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Research report

Converging evidence from fMRI and aphasia that the left temporoparietal cortex has an essential role in representing abstract semantic knowledge

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ABSTRACT

While the neural underpinnings of concrete semantic knowledge have been studied extensively, abstract conceptual knowledge remains enigmatic. We present two experiments that provide converging evidence for the involvement of key regions in the temporoparietal cortex (TPC) in abstract semantic representations. First, we carried out a neuroimaging study in which participants thought deeply about abstract and concrete words. A functional connectivity analysis revealed a cortical network, including portions of the TPC, that showed coordinated activity specific to abstract word processing. In a second experiment, we tested participants with lesions involving the left TPC on a spoken-to-written word matching task using abstract and concrete target words presented in arrays of related or unrelated distractors. The results revealed an interaction between concreteness and relatedness: participants with TPC lesions were significantly less accurate for abstract words presented in related arrays than in unrelated arrays, but exhibited no effect of relatedness for concrete words. These results confirm that the TPC plays an important role in abstract concept representation and that it is part of a larger network of functionally cooperative regions needed for abstract word processing.

1. Introduction

Concreteness is a critical organizing factor in semantic memory and recognition of the dichotomy between abstract and concrete concepts has a long history in psychology and philosophy. While concrete concepts have been the focus of much psychological and physiological research, abstract concepts remain enigmatic.

An extensive empirical literature supports the dichotomy between abstract and concrete concepts. The “concreteness effect” – concrete concepts are easier to learn, use, recall and recognize – is a robust effect that has been demonstrated across populations and tasks. Typical participants show a

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general advantage for concrete concepts, processing them faster and more accurately than abstract concepts, in a variety of tasks such as lexical decision and semantic categorization (Bleasedale, 1987; Day, 1977; de Groot, 1989; Howell & Bryden, 1987; James, 1975; Kroll & Merves, 1986; Rubin, 1980; Whaley, 1978). The neurological distinction between abstract and concrete concepts has also been supported by a large EEG literature, which has consistently identified differences in the N400 component when processing abstract and concrete words (Adorni & Proverbio, 2012; Holcomb, Kounios, Anderson, & West, 1999; Kanske & Kotz, 2007; Kounios & Holcomb, 1994; Nittono, Suehiro, & Hori, 2002; Renoult, Brodeur, & Debruille, 2010; Tolentino & Tokowicz, 2009; Tsai et al., 2009; West & Holcomb, 2000; Zhang, Guo, Ding, & Wang, 2006).

However, attempts to localize neural differences between abstract and concrete concepts have been largely unsuccessful. This is partially due to the fact that patients with acquired language deficits almost always exhibit greater impairments with abstract words than with concrete words, and sometimes exhibit exclusively abstract word impairments. This has been repeatedly demonstrated in patients with deep dyslexia when reading abstract and concrete words (Coltheart, 1980) as well as in word repetition tasks (Katz & Goodglass, 1990; Martin & Saffran, 1992). Patients with aphasia and short-term memory deficits also show a strong disadvantage with abstract concepts (Goodglass, Hyde, & Blumstein, 1969; Saffran & Martin, 1990). Furthermore, the typical pattern in degenerative neurological diseases that affect semantic memory, such as semantic dementia, involves early loss of the ability to use and recognize abstract concepts (Hoffman & Lambon Ralph, 2011).

Much more unusual is the reverse effect – a specific deficit for concrete words leaving abstract words intact (termed *the reversal of the concrete effect*; Warrington, 1975). This deficit has been identified in patients with a range of lesion foci and disorders, including aphasia, semantic dementia, and acquired dyslexia (Bonner et al., 2009; Breedin, Saffran, & Coslett, 1994; Cipolotti & Warrington, 1995; Gvion & Friedmann, 2013; Sirigu, Duhamel, & Poncet, 1991; Warrington, 1981; Warrinton & Shallice, 1984; Yi, Moore, & Grossman, 2007). Bonner et al. (2009) found that the peak neurological degeneration associated with this specific concrete-word deficit was found in a portion of the ventral surface of the anterior temporal lobes. It has also been suggested that in some cases, cortical damage in sensory-information integration regions, such as the ventral temporal lobe, produce the unusual deficit for specifically concrete (or visual) concepts, or alternatively that some patients may have had unusual prior expertise with abstract concepts, which allowed certain abstract concepts to be resilient to cortical insult (Hoffman & Lambon Ralph, 2011). However, these hypotheses can only account for a few of the patients who exhibit the reversal of the concreteness effect and the cortical organization of abstract and concrete semantic knowledge remains mysterious. Nevertheless, this double dissociation in ability to process abstract and concrete concepts after brain injury suggests that abstract and concrete concepts rely on somewhat distinct neurological systems.

Neuroimaging has been a valuable tool for understanding the organization of semantic memory as a whole (Binder, Desai, Graves, & Conant, 2009), but findings on the abstract-concrete distinction are largely inconsistent. For example, some neuroimaging studies have shown stark distinctions in regional activity throughout the brain for concrete and abstract concepts, with almost no overlap (Binder, Westbury, McKiernan, Possing, & Medler, 2005; D'Esposito et al., 1997; Wise et al., 2000). Many others, however, have failed to identify any regional differences, with all activations completely overlapping (Beauregard et al., 1997; Fiebach & Friederici, 2003; Friederici, Opitz, & von Cramon, 2000; Grossman et al., 2002; Kiehl et al., 1999; Noppeney & Price, 2004; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Skipper & Olson, 2014).

Two large meta-analyses of the neuroimaging literature on semantic memory reported some similar and some distinct findings. Binder et al. (2009) found that abstract concepts were associated with activity in the left inferior frontal gyrus (IFG), superior aspects of the left anterior temporal lobe (ATL), and in the superior temporal sulcus (STS), while concrete concepts were more distributed across both hemispheres, including bilateral angular gyrus (AG), bilateral dorsomedial prefrontal cortex, left posterior cingulate and left inferior temporal lobe in fusiform cortex. A meta-analysis by Wang, Conder, Blitzer, and Shinkareva (2010) examined 19 neuroimaging studies, only nine of which overlapped with the Binder analysis. In this meta-analysis, only left hemisphere regions were identified. Abstract concepts were again found to activate the left IFG, as well as the entire left temporal pole (TP). Concrete concepts activated the left AG, left posterior inferior temporal cortex, and posterior anterior cingulate.

In sum, neuroimaging and neuropsychological studies have failed to identify unequivocal "nodes" of abstract and concrete semantic neural representation. Subtraction analyses are designed to identify just that – "nodes" that respond to or prefer one stimulus while disregarding another. Subtraction analyses are very useful to neuroimaging, and can be used to answer certain specific questions, such as whether certain regions respond to both abstractness and emotional content (for example, Skipper & Olson, 2014). However, subtraction analyses have unfortunately demonstrated little utility in mapping the whole-brain organization for abstract, compared to concrete, concept knowledge. Before concluding that abstract and concrete semantic representations are indistinguishable, it may be useful to take a different approach in order to examine the *organization* of abstract (and concrete) semantic knowledge – one that looks beyond just sites with stimuli-specific preferences.

1.1. Goals of this study

The primary goal of this study is to explore neural networks of sites that coordinate during abstract and concrete conceptual processing using functional magnetic resonance imaging (MRI). As an alternative to the subtraction approach, in Experiment 1 we used functional connectivity to identify regions that respond in coordination with each other during abstract and concrete processing, regardless of whether each site "preferred" abstract or concrete words. Our motivation is that a network-connectivity approach can offer novel insights into the network organization of abstract semantic memory beyond those provided by abstract-versus-concrete subtraction analyses. In order to explore these networks, we carried out an fMRI study in which participants were instructed to think deeply and answer meaningful questions about abstract and concrete words.

The second goal of this study was to validate the fMRI findings in participants with focal lesions overlapping with one of the key abstract semantic "nodes" found in Experiment 1. To that end, we recruited a group of individuals with lesions in a region that was identified as part of the abstract network in our neuroimaging study. These participants were tested on a spoken-to-written word matching task using abstract and concrete words in related and unrelated arrays. By combining neuroimaging and neuropsychological methods we aim to provide converging evidence that will be stronger than either method alone.

2. Experiment I

2.1. Methods

2.1.1. Participants

Twenty young adults were recruited to participate through Temple University (11 female, mean age = 23 years, range: 19–28 years). All participants were neurologically and psychologically healthy, native English speakers, and right handed. Data collected from these participant's MRI sessions have been previously described (Skipper & Olson, 2014), using different analyses and testing a distinct hypothesis.

2.1.2. Stimuli

Stimuli consisted of 164 nouns collected from the MRC psycholinguistic database (Wilson, 1988). The words were either abstract (concreteness <350, $n = 82$) or concrete (concreteness > 550, $n = 82$) and also varied along the dimension of imageability, such that abstract words had low imageability scores and concrete words had high imageability scores. A complete list of the verbal stimuli used in this experiment can be found in the Supplementary Materials. The stimuli also included a set of pronounceable nonwords, matched for length with the real word stimuli (selected from the set used by Binder, Westbury, et al., 2005).

Both the abstract and concrete words could be equally divided into emotionally valenced and neutral subsets such that emotional valence and arousal were matched across the abstract and concrete conditions (analyses of this dimension are reported elsewhere: Skipper & Olson, 2014). Stimuli were also matched for word length (number of letters and number of phonemes), word frequency (SUBTLEX: Brysbaert & New, 2009; Brown Corpus: Kučera & Francis, 1967), familiarity (MRC psycholinguistic database: Coltheart, 1981), orthographic neighborhood size, sum bigram frequency, and number of morphemes (English Lexicon Project: Balota et al., 2007). Age of acquisition was examined post-hoc using the recent Kuperman norms (Kuperman, Stadthagen-Gonzalez, & Brysbaert, 2012), and concrete and abstract words did differ: concrete words were learned at a younger age than abstract words, which is typical for abstract and concrete nouns (Maguire, Hirsh-Pasek, & Michnick Golinkoff, 2006). Table 1 shows the mean scores on psycholinguistic variables for each condition.

