being performed. Their comprehension is strongly influenced by the degree of competition between concepts and the extent to which the task constrains semantic processing, reducing the need for internally-generated control (Corbett et al., 2009a; Gardner et al., 2012; Jefferies and Lambon Ralph, 2006; Jefferies et al., 2008; Noonan et al., 2010). While semantic aphasia patients have large lesions, neuroimaging and TMS studies of healthy participants also show effects of executive-semantic demands in LIFG and pMTG (Badre et al., 2005; Noonan et al., 2013b; Whitney et al., 2011a, 2011b). The literature therefore suggests that LIFG and pMTG work together to underpin controlled semantic retrieval, while ATL is involved in semantic representation (for review see Jefferies, 2013). This distinction is also broadly consistent with the findings of fMRI studies that have used multi-voxel pattern analysis to investigate brain areas representing specific semantic features and concepts: several studies using simple tasks without marked control demands have found that features and concepts can be classified by responses in ATL but not LIFG (Correia et al., 2014; Coutanche and Thompson-Schill, 2014; Peelen and Caramazza, 2012; but see Simanova et al., 2014).

A crucial question for this investigation concerns how this distributed functional system appropriately shapes semantic cognition for word and picture inputs. A recent activation likelihood estimation (ALE) meta-analysis examining tasks tapping semantic control in different ways (for example, understanding ambiguous words, retrieving distant semantic relationships or dealing with strong distractors) revealed a common response within bilateral IFG (extending to inferior frontal sulcus (IFS) and premotor cortex), left pMTG, dorsomedial prefrontal cortex (pre-SMA), and left dorsal angular gyrus (dAG) bordering on intraparietal sulcus (IPS) (Noonan et al., 2013b). These regions were commonly activated when semantic processing was difficult; however, the vast majority of these studies employed words (85% used verbal stimuli; 13% used a combination of words and pictures; with next-to-no studies examining picture-only tasks). The meta-analysis also explored which of these regions additionally showed activation for control-demanding phonological tasks: substantial overlap was seen in posterior parts of LIFG/premotor cortex, consistent with the view that these sites contribute to controlled aspects of linguistic processing more broadly, while anterior LIFG and pMTG showed a specifically semantic response (see also Gough et al., 2005; Wagner et al., 2001). Several of the sites identified by this meta-analysis – namely inferior frontal sulcus, IPS and pre-SMA – form a distributed frontoparietal control network supporting executive control across multiple domains and tasks (e.g., the multi-demand network described by Duncan, 2010; Duncan and Owen, 2000); it is therefore unsurprising that these regions are recruited during challenging conceptual tasks, and we would expect these regions to be recruited for more difficult judgements to both words and pictures. However, left anterior IFG and pMTG fall outside this multi-demand system (Blank et al., 2014; Fedorenko et al., 2012; Noonan et al., 2013b) and could conceivably show a differing response across input modalities or different types of tasks.

To develop hypotheses about the way in which the recruitment of semantic control regions might vary with modality, we first discuss the contribution that IFG and pMTG make to the executive control of semantic cognition in verbal tasks. The control of semantic cognition is multi-faceted: for example, in the case of goal-driven semantic control, attention can be focussed on specific aspects of knowledge according to the task instructions, while irrelevant features are suppressed (e.g., to answer the question "do pianos and penguins have the same colour?", retrieval must be focussed on colour knowledge). Additionally, a representation of the current context (e.g., "we are moving house") can be used to shape the conceptual response to inputs (e.g., on hearing the word "piano", attention can be focussed on size and weight features, as opposed to its function as a musical instrument). Nevertheless, the meta-analysis of Noonan et al. (2013b) found that broadly the same network was recruited across tasks – and perhaps this is unsurprising since, in all cases, there is a need to use a goal or context to shape competitive processes such that relevant aspects of knowledge receive greater activation, and irrelevant information is supressed. Noonan et al. (2013b) suggested that co-activation of IFG and pMTG is crucial for the establishment, maintenance and efficient application of task, goal and context representations to ongoing conceptual processing, such that semantic cognition is biased towards aspects of meaning which are currently relevant. Nevertheless, we might still see graded specialisation of function within and between these regions (Badre et al., 2005; Noonan et al., 2013b). Below, we develop predictions about potential differences between words and pictures concerning (i) anterior and posterior IFG; (ii) left and right IFG and (iii) left IFG and pMTG.

Anterior vs. posterior IFG: Following the early debate about whether the contribution of LIFG to semantic cognition is best characterised as "selection" or "controlled retrieval" (Thompson-Schill et al., 1997; Wagner et al., 2001), Badre et al. (2005) suggested that *posterior* parts of LIFG are crucial for selection, while anterior parts of LIFG are more crucial for controlled retrieval. By this view, posterior IFG might bias competitive processes within the semantic system in favour of task- or context-relevant aspects of knowledge and away from strong distracters, while anterior IFG might be more important for establishing which aspects of conceptual knowledge should be the focus of ongoing processing (see also Bookheimer, 2002). This distinction is broadly consistent with proposals about the general organisation of cognitive control, which suggest that anterior parts of PFC maintain high-level goals which determine which features of representations are currently relevant for action or cognition, while posterior parts of PFC instantiate mechanisms that resolve competition between competing alternative responses (Badre and D'Esposito, 2009; Demb et al., 1995; Gabrieli et al., 1998). Since words occur in different contexts and have flexible meanings, we might hypothesise that generating