2.1.3. Task

This experiment was carried out in a block design to maximize power. Each block lasted for 12 sec, followed by a 4-sec question screen. Each block began with the presentation of a single word in black sans serif font the center of the screen, which remained on the screen for 3500 msec. The participants were instructed to think deeply about the concept that the word represents during this time, but participants were not informed that the words were blocked based on imageability or concreteness. The word was then removed, and a fixation appeared for 500 msec, followed by another word, again presented for 3500 msec. In total, three words and three fixations appeared consecutively within a single block, totaling to 12 sec. Following the third and final fixation, a question screen appeared and remained on the screen for 4000 msec. The participants' task was to respond with a "yes" or "no" to the question in reference to the three words in that block. For example, a question may be "Is one a member of a family?" or "Is one found in a store?" The questions were simply intended to encourage participants to engage semantic representations while thinking about the words and were not controlled on any psycholinguistic variables because the question screen was not included in the imaging analyses; only the 12 sec block was modeled. However, if the participant answered the question incorrectly, the preceding block was removed from analysis. In total, each participant experienced 40 blocks in the concrete condition, 40 blocks in the abstract condition, and 20 blocks in the nonword condition, in a counterbalanced order.

All subjects were given a practice version of the task prior to entering the MRI scanner. The practice task was simply a shorter version of a single run, and utilized words and nonwords not used in the main MRI task.

2.1.4. Imaging parameters

Neuroimaging sessions were conducted at the Temple University Hospital on a 3.0 T S Verio scanner (Erlangen, Germany) using a twelve-channel Siemens head coil.

Table 1 – Mean scores on psycholinguistic variables for each condition, standard error in parentheses.

Psycholinguistic variables	Abstract	Concrete
Concreteness*	307 (6)	544 (5)
Imageability*	338 (5)	567 (7)
Hedonic valence	.85 (.08)	.73 (.07)
Arousal	3.81 (.12)	3.58 (.12)
Age of acquisition*	9.72 (.24)	7.35 (.29)
Kučera-Francis verbal frequency	33.34 (4.00)	30.97 (4.76)
log SUBTLEX WF	2.3 (7.4)	2.6 (9.1)
Orthographic neighbors	1.28 (.31)	1.35 (.32)
Sum bigram frequency	14,263 (756)	14,113 (777)
Number of morphemes	1.73 (.08)	1.66 (.08)
Number of phonemes	6.73 (.22)	6.38 (.23)
Number of letters	7.58 (.22)	7.60 (.23)

Note: Asterisk indicates measures in which the abstract and concrete stimuli were significantly different.

Functional T2*-weighted images sensitive to blood oxygenation level-dependent contrasts were acquired using a gradient-echo echo-planar pulse sequence (repetition time (TR), 2 sec; echo time (TE), 19 msec; FOV = 240 × 240; voxel size, 3 × 3 × 3 mm; matrix size, 80 × 80; flip angle = 90°) and automatic shimming. This pulse sequence has been optimized for ATL coverage and sensitivity based on pilot scans performed for this purpose, details of which are reported in Ross and Olson (2010). Participants underwent five functional runs, each consisting of 165 TR, including the introduction and closing slides. Forty slices were collected, and the bottom slice was fitted to cover the inferior aspects of the ATL. Temporal lobe function is of particular interest to this study because it has been proposed that the ATL serves as a hub in the semantic system (Patterson, Nestor, & Rogers, 2007), and the design presented here optimizes coverage of the entire temporal lobe, sometimes at the cost of losing portions of the superior parietal lobe.

The five functional runs were preceded by a high-resolution structural scan. The scanning procedure began with an approximately 10 min long high-resolution anatomical scan. The anatomical image was used to fit the volume of covered brain tissue acquired in the functional scan. The T1-weighted images were acquired using a three-dimensional magnetization-prepared rapid acquisition gradient echo pulse sequence (TR, 3 sec; TE, 3 msec; FOV = 201 × 230 mm; inversion time, 900 msec; voxel size, 1 × 0.9000 × .9000 mm; matrix size, 256 × 256 × 256; flip angle = 15°, 160 contiguous slices of .9 mm thickness). Visual stimuli were shown through a projection system, and participants viewed the screen through mirrors mounted on the head coil. The stimulus delivery was controlled by E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA) on a Windows laptop located in the scanner control room.

2.1.5. *Image preprocessing*

fMRI data were preprocessed and analyzed using FSL software (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). The preprocessing of the functional data included a correction for head motion (trilinear/sinc interpolation), the removal of linear trends and high-pass temporal filtering. The resulting volumetric time course data were then smoothed using a 6 mm FWHM Gaussian kernel.

For all blocks, a canonical hemodynamic response function (HRF) was modeled spanning the 12 sec for each block. Predictors were built by convolving the boxcar waveform for each condition with a double-gamma hemodynamic response function. Standard motion parameters were included as covariates in the regression. Any remaining head motion artifacts were unlikely to be substantial because there were no runs in which subject head motion displacement exceeded an *a priori* cut-off of 1.5 mm.

2.1.6. *Analysis of imaging data*

Subtraction analyses were carried out to compare our data to the findings previously reported in the literature. The findings of this subtraction analyses are reported elsewhere (Skipper & Olson, 2014; see Fig. 2A and Table 4) and briefly summarized in the Results section.

Task-dependent functional connectivity was then assessed using a psychophysiological interaction (PPI) analysis. PPI analysis requires the creation of an interaction term, which is simply the multiplication of the psychological variable (for example, a binary variable representing abstract-*vs*-concrete concept trials) with the physiological variable (time course in the seed region) (Friston et al., 1997). A whole-brain search identifies all voxels whose variance in activation can be explained by the psychophysiological interaction term. Regions identified as significant by the connectivity analysis are shown to be functionally connected to the seed region (left aIFG) during the task of interest (abstract/concrete word processing).

The connectivity analysis was carried out twice, first using abstract concepts as the psychological predictor and the second time using concrete concepts as the psychological predictor. For example, the connectivity analysis for abstract words used *abstract blocks > nonword blocks* as the psychological predictor and *activity in the left aIFG* as the physiological predictor. This analysis allows for the identification of a network supporting abstract knowledge, and then independently identifying a network supporting concrete knowledge in a separate analysis.

All results were examined at an FDR corrected $q < .05$. A cluster-based correction was applied, in which the z-threshold (2.3) was used to estimate contiguous clusters. Each cluster's significance level was estimated, using gradient random field theory, and compared with the cluster probability threshold, using standard FSL procedures (Jenkinson et al., 2012).

2.1.7. *Seed region*

The left aIFG was selected as a seed region because it has been identified as part of a larger region, the overall IFG, that may play a critical role in lexical processes such as tying phonology to semantics (Badgaiyan, Schacter, & Alpert, 2002; Badre & Wagner, 2002; Bodke, Tagamets, Friedman, & Horwitz, 2001; Devlin, Matthews, & Rushworth, 2003; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003), regardless of concreteness. The posterior IFG has been implicated in maintenance of phonological codes, phonemic classification, and simple word reading (Awh et al., 1996; Davachi, Maril, & Wagner, 2001; Paulesu, Frith, & Frackowiak, 1993; Poldrack et al., 1999). The aIFG has been shown to be responsive in semantic generation and semantic classification tasks, and to modulate the activity of its posterior counterpart (Bodke et al., 2001). Recently, it has been hypothesized that inferior frontal cortex controls goal directed activation of the rest of the semantic system, based on stimulus and task demands (Binder & Desai, 2011). The IFG is commonly activated when task demands induce deeper semantic processing, typically for both abstract and highly concrete stimuli (Badgaiyan et al., 2002; Badre & Wagner, 2002; Costafreda et al., 2006; Demb et al., 1995; Gabrieli, Poldrack, & Desmond, 1998; Mestres-Missé, Münte, & Rodriguez-Fornells, 2009; Poldrack et al., 1999), and TMS applied to the anterior left IFG leads to slowed RTs for concrete as well as abstract word stimuli (Devlin et al., 2003; Gough, Nobre, & Devlin, 2005). These studies support the hypothesis that the aIFG plays a significant role in processing the semantics of both abstract and concrete words.

The aIFG ROI used in this study was drawn so that it was restricted to a region ventral to the inferior frontal sulcus,

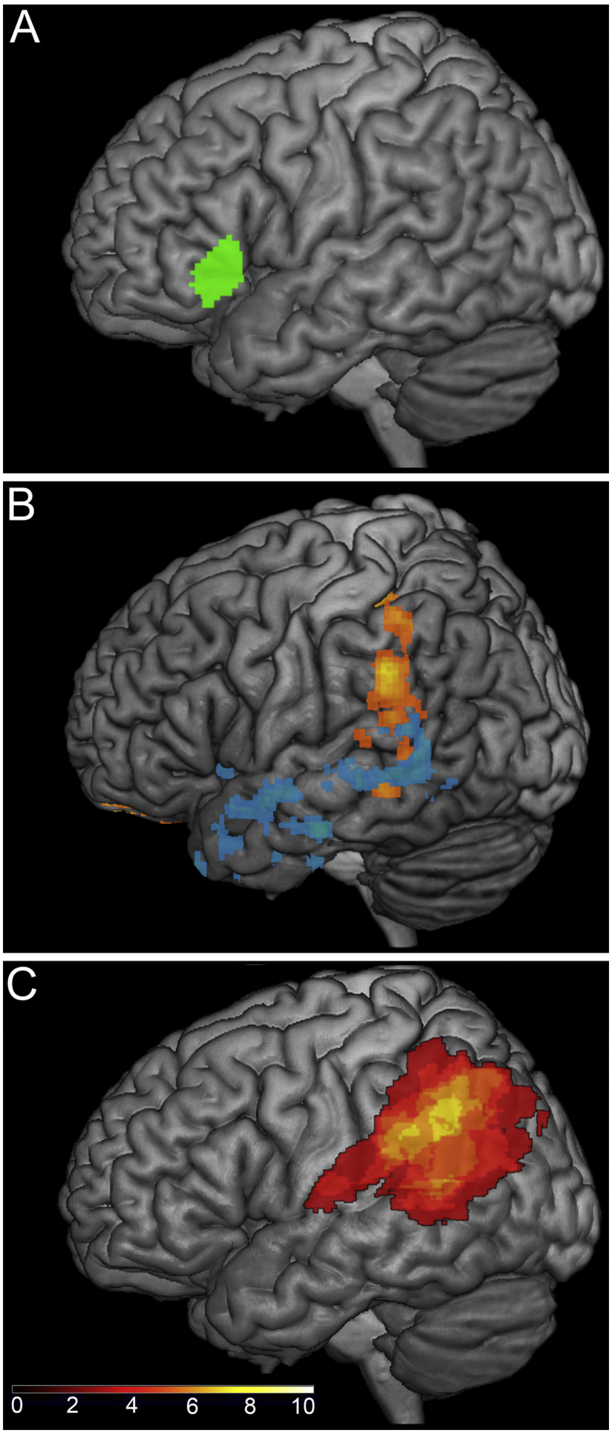

Fig. 1 – (A) Seed region, corresponding to the left aIFG, used in the connectivity analysis in Experiment 1. (B) Results of the connectivity analysis from Experiment 1. The network identified for abstract concepts is shown in red, and the network identified for concrete concepts is shown in blue. All results are presented at an FDR and cluster corrected $p < .05$. (C) An overlay map of the cortical lesions identified in the ten participants in the lesion group in Experiment 2. The scale shown represents number of participants with a lesion including that voxel.

including the pars triangularis but excluding the pars orbitalis and pars opercularis. The ROI was drawn on a cortical map that was spatially normalized to the MNI template, and consisted of 280 $1 \times 1 \times 1$ mm voxels. The aIFG ROI was then transformed into the individual subject space for the connectivity analyses, and the final results were transformed into standard MNI space for presentation and group level analyses. The ROI is shown in green in Fig. 1A.

2.2. Results

2.2.1. Behavioral results

Participants' behavioral performance while in the scanner was analyzed using a one-way ANOVA. A main effect of condition was found for accuracy on the question at the end of each block, $F(2,36) = 10.56$, $p < .001$, due to higher accuracy in the concrete condition and the abstract condition compared to the nonword condition (both p's $< .05$). Accuracy in the concrete condition was only marginally higher than in the abstract condition, $p = .06$. Across subjects, an average of 5.75 abstract blocks and 4.46 concrete blocks were removed from analyses due to inaccurate responses, out of 40 total for each participant.

A one-way ANOVA also revealed an effect of concreteness on response time (RT), $F(2, 36) = 3.79$, $p < .05$, due to faster RTs in the concrete condition compared to both the abstract condition and nonword condition (both p's $< .05$). There was no significant difference between the RTs for abstract words and nonwords, $t(18) = .99$, $p > .30$. Average performance on all three conditions is reported in Table 2.

2.2.2. Brief summary of subtraction analyses

First, we carried out two subtraction analyses in the whole brain, the results of which are briefly described here. The first analysis contrasted abstract words to nonwords. Regions responding to abstract concepts included the left and right STS extending into the TP, left posterior middle temporal gyrus (MTG), just inferior to the AG. Activation for abstract words in the right hemisphere was found in the most posterior portion of the STS, extending into the AG as well as a small cluster in the anterior MTG. The second analysis contrasted concrete words to nonwords. A great deal of activation for this contrast overlapped with the results from the abstract subtraction. Overlapping activations were found in the left TP and STS, as well as the left posterior MTG, medial OFC and medial occipital cortex, and the right posterior STS/temporoparietal cortex. Areas that responded uniquely to concrete concepts were found in the left inferior surface of the ATL, posterior cingulate cortex and medial superior frontal cortex. Areas that responded uniquely to abstract concepts were the right STS, right superior TP, and left parahippocampal gyrus. A more detailed description of these subtraction results, and figures depicting these results, can be found in Skipper and Olson (2014).

2.2.3. Connectivity during abstract word processing

A whole brain connectivity analysis examining regions that were functionally connected to the left aIFG during abstract word processing identified a bilateral network, with the largest peak at the intersection of the posterior superior

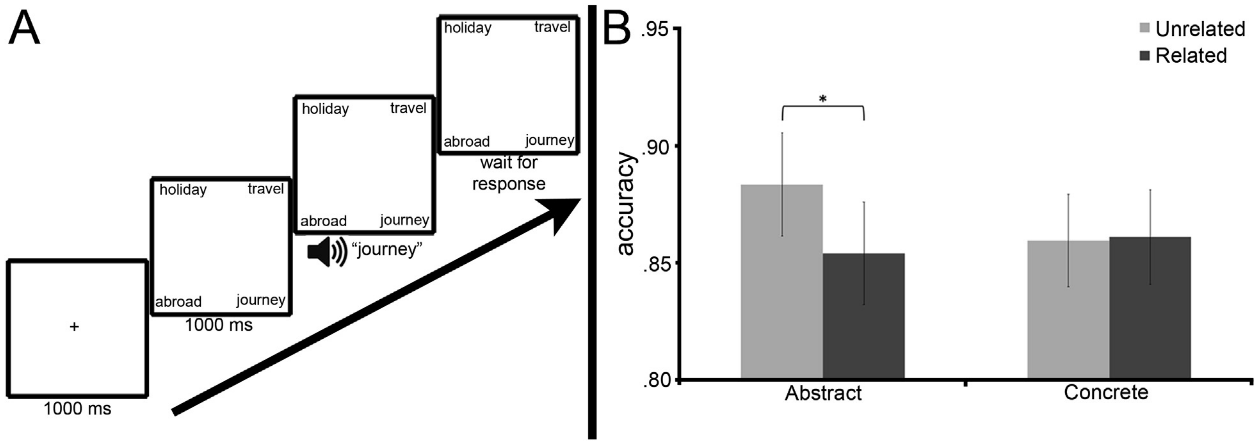

Fig. 2 – (A) A schematic diagram of a single trial in Experiment 2. The example shown is from the abstract-related condition. (B) Accuracy results for participants in the lesion group across the abstract and concrete, related and unrelated conditions.

temporal lobe and parietal lobe. Significantly connected regions included the left posterior STS extending into posterior MTG. The activation also included the left supramarginal gyrus (SMG) and AG. We will refer to this region as temporoparietal cortex (TPC). In addition to the left TPC, the small clusters in the abstract network were identified in the bilateral orbitofrontal cortex (OFC) and in the superior portion of the TP.

2.2.4. *Connectivity during concrete word processing*

A second connectivity analysis examined regions that were functionally connected to the left aIFG during concrete word processing, independently from the previous analysis. The concrete network was entirely left lateralized, and largely constrained to the temporal lobe. A significant cluster was found extending over the left STS, with the peak in the anterior STS. A peak was also found in the ventral temporal lobe, in the left inferior temporal gyrus, and a small cluster in the left medial OFC.

The abstract and concrete networks overlapped in a small area in the posterior MTG, and near-adjacent activation for the two networks was identified in the STS. However, the concrete network was largely ventral to the abstract network.

The results of both functional connectivity analyses are presented in Fig. 1B, and peak activations are reported in MNI space in Table 3.

3. Discussion

The results of the subtraction analysis, reported briefly here and in more detail in another publication (Skipper & Olson, 2014) aligned closely with the findings of two recent meta-analyses of subtraction-based fMRI experiments using abstract and concrete words (Binder et al., 2009; Wang et al., 2010). In addition to these findings, our connectivity analysis identified a wider network of regions that coordinate together specifically during abstract and concrete words processing.

We used functional connectivity analyses to identify two functionally coordinated, independent cortical networks for abstract and concrete word processing. A dorsal/posterior network including a large portion of temporoparietal cortex was found to coordinate with the left aIFG during abstract word processing. A more ventral network extending along the inferior and middle temporal lobe was found to coordinate with the left aIFG during concrete word processing. Interestingly, the left inferior parietal lobe has been found in previous neuroimaging studies to be responsive to concrete, or highly sensory, words (Binder, et al., 2009; Wang et al., 2010, and our own subtraction analysis). However, in our connectivity

Table 2 – Average accuracy and response times on the question screen for all conditions in Experiment 1. Standard deviation shown in parentheses.

	Accuracy	RT
Abstract	.86 (.09)	2071 (264)
Concrete	.89 (.09)	1988 (262)
Nonword	.79 (.10)	2128 (331)

Table 3 – MNI coordinates of the peak activations for the connectivity analyses for the abstract and concrete conditions.

Region	BA	x	y	z
Abstract network				
Left supramarginal gyrus	40	−52	−40	32
Left posterior superior temporal sulcus	22	−50	−38	−4
Left postcentral gyrus	3	−32	−40	44
Left medial orbitofrontal cortex	11	−2	56	−20
Left posterior middle temporal gyrus	37	−48	−40	−6
Left angular gyrus	39	−50	−48	18
Right lateral orbitofrontal cortex	11	22	38	−20
Right temporal pole, superior temporal sulcus	38	54	14	−14
Concrete network				
Left middle insula	52	−36	−16	−10
Left middle temporal gyrus	21	−50	−16	−18
Left anterior superior temporal sulcus	22	−44	−2	−28
Left posterior superior temporal sulcus	22	−44	−28	0
Left posterior inferior temporal gyrus	37	−42	−44	−8
Left temporal pole, superior temporal sulcus	38	−54	10	−14
Left medial orbitofrontal cortex	11	−10	42	−14

analysis, we found a large region posterior and inferior to those concrete activations was part of an abstract concept network. This posterior temporal region will be described generally as the TPC.

Our next aim was to evaluate our finding that the TPC is involved in abstract word processing using converging evidence from individuals with lesions to this area. This is important because the existing neuroimaging literature on the role of the TPC in semantic memory is a confusing mixture of findings. For instance, each of the three possible claims about TPC have been supported by subtraction analyses: that it is involved in processing of highly concrete concepts (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Fliessbach, Weis, Klaver, Elger, & Weber, 2006; Wallentin, Østergaard, Lund, Østergaard, & Roepstorff, 2005), that it is equally involved in processing concrete and abstract concepts (Binder, Westbury, et al., 2005; Kiehl et al., 1999; Moseley, Carota, Hauk, Mohr, & Pulvermüller, 2012; Tettamanti et al., 2008; subtraction analysis of the present data: Skipper & Olson, 2014), and that portions of the TPC are more responsive to abstract concepts than to concrete concepts (Noppeney & Price, 2003, 2004; Perani et al., 1999; Pexman, Hargreaves, Edwards, Henry, & Goodyear, 2007; Sabsevitz et al., 2005). Our functional connectivity results suggest that rather than asking whether TPC is involved in processing concrete or abstract concepts, we should ask what functional role this region might have in processing abstract concepts.

The network identified in our analyses of abstract word processing bears a striking resemblance to regions identified in studies of thematic and event-based semantic relationships (Bedny, Dravida, & Saxe, 2013; de Zubicaray, Hansen, & McMahon, 2013; Kalénine et al., 2009; Mirman & Graziano, 2012; Schwartz et al., 2011). Thematic relationships have been hypothesized to be especially important for abstract concept knowledge, in a framework dubbed the Qualitatively Different Representations (QDR) theory. QDR theory (Crutch, 2006) proposes that concrete and abstract words are stored and accessed through different types of networks: that concrete words are associated with "semantically-related" or taxonomic networks, and abstract concepts are associated with "semantically-associated", or thematic, networks. Concepts are thematically related if they perform complementary roles or frequently occur together in a shared scenario or event (for a review, see Estes, Galonka, & Jones, 2011). QDR theory suggests that when accessing an abstract concept, such as *comedy*, spreading activation will activate concepts that are thematically associated with the target (e.g., *laughter*). A great deal of neuropsychological evidence has accrued for this theory (Crutch, Ridha, & Warrington, 2006; Crutch, Troche, Reilly, & Ridgeway, 2013; Crutch & Warrington, 2010) However, these studies tested individuals with very large, non-focal left hemisphere lesions, so they have not linked any specific brain region to either concreteness or to particular kinds of conceptual relationships. Furthermore, several neuropsychological and behavioral studies have failed to support the QDR hypothesis (Brozdowski, Gordils, & Magnuson, 2013; Hamilton & Coslett, 2008; Papagno, Martello, & Mattavelli, 2013).

Based on our connectivity results and previous evidence that TPC is particularly important for thematic semantics and that thematic relations are particularly important for abstract concepts, we hypothesized that the TPC plays a role in accessing and using thematic semantic relationships and that this cognitive function may be crucial to abstract word processing. More specifically, to test this hypothesis, in Experiment 2 we tested individuals with focal lesions in the TPC following stroke on two tasks using abstract and concrete words. The first task was a simple lexical decision task using the same stimuli used in Experiment 1. We predicted that patients with TPC lesions would be more impaired on the abstract words used in the imaging experiment. However, patients with a variety of lesions are impaired with (arguably more difficult) abstract words in lexical decision. In order to strictly test our hypothesis about abstract concepts in the TPC, we tested the patients in a second task in which the same abstract and concrete words were tested in semantically noncompetitive (unrelated) and competitive (related) arrays. We used the task previously employed by Crutch and Warrington (2005): participants were asked to perform a spoken-to-written word matching task in which the target words could be either abstract or concrete, and were presented in related and unrelated arrays. Our specific prediction was that participants with focal TPC lesions should show impaired performance on abstract words presented with semantically related distracters. These participants may also exhibit an overall deficit for abstract words, but since abstract concepts are generally more difficult and abstract impairments are typical with any neurological injury affecting language, the critical prediction was that the deficit would be significantly greater for abstract words in related arrays (i.e., a word type by distracter relatedness interaction). This finding would suggest that patients have a semantic deficit with abstract word recognition, beyond the baseline difficulty of abstract words compared to concrete words.

4. Experiment 2

4.1. Methods

4.1.1. Participants

Ten participants with diagnoses of aphasia following left hemisphere stroke (3 female, mean age = 58.9 years, mean education = 15.8 years, mean time since injury = 48.9 months) were recruited to participate from the Neuro-Cognitive Rehabilitation Research Patient Registry at the Moss Rehabilitation Research Institute (Schwartz, Brecher, Whyte, & Klein, 2005). In order to be included in this group, the participant's lesion could not extend past the central sulcus or extend into the inferior temporal lobe. Fig. 1C shows a lesion overlay map, and depicts the degree to which the lesions overlapped with the abstract network from Experiment 1.

Diffusion-tensor imaging data was not collected on these participants. However, the degree to which white matter connectivity to the frontal lobes was affected by the lesion was of particular interest to this study, given the results of the PPI analysis in Experiment 1. In order to estimate whether key white matter tracts were affected, the lesion tracings, warped into standard space, were overlaid onto the John Hopkins University Diffusion Tractography Atlas (Hua et al., 2008). We

Table 4 – Demographic information and performance on a range of memory tasks for participants in the lesion group for Experiment 2. Participants in the neurologically intact control group were matched on age, gender, education and ethnicity, to these participants on an individual basis. Means are shown below. The bottom row shows normal performance (mean and standard deviation) based on an independent sample of 20 older adults with no neurological or psychiatric conditions. WAB AQ = Western Aphasia Battery Aphasia Quotient; PRT = Philadelphia Repetition Test; PNT = Philadelphia Naming Test; STM = Short Term Memory; ISR = Immediate Serial Recall.

	Age	Gender	Education	WAB AQ	Time since injury (in months)	PRT accuracy	PNT accuracy	Nonword repetition accuracy	Category STM span	Phonological STM span	ISR STM span
1	63	F	16	91.5	55	96	86	52	4.44	3.67	3
2	69	M	14	41.4	40	39	25	8	0.5	0.5	1.2
3	53	F	14	87.8	58	95	93	75	3.32	3	3.8
4	52	M	14	65	53	97	55	37	2	3	2.8
5	34	F	19	78.7	41	77	93	32	1.62	2	2
6	67	M	19	94.5*	33	99	98	78	6	3.8	4
7	77	M	21	80.8	72	98	93	70	2.65	6.18	3
8	57	M	12	85.6	62	84	81	35	2.46	5	4
9	63	M	17	84.7	17	98	83	78	2.55	2	3.6
10	54	M	12	76.6	58	66	75	13	2.79	2	2.4
–	59	3 F/7 M	16	76.9	49	84.9	78.2	47.8	2.8	3.1	3.0
Performance in controls ($n = 20$):				97.2 (2.7)	82.6 (10.5)	5.4 (1.3)	6.5 (1.6)	4.8 (.3)			

Note: Participant #6 in the lesion group would be classified as "recovered" by standard WAB AQ criteria (Kertesz, 1982).

examined the superior longitudinal fasciculus (SLF), of which the arcuate fasciculus is part, at a relatively liberal threshold of 50%, meaning that we included voxels in which at least 50% of the JHU sample had identifiable SLF. Of our ten participants, five had lesions overlapping with SLF.

Ten neurologically typical control participants were also recruited, who were individually matched to the participants with lesions on gender, age, education and ethnicity. All control participants scored 26 or higher (mean = 28.4) on the mini-mental status exam (Folstein, Folstein, & McHugh, 1975). All participants were right handed.

Table 4 presents demographic information for the participants in the lesion group. The participants in the lesion group were impaired on measures of short term memory and phonological processing, such as non-word reading. They were relatively less impaired on an object naming test. The performance of the participants in the lesion group on these tests are shown in Table 4, and compared to performance on a normative sample of 20 age-matched control participants.

4.1.2. *Lexical decision task*

Each participant was tested on a simple lexical decision task, using the same words and nonwords used in Experiment 1. In each trial, a word appeared in the center of the screen and the participant was asked to indicate whether the display showed a real word or not a real word. Participants were given unlimited time to respond, using the "1" or "2" key on the top of a typical keyboard with their left forefinger and middle finger.

The number assigned to the word/nonword response was counterbalanced across participants. Once a response was given, the word disappeared and a fixation appeared for 1000 msec, until the start of the next trial. Words were presented in a random order for each participant.

4.1.3. *Spoken-to-written word matching stimuli*

Stimuli were the same as those used by Crutch and Warrington (2005) in their Experiments 4 and 5. The stimuli were a set of abstract and concrete words, collected into arrays that were all related or unrelated to each other. Crutch and Warrington found an interaction of concreteness with type of relationship (similarity-based *vs* thematic/associative). However, we found no interactions with relationship type, so we will not discuss that variable further. Related arrays were made up of four words that were all related to each other in a semantically meaningful way, either taxonomically or through associations. Unrelated arrays were created by shuffling words from related arrays. The full list of stimuli can be found in Supplementary Materials. This resulted in a 2 × 2 design, with the factors being concreteness (abstract/concrete), and relatedness (unrelated/related). The unrelated arrays were made up of the same exact items as the related arrays in the same concreteness condition. For example, all of the words that served as targets and distracters for abstract-related trials, also served as targets and distracters for the abstract-unrelated condition, but were arranged in such a way that the distracters were not related to the target in the unrelated condition. Furthermore, each array, regardless of condition, was created so that it contained no orthographic or phonological neighbors, meaning that words in each array were different from each other by at least two letters or phonemes. This ensured that any differences found between conditions could not be attributed to difficulty with phonologically or orthographically similar distractors.

Each word was recorded in a quiet room by a female native speaker of American English at 44.1 kHz. To make the stimuli more natural, the words were recorded in a carrier phrase "select the word ...". Background noise reduction was carried out using Audacity software (http://audacity.sourceforge.net/), then each word was isolated from the complete recording. The words in each condition were then matched on intensity and did not differ significantly in duration (mean: 823 msec, range: 520–1170 msec).

4.1.4. *Spoken-to-written matching task*

Each testing session began with a set of practice items, made up of unique words not used in the main stimulus set. Neurologically intact control participants were given a minimum of 4 practice trials, but based on pilot testing, the lesion group was given a minimum of 15 practice trials. Participants in the lesion group were also informally pressured to perform as quickly as possible during the practice, based on their own ability, but using a prepared script. After the first practice, participants in both groups were given the opportunity to do another set of practice items or to continue on to the main experiment at their own discretion. Once the main experiment began, the experimenter remained in the room but did not communicate with the participant until the testing session ended.

In the experiment, each trial began with a fixation screen that remained visible for 1000 msec, followed by an array of written words appearing on the screen. Each of the four words appeared in a different corner of the screen, and the arrangement of the array was randomized for each trial. The array was presented for a 1000 msec preview, after which a pre-recorded spoken word was played through the speakers on the computer at a comfortable volume and participants indicated which word on the screen had been spoken. The array remained on screen during the spoken word presentation and until the participant made a response. Healthy control participants made their selection using a computer mouse and viewed the experiment on a 17-inch computer monitor. To simplify the manual response demands, participants in the lesion group viewed the experiment on a 17-inch touch-sensitive monitor with the same display ratio and resolution (1024×768) as the monitor used by the control participants, and made their response by touching the word they wanted to select. A schematic of a single trial is presented in Fig. 2A.

The trials were blocked by array, such that participants viewed the same array of four words over four successive trials, but in each trial they were asked to select a different target and the arrangement of the array on the screen was randomized. The blocks were presented in a pseudo-random counterbalanced order. Altogether there were 520 trials (128 per condition, with the exception of abstract conditions, which had 132 trials due to an extra array in the original stimuli set). The trials were split into two blocks (260 trials each) and all were given the opportunity to take a break between blocks. Practice items preceded both halves of the experiment.

One possible criticism of this design is that the task was not explicitly semantic, and could hypothetically be carried out using only a phonological-to-orthographic mapping strategy. However, the same words were used in the related and unrelated conditions, so the phonological and orthographic demands were exactly matched and only the semantic processing demands differed. Therefore, although phonological or orthographic deficits could have contributed to overall difficulty with the task, only a semantic deficit affecting abstract words could have produced the specific deficit for abstract words when they were presented with semantically related distractors.

The stimuli in the spoken-to-written word matching task were selected because they had previously been validated in similar neuropsychological experiments (Crutch & Warrington, 2005). Using the same words for the related and unrelated arrays provides the optimal test of the effect of relatedness by precisely controlling all other lexical, phonological, and orthographic factors. However, the constraints of the task (creating sets of 4 words that are sufficiently matched on relatedness) make it difficult to match the abstract and concrete words to each other as precisely as they were matched in the lexical decision task. That is, the lexical decision task provides the best test of whether the TPC lesion group exhibited an overall difference between abstract and concrete words whereas the spoken-to-written word matching task provides the best test of our more specific hypothesis that participants with TPC lesions will exhibit impairment when selecting abstract words from semantically related distractors. In statistical terms, this hypothesis predicts a word type (abstract *vs* concrete) by relatedness interaction; that is, presenting words in semantically related arrays compared to unrelated arrays will have a bigger effect on recognition accuracy of abstract words than of concrete words.

4.2. *Results and discussion*

4.2.1. *Lexical decision results*

A two-way repeated measures ANOVA was carried out on the accuracy rates, using participant group (control/lesion) as a between-subjects independent variable, and word type (concrete/abstract) as the within-subjects independent variable. There was a main effect of word type, $F(1,18) = 13.34$, $p < .01$, due to higher accuracy in the concrete words (mean = .97) than in abstract words (mean = .95). There was a marginal effect of participant group, $F(1,18) = 3.83$, $p = .06$, due to higher accuracy in the control group (mean = .98) than in the lesion group (mean = .94). However, overall both groups performed very well on the task. There was a significant interaction between participant group and word type, $F(1,18) = 5.58$, $p < .05$. This effect was due to marginally worse performance in the lesion group compared to controls on abstract words, $t(9) = 2.11$, $p = .06$, but no significant difference in performance between groups on concrete words, both $p > .10$.

These results are consistent with the fMRI connectivity results, in that our sample of participants with lesions in the identified abstract network performed worse than controls on abstract word recognition, but not concrete word identification. However, patients with language impairments are typically more impaired with abstract words regardless of lesion size or location because abstract words were arguably more difficult than concrete words. For this reason, we also examined the data from the spoken-to-written word matching task, which allowed us to examine how semantic competitors affected performance for patients with TPC lesions, compared to their own performance with the same words in a noncompetitive baseline condition.

4.2.2. *Typical control group*

Control participants performed at ceiling on accuracy (>99% correct in all conditions), so their data were analyzed independently from the lesion group, who made substantially more errors (average accuracy across all conditions = 86%). Mean accuracy and RTs in all conditions for both the typical control group and the lesion group can be found in Table 5.

We carried out separate two-way repeated measures ANOVAs on accuracy and RT, using concreteness (concrete, abstract) and relatedness of the arrays (related, unrelated) as factors. There were no statistically significant effect in the accuracy data (all p's > .10). For RT, there was no effect of concreteness, $F(1,9) = 3.14$, $p > .10$ and the interaction between concreteness and relatedness was not significant ($F < 1$). However, there was a main effect of relatedness, $F(1,9) = 5.05$, $p = .05$, due to slightly faster (22 msec) responses in the unrelated conditions than in the related condition, suggesting interference or competition from related words.

4.2.3. *Aphasia patient group*

A two-way repeated measures ANOVA was carried out on the accuracy rates of the participants in the aphasia patient group. There was no main effect of concreteness on accuracy for the patient group, $F < 1$. A marginal main effect of relatedness was found, $F(1,9) = 4.05$, $p = .07$, due to lower accuracy when related words were present as compared to unrelated words (M = .858 *vs* .872). The critical interaction between concreteness and relatedness was significant, $F(1,9) = 5.03$, $p = .05$. This interaction was driven by the significant effect of relatedness on abstract trials, $t(9) = 3.15$, $p < .05$, but not for concrete trials, $t(9) = .15$, $p > .85$ (see Fig. 2B). Specifically, the TPC lesion group performed worse on abstract words in the context of related distractors than in the context of unrelated distractors, but recognition of concrete words was not affected by the relatedness of the distractors.

In a post-hoc analysis, we compared accuracy in participants whose lesions overlapped with the SLF in the Johns Hopkins University DTI Atlas to participants with lesions that did not overlap with SLF. No significant differences were found between these groups in any condition (abstract-unrelated, abstract-related, concrete-unrelated, concrete-unrelated; all p's > .12). This preliminary, post hoc analysis did not reveal an effect of SLF damage on semantic processing, but future finer-grained studies using DTI and functional connectivity measures will be in a stronger position to evaluate the role of SLF in semantic cognition.

Turning to RTs, a main effect of concreteness on RTs was found, $F(1,9) = 9.90$, $p < .05$, due to relatively faster RTs in the concrete conditions compared to the abstract conditions (M = 2778 msec *vs* 2842 msec), reflecting the standard concreteness effect. The main effect of relatedness, and the interaction of concreteness and relatedness were not significant, $F < 1$.

The results of Experiment 2 show that, in our sample, participants with lesions to the left TPC had more difficulty processing abstract words presented in arrays of meaningfully related words than in unrelated arrays, but did not exhibit the same relatedness effect for concrete words. Their overall accuracy for concrete and abstract words was not significantly different, suggesting that the results are not simply due to baseline word difficulty. The selective impairment emerged when participants were required to select abstract words from a set of distracters with semantically similar representations but not when the distracters were semantically unrelated, further implicating a semantic deficit rather than other lexical, phonological, or orthographic factors. Specific difficulty in matching tasks when stimuli are presented with related distracters is a hallmark of semantic deficits in aphasia (for a recent review see Mirman & Britt, 2014) as well as semantic dementia (e.g., Hurley, Paller, Rogalski, & Mesulam, 2012). The results of Experiment 2 suggest that, in our sample, the TPC is specifically involved in representing and *differentiating* abstract, but not concrete, concepts, converging with results from Experiment 1 to indicate that TPC plays an important role in processing abstract concepts.

Participants had to hold the spoken word in short-term memory while reading the response options, so it is possible that STM deficits contributed to our finding. In fact, the participants in the lesion group were relatively impaired on short-term memory tasks (see Table 4). Since abstract words are typically read more slowly than concrete words, they could potentially require more short term memory capacity during the period between hearing the word and making the selection. However, despite the difference in accuracy, participants in the lesion group were, on average, only 84 msec slower with abstract than concrete words in the unrelated condition, and only 44 msec slower in the related condition (see Table 5). These very small differences (relative to an overall average RT of about 2800 msec) are unlikely to produce substantially greater short term memory load for abstract words. Furthermore, providing more lexical context, and therefore more words to remember, decreases RTs in abstract words so that they match concrete words (Schwanenflugel, Akin, & Luh, 1992). It is therefore not clear that short term memory load plays a significant role in the processing differences identified between abstract and concrete words in general. In addition, a specific deficit of holding abstract words

Table 5 – Mean accuracy and response times in Experiment 2. Standard deviations reported in parentheses.

	Accuracy		RT	
	Abstract	Concrete	Abstract	Concrete
Control group				
Unrelated	.998 (.006)	.998 (.006)	2737 (275)	2711 (251)
Related	.998 (.006)	.995 (.011)	2759 (267)	2731 (253)
Lesion group				
Unrelated	.883 (.064)	.859 (.064)	2849 (545)	2765 (449)
Related	.854 (.065)	.861 (.061)	2835 (525)	2791 (505)

(but not concrete words) in STM is an STM-based version of the our general interpretation that TPC damage impairs processing abstract words presented in arrays of meaningfully related words.

Like many neuropsychological studies, this study included a limited sample size of ten participants in each group. The hypothesis was formed *a priori*, based on functional imaging data in an independent sample of healthy adults, so the convergence between the two studies strengthens the conclusions despite the small sample size. Future studies using larger samples and voxel-based lesion symptom mapping techniques, would further strengthen these conclusions.

Finally, in the unrelated conditions in the spoken-to-written word matching task, participants performed slightly, but not statistically significantly, worse on concrete words compared to abstract words. This is in contrast to the results of the lexical decision task, in which the abstract and concrete words were more tightly controlled for a range of psycholinguistic variables, and in which the participants in the lesion group demonstrated the classic greater impairment for abstract words. The participants in the lesion group had relatively mild impairments across our tests, and performance on the concrete-unrelated condition was relatively high (mean accuracy = .859). Thus it is unlikely that a floor effect limited our ability to find a relatedness effect for concrete words.

5. General discussion

The primary goal of this study was to explore neural networks of sites with coordinated activity during abstract and concrete concept processing using fMRI and to validate these findings in participants with focal lesions. Our first experiment found functionally distinct neural networks for abstract and concrete words. Thinking about abstract words activated a functionally connected network involving the aIFG and the AG and posterior STS, while regions in the MTG and left TP were integrated with the left aIFG during concrete word processing. These finding support the idea that abstract and concrete concepts rely on (partially) independent neural processing networks. Our second experiment confirmed our finding that the temporoparietal cortex, which included the AG, was specifically involved in abstract word representation. In our sample, participants with lesions in this area had more difficulty matching abstract spoken words to their printed forms when the words were presented in arrays of semantically related distracters but not when the same words were presented in arrays of unrelated distracters. These participants did not show the same effect of distracter relatedness for concrete words, indicating that they had specific difficulty differentiating the meanings of abstract words but not concrete words. Based on these findings, we propose the existence of two distinct networks for abstract and concrete conceptual representations that overlap in key nodes such as the left aIFG and may at times cooperate depending on the type of semantic information required by a task.

The hypothesis that abstract and concrete concepts depend on at least somewhat independent neural networks sets our proposal apart from other general accounts of the neural representation of semantic memory, in which abstract knowledge is represented within a subset of regions that belong to a larger, more complex concrete semantic network (Binder & Desai, 2011; Pulvermüller, 2013; Rogers et al., 2004). However, independent neural representation for abstract concepts is necessary to account for data from neuropsychological research, specifically the reversal of the concreteness effect.

The reversal of the concreteness effect is demonstrated when an individual with a neurological deficit is impaired on concrete words, but is relatively unimpaired or less impaired on abstract words. The first such case in the literature was reported by Warrington (1975), describing patient A.B., who likely suffered from semantic dementia. A.B. was able to provide definitions for abstract words like *vocation* and *supplication* but could not remember the meaning of concrete words, such as *acorn* or *needle*. Since this report, there have been many case studies of patients with selective impairments for concrete words; a disproportionate number of these cases have been of patients with semantic dementia or herpes simplex encephalitis (Breedin et al., 1994; Cipolotti & Warrington, 1995; Macoir, 2009; Papagno, Capasso, & Miceli, 2009; Sirigu et al., 1991; Warrington & Shallice, 1984). These case studies provide important constraints, but caution is required when drawing inferences from single case studies. For example, it is possible that these patients differed in their premorbid experiences and that this protected abstract representations or made concrete representations more vulnerable, and thus generalizations drawn from these cases may be invalid (Hoffman & Lambon Ralph, 2011). However, two recent patient studies have demonstrated the reversal of the concreteness effect in relatively significant samples. Loiselle et al. (2012) tested a sample of seven patients with ATL resections and found that they were significantly more impaired on concrete words than abstract words, relative to patients with hippocampal resections who were impaired equally on both. Similarly, Yi et al. (2007) examined a sample of 41 semantic dementia patients, and demonstrated that they were more impaired with relatively concrete motion verbs, like *push*, than with abstract cognition verbs, such as *concede*, and the patients performed only marginally worse with abstract, compared to concrete, nouns.

This growing body of evidence for the reversal of the concreteness effect is problematic for theories that propose that abstract concept representations are merely a subset of the features or brain regions involved in representing concrete concepts. The double dissociation of impairment on either abstract or concrete words suggests that abstract concepts are, at least in part, dependent on systems that are independent from concrete processing. Shallice and Cooper (2013) recently suggested that an independent neural system for abstract words is necessary because abstract representations require more complex feature compilations. They argue that abstract words are more flexibly represented and that their features must be more probabilistic and subject to contextual influences, compared to concrete words. For example, a necessary feature of a concrete concept, like “bicycle” is that it *does have wheels*. In contrast, abstract words like *hope* are meaningfully captured by tendencies, such as *likely involves belief in a possibility*. Based on neuroimaging findings in this literature (Binder, Westbury, et al., 2005; Friederici et al., 2003;

Perani et al., 1999; and others discussed in detail in the introduction), Shallice and Cooper suggest the left IFG as a potential site for these probabilistic processes.

We concur with their hypotheses that abstract concepts need a distinct network from concrete concepts and that abstract words require more flexible representational processes, but we instead point to the TPC as a stronger candidate for the site of these abstract representational processes. Our results from the first experiment support this notion of partially independent neural networks for abstract and concrete processing. More specifically, we identified functional connections, including between the aIFG and the AG and posterior STS that were only involved during abstract processing. Other functional connections, such as between the aIFG and the left TP and anterior MTG, were only involved during concrete processing.

5.1. *A role for temporal parietal cortex in abstract conceptual representation*

We found that subregions of the TPC played a significant role in abstract conceptual processing in both the neuroimaging and neuropsychological experiments. This is particularly interesting because this region, particularly the AG, frequently shows greater activation in response to concrete, over abstract, word processing (Binder et al., 2009; Wang et al., 2010). Notably, the area predicted by the interaction term for the abstract condition in our study is significantly anterior to those identified as responsive to concrete concepts, but it is still part of the same general cortical area. Furthermore, just inferior to the TPC in posterior MTG, we found overlapping networks for abstract and concrete conceptual processing.

This raises the question, why do neighboring subregions subserve these separate classes of words? Functional connectivity analyses are not superior to subtraction analyses, and our results should be interpreted in conjunction with the prior neuroimaging literature. Fortunately, our results do not contradict the finding that posterior and somewhat superior regions of the TPC respond to concrete words. A significant behavioral literature suggests that our experience with concrete words and concepts are much richer (Paivio, 1991), and thus increased activation may be in part driven by this experiential information. However, when examining how regions of the brain work together, we observe that a large area in the TPC that selectively links with other critical language areas during abstract word processing. This finding is also supported by TMS research. Papagno, Fogliata, Catricalà, and Miniussi (2009) demonstrated that highly focal transient lesions induced in the posterior STS, within the abstract network that we identified, leads to significant increase in errors recognizing abstract, but not concrete words – and a separate stimulation site in the nearby parietal lobe produced no such effect. Thus, while some subregions in the posterior/dorsal TPC show response to rich, salient lexical stimuli such as concrete words, the larger region is selectively connected to key sites in the cortical language network during abstract word processing.

We therefore propose that the TPC is part of a larger network of regions involved in abstract processing. Specifically, left TPC may be involved in actively forming, updating, and differentiating abstract representations through a complex process that includes combining contextual information (which is flexible and temporal) and associative information (which is relatively stable) to assign meaning to abstract words, and furthermore weighing feature information to distinguish closely-related concepts.

What feature and contextual information the TPC may be accessing specifically for abstract words remains an open question. There is significant evidence that abstract words rely to a greater extent on the verbal context they appear in (Schwanenflugel et al., 1992), and understanding the subtle meanings of abstract concepts can be highly reliant on contextual information and individual experience (Ohlsson & Lehtinen, 1997). There is also evidence that accessing abstract words leads to spreading activation to concepts whose relationship are unique, compared to concrete words (Crutch, 2006; Crutch et al., 2006; Crutch et al., 2013; Crutch & Warrington, 2010), and the TPC may play a role specifically in the associative (rather than categorical) relationships that support abstract word meaning. Recent research suggests that abstract concepts may have an emotional basis (Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011). While this may be true for some types of abstract words and not others (Skipper & Olson, 2014), it reveals a significant variable that is frequently overlooked in the study of abstract semantics. Like concrete concepts, the everyday use of abstract concepts requires us to not only know the dictionary difference between related words, but also to recognize how contextual, relational, and feature information influences appropriate interpretations.

The TPC is traditionally considered heteromodal association cortex, meaning that it is not primarily sensory or motoric, but instead devoted to the integration of multiple sources of information (Binder & Desai, 2011; Mesulam, 1985). Diffusion tensor imaging has revealed that this region is highly interconnected with regions throughout the frontal, parietal and temporal lobes (Turken & Dronkers, 2011). This region has been linked to a range of functions such as translating visual numerical symbols into abstract representations of quantity (Cappelletti, Lee, Freeman, & Price, 2010) and in understanding conceptual metaphors and proverbs, which require assigning an abstract meaning to concrete words and phrases (Chen, Widick, & Chatterjee, 2008; Ramachandran & Hubbard, 2003). Other findings, scattered across diverse literature, also lend to the idea that the left TPC is involved in translating and contextualizing thoughts, ideas, and language. For example, this region has been implicated in following narrative structures (Xu, Kemeny, Park, Frattali, & Braun, 2005), which requires actively updating representations and relationships between them as the story continues. It has been repeatedly shown to activate in response to language-based social stimuli, such as vignettes used in the theory of mind literature (Saxe & Kanwisher, 2003; Völlm et al., 2006). These require understanding and updating abstract representations of shared knowledge, intention, and social goals, as well as sociocultural norms. Furthermore, voxel based lesion symptom mapping has demonstrated that damage to the TPC is associated with impairments in using syntactical information in reversible sentence comprehension ("the man serves the woman," or "the woman serves the man") (Thothathiri, Kimberg, & Schwartz, 2012; see also, Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Race, Ochfeld, Leigh, & Hillis, 2012), a task that requires the use of context to understand the relationships between objects and people.

Patients with lesions in the left TPC tend to make thematically based semantic production errors (Schwartz et al., 2011) and thematic interference in picture naming has been associated with activation in the left AG (de Zubicaray et al., 2013). It is notable that thematic relationships typically do not rely on physical features of concepts (Estes et al., 2011) and may be of particular importance for abstract conceptual knowledge (Crutch & Warrington, 2005). Even as early as the 1950's, MacDonald Critchley, describing the work by Sir Henry Head, commented that left parietal lobe lesions led to defects that were characterized "by lack of recognition of the full significance of words and phrases apart from their immediate verbal meaning" (Critchley, 1953).

All of these findings point to the TPC involvement in a diverse range of cognitive tasks, all of which appear to be united by the need for flexible translation between representations and contextualizing of abstract conceptual representations. While both concrete and abstract semantic knowledge are associated with the TPC, the specific functions of flexibly modifying representations, gleaning information from context, representing relationships, and making thematic associations may be particularly important for abstract concepts (Crutch & Warrington, 2005; Shallice & Cooper, 2013). The TPC is not the "site" of abstract concepts, but rather its general role in semantic memory is crucial for abstract conceptual representation.

5.2. *The importance of white matter and connectivity with the TPC*

In Experiment 1, we found functional connectivity between the left inferior frontal lobe and the left TPC during abstract word processing. In Experiment 2, we found that lesions to the left TPC, in a relatively small sample of participants, led to impaired performance in selecting abstract words from semantically related distractors. However, we were unable to determine whether structural connectivity between the left frontal lobes and TPC was responsible for this impairment. This is in large part because we lack diffusion tensor data for the participants, and could only estimate whether underlying white matter tracts were affected based on an atlas. Based on the functional imaging findings, we hypothesize that the connectivity between these regions that support abstract conceptual processing are flexible, and the role of the TPC is to synchronize with frontal regions specifically when accessing abstract concepts. However, it is not clear that this functional connectivity should implicate a single white matter tract such as the SLF or arcuate fasciculus. A recent study of 99 participants with aphasia following left hemisphere stroke found that deficits in recognizing semantic relationships were associated with damage to a frontal "white matter bottleneck" that affected the inferior fronto-occipital fasciculus, the uncinated fasciculus, and the anterior thalamic radiations (Mirman, Chen, et al., 2015; Mirman, Zhang, Wang, Branch Coslett, & Schwartz, 2015). Mirman et al. interpreted this result to mean that semantic cognition requires widespread connectivity between frontal regions and other brain regions involved in semantic memory, rather than a single connection between any two regions. Future studies will need to collect more detailed structural and functional connectivity data in order to fully evaluate these hypotheses.

5.3. *A possible role for the ventral ATL in concrete conceptual representation*

Our neuroimaging results revealed that the left ventral and ATLs may be functionally connected to a wider semantic network during concrete semantic processing. The region has previously been identified as involved in integrating visual and semantic information (Skipper, Ross, & Olson, 2011) and receives projections from higher order visual cortex as the endpoint of the ventral visual stream (Blaizot et al., 2010; Ding, Van Hoesen, Cassell, & Poremba, 2009).

This region is perhaps best understood through the results of semantic dementia, a neurodegenerative disease associated with widespread cell loss that is more concentrated in the ventral ATLs (Hodges, Patterson, Oxbury, & Funnell, 1992), especially perirhinal cortex (Mion et al., 2010). Patients with semantic dementia demonstrate dramatic semantic memory loss, not limited to any single modality. When asked to provide definitions for concrete objects, patients with semantic dementia will focus on functional information and fail to produce visual feature information (Lambon Ralph, Graham, & Patterson, 1999; McCarthy & Warrington, 1988), though they are markedly impaired on both.

The reversal of the concreteness effect also has interesting implications for the region, as the reversal appears disproportionately in cases of semantic dementia and herpes simplex encephalitis, which tend to cause focal medial and ATL damage (Kapur et al., 1994). Some have demonstrated that semantic dementia patients do typically perform worse with abstract than with concrete words (Hoffman & Lambon Ralph, 2011). However, the reversal of the concreteness effect does not require better performance on abstract words compared to concrete, because even the healthy brain is biased towards concrete words and a significant impairment for concrete words alone could be demonstrated even if performance is better for them than for abstract words. That is, a reversal of the concreteness effect can be demonstrated through a greater impairment for concrete words than abstract words, relative to neurologically intact participants. Furthermore, the concreteness effect studies in SD rarely include a control group or baseline task, thus it is not possible to compare these results to the performance of the SD patients with any other kind of impairment of the semantic system. Our study differed from these because we employed a baseline (no semantically-related distractors) task, allowing us to assess the participants' semantic impairment with abstract words against their own performance in a nonsemantic condition.

A recent study compared the performance of seven patients who had undergone resection of the ATL to a group of 15 patients with unilateral surgical resection of the amygdala and hippocampus (Loiselle et al., 2012). Compared to healthy controls, both patient groups were significantly impaired on both abstract and concrete words. However, when the scores were normalized, it was discovered that patients in the anterior temporal lobectomy group were significantly more impaired on concrete than abstract words, while the hippocampectomy patients were equally impaired on both. Although these are relative effects, and not an absolute reversal, the evidence points to a possible role for the TP/ATL, specifically ventral subregions, in processing concrete and highly imageable semantic stimuli. If our experimental approach were used to test participants with TP/ATL damage, it may similarly reveal a greater effect of distractor relatedness on concrete words than on abstract words; that is, a complementary relatedness-by-concreteness interaction to the one we observed for individuals with TPC damage.

5.4. *The QDR theory*

The spoken-to-written word matching task used in Experiment 2 also tested the QDR theory for abstract and concrete concept representation (Crutch, 2006; Crutch et al., 2006; Crutch et al., 2013; Crutch & Warrington, 2010), but we failed to support the QDR hypothesis. Specifically, we found no interaction between concreteness (abstract/concrete) and type of relationship (thematic/taxonomic). Other recent neuropsychological and behavioral studies have also failed to find support for the QDR theory as well (Brozdowski et al., 2013; Hamilton & Coslett, 2008; Papagno et al., 2013). However, the evidence for the QDR model is heavily based on patients with large non-focal lesions (Crutch, 2006; Crutch et al., 2006) and thus our patients may not have had severe enough impairments to show the critical effect. Furthermore, our sample, and effects, were relatively small, and we may have lacked the power to identify the effect predicted by the QDR model. Although not conclusive, our negative results add to the ongoing evaluation of the QDR theory.

5.5. *Conclusions*

In the study of semantic and conceptual knowledge, abstract concepts are frequently overlooked, and studies of the neural basis of abstract words have produced diverse and difficult to interpret results. However, the double dissociation that can be found in the neuropsychological patients, where most are impaired on abstract words, but some are unusually impaired on concrete words, suggests that a partially distinct system for abstract words is necessary. Using functional connectivity analyses of neuroimaging data from neurologically intact participants, we identified two unique networks for abstract and concrete word knowledge. The abstract network involved functional connections between aIFG and subregions of the temporoparietal cortex, including the AG and posterior STS. In a second experiment, we found that participants with lesions in the left temporoparietal cortex had degraded representations for abstract concepts. We propose that abstract concepts are represented through neural networks that are partly independent of those involved in concrete conceptual representation, and that the temporoparietal cortex may be involved in flexible translation and contextual updating of abstract representations.

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Supplementary data

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REFERENCES

Adorni, R., & Proverbio, A. M. (2012). The neural manifestation of the word concreteness effect: an electrical neuroimaging study. *Neuropsychologia, 50*, 880–891.

Awh, E., Jonidas, J., Smith, E. E., Schumacher, E. J., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: evidence from positron emission tomography. *Psychological Science, 7*, 25–31.

Badgaiyan, R. D., Schacter, D. L., & Alpert, N. M. (2002). Retrieval of relational information: a role for the left inferior prefrontal cortex. *NeuroImage, 17*, 393–400.

Badre, D., & Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and Cognitive Neuroscience Reviews, 1*, 206–218.

Balota, D. A., Yap, M. J., Cortese, M. J., Hutchison, K. A., Kessler, B., Loftis, B., et al. (2007). The English lexicon project. *Behavior Research Methods, 39*, 445–459.

Beauregard, M., Chertkow, H., Bub, D., Murtha, S., Dixon, R., & Evans, A. (1997). The neural substrate for concrete, abstract and emotional word lexica: a positron emission tomography study. *Journal of Cognitive Neuroscience, 9*, 441–461.

Bedny, M., Dravida, S., & Saxe, R. (2013). Shindigs, brunches, and rodeos: the neural basis of event words. *Cognitive, Affective and Behavioral Neuroscience*. http://dx.doi.org/10.3758/s13415-013-0217-z.

Binder, J., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*, 527–536.

Binder, J., Desai, R. H., Graves, W. W., & Conant, L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*, 2767–2796.

Binder, J., Medler, D. A., Desai, R., Conant, L. L., & Liebenthal, E. (2005). Some neurophysiological constraints on models of word naming. *NeuroImage, 27*, 677–693.

Binder, J., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience, 17*, 905–917.

Blaizot, X., Mansilla, F., Insausti, A. M., Constans, J. M., Salinas-Alaman, A., Pro-Sistiaga, P., et al. (2010). The human parahippocampal region: I. Temporal pole cytoarchitectonic and MRI correlation. *Cerebral Cortex, 20*, 2198–2212.

Bleasedale, F. A. (1987). Concreteness-dependent associative priming: separate lexical organization for concrete and abstract words. *Journal of Experimental Psychology: Learning, Memory and Cognition, 13*, 582–594.

Bodke, A. L., Tagamets, M., Friedman, R. B., & Horwitz, B. (2001). Functional interactions of the inferior frontal cortex during the processing of word and word-like stimuli. *Cortex, 30*, 609–617.

Bonner, M. F., Vesely, L., Price, C., Anderson, C., Richmond, L., Farag, C., et al. (2009). Reversal of the concreteness effect in semantic dementia. *Cognitive Neuropsychology, 26*, 568–579.

Breedin, S. D., Saffran, E. M., & Coslett, H. B. (1994). Reversal of the concreteness effect in a patient with semantic dementia. *Cognitive Neuropsychology, 11*, 617–660.

Brozdowski, C. R., Gordils, J., & Magnuson, J. S. (2013). Contra the qualitatively different representation hypothesis (QDRH), concrete concepts activate associates faster than abstract concepts. *Abstracts of the Psychonomic Society, 18*, 68.

Brysbaert, M., & New, B. (2009). Moving beyond Kučera and Francis: a critical analysis of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods, 41*, 977–990.

Cappelletti, M., Lee, H. L., Freeman, E. D., & Price, C. J. (2010). The role of the right and left parietal lobes in the conceptual processing of numbers. *Journal of Cognitive Neuroscience, 22*, 331–346.

Chen, E., Widick, P., & Chatterjee, A. (2008). Functional-anatomical organization of predicate metaphor processing. *Brain and Language, 107*, 194–202.

Cipolotti, L., & Warrington, E. K. (1995). Semantic memory and reading abilities: a case report. *Journal of the International Neuropsychological Society, 1*, 104–110.

Coltheart, M. (1980). Deep Dyslexia: a right-hemisphere hypothesis. In M. Coltheart, K. Patterson, & J. C. Marshall (Eds.), *Deep dyslexia* (pp. 326–380). London: Routledge & Kegan Paul.

Coltheart, M. (1981). The MRC psycholinguistic database. *Quarterly Journal of Experimental Psychology, 33A*, 497–505.

Costafreda, S. G., Yu, C. H. Y., Lee, L., Everitt, B., Brammer, M. J., & David, A. S. (2006). A systematic review and quantitative appraisal of fMRI studies of verbal fluency: role of the left inferior frontal gyrus. *Human Brain Mapping, 27*, 799–810.

Critchley, M. (1953). *The parietal lobes*. Oxford: Williams and Wilkins.

Crutch, S. J. (2006). Qualitatively different semantic representations for abstract and concrete words: further evidence from the semantic reading errors of deep dyslexic patients. *Neurocase, 12*, 91–97.

Crutch, S. J., Ridha, B. H., & Warrington, E. K. (2006). The differential frameworks underlying abstract and concrete knowledge: evidence from a bilingual patient with a semantic refractory access dysphasia. *Neurocase, 12*, 151–163.

Crutch, S. J., Troche, J., Reilly, J., & Ridgeway, G. R. (2013). Abstract conceptual feature ratings: the role of emotion, magnitude, and other cognitive domains in the organization of abstract conceptual knowledge. *Frontiers in Human Neuroscience, 7*(186), 1–14.

Crutch, S. J., & Warrington, E. K. (2005). Abstract and concrete concepts have structurally different frameworks. *Brain, 128*, 615–627.

Crutch, S. J., & Warrington, E. K. (2010). The differential dependence of abstract and concrete words upon associative and similarity-based information: complementary interference and facilitation effects. *Cognitive Neuropsychology, 27*, 46–71.

Davachi, L., Maril, A., & Wagner, A. D. (2001). When keeping in mind supports later bringing to mind: neural markers of phonological rehearsal predict subsequent remembering. *Journal of Cognitive Neuroscience, 13*, 1059–1070.

Day, J. (1977). Right-hemisphere language processing in normal right-handers. *Journal of Experimental Psychology: Human Perception and Performance, 3*, 518–528.

Demb, J. B., Desmond, J. E., Wagner, A. D., Vaidya, C. J., Glover, G. H., & Gabrieli, J. D. E. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *Journal of Neuroscience, 15*, 5870–5878.

Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience, 15*, 71–84.

Ding, S. L., Van Hoesen, G. W., Cassell, M. D., & Poremba, A. (2009). Parcellation of the human temporal polar cortex: a combined analysis of multiple cytoarchitectonic, chemoachitectonic and pathological markers. *Journal of Computational Neurology, 514*, 595–623.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*, 145–177.

D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., et al. (1997). A functional MRI study of mental image generation. *Neuropsychologia, 35*, 725–730.

Estes, Z., Galonka, S., & Jones, L. L. (2011). Thematic thinking: the apprehension and consequences of thematic relations. In B. Ross (Ed.), *The psychology of learning and motivation* (vol. 54, pp. 249–294). Burlington: Academic Press.

Fiebach, C. J., & Friederici, A. D. (2003). Processing concrete words: fMRI evidence against a specific right-hemisphere involvement. *Neuropsychologia, 42*, 62–70.

Fliessbach, K., Weis, S., Klaver, P., Elger, C. E., & Weber, B. (2006). The effect of word concreteness on recognition memory. *NeuroImage, 32*, 1413–1421.

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). Mini-mental state: a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research, 12*, 189–198.

Friederici, A. D., Opitz, B., & von Cramon, Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cerebral Cortex, 10*, 698–705.

Friederici, A. D., Rüschemeyer, S., Hahne, A., & Fiebach, C. J. (2003). The role of the left inferior frontal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral Cortex, 13*, 170–177.

Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysical and modulatory interactions in neuroimaging. *NeuroImage, 6*, 218–229.

Gabrieli, J. D. E., Poldrack, R. A., & Desmond, J. E. (1998). The role of the left inferior frontal cortex in language and memory. *Proceedings of the National Academy of Sciences USA, 95*, 906–913.

Goodglass, H., Hyde, M. R., & Blumstein, S. (1969). Frequency, picturability and availability of nouns in aphasia. *Cortex, 5*, 104–119.

Gough, P. M., Nobre, A. C., & Devlin, J. T. (2005). Dissociating linguistic processes in the left inferior frontal cortex with transcranial magnetic stimulation. *The Journal of Neuroscience, 25*, 8010–8016.

de Groot, A. M. B. (1989). Representational aspects of word imageability and word frequency as assessed through word association. *Journal of Experimental Psychology: Learning, Memory and Cognition, 15*, 824–845.

Grossman, M., Smoth, E. E., Koenig, P., Glosser, G., Devita, C., Moore, P., et al. (2002). The neural basis for categorization in semantic memory. *NeuroImage, 17*, 1549–1561.

Gvion, A., & Friedmann, N. (2013). A selective deficit in imageable concepts: a window to the organization of the conceptual system. *Frontiers in Human Neuroscience, 7*(226), 1–13.

Hamilton, A. C., & Coslett, H. B. (2008). Refractory access disorders and the organization of concrete and abstract semantics: do they differ? *Neurocase, 14*, 131–140.

Hodges, J. R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia: progressive fluent aphasia with temporal lobe atrophy. *Brain, 115*, 1783–1806.

Hoffman, P., & Lambon Ralph, M. A. (2011). Reverse concreteness effects are not a typical feature of semantic dementia: evidence for the hub-and-spoke model of conceptual representation. *Cerebral Cortex, 21*, 2103–2112.
Holcomb, P. J., Kounios, J., Anderson, J. W., & West, W. C. (1999). Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electrophysiological investigation. *Journal of Experimental Psychology: Learning, Memory and Cognition, 25*, 721–742.
Howell, J. R., & Bryden, M. P. (1987). The effects of word orientation and imageability on visual half-field presentation with a lexical decision task. *Neuropsychologia, 25*, 527–538.
Hua, K., Zhang, J., Wakana, S., Jiang, H., Li, X., Reich, D. S., et al. (2008). Tract probability maps in stereotaxic spaces: analyses of white matter anatomy and tract-specific quantification. *NeuroImage, 39*, 336–347.
Hurley, R. S., Paller, K. A., Rogalski, E. J., & Mesulam, M. M. (2012). Neural mechanisms of object naming and word comprehension in primary progressive aphasia. *Journal of Neuroscience, 32*, 4848–4855.
James, C. T. (1975). The role of semantic information in lexical decisions. *Journal of Experimental Psychology: Human Perception and Performance, 1*, 130–136.
Jenkinson, M., Beckmann, C. F., Behrens, T. E., Woolrich, M. W., & Smith, S. M. (2012). FSL. *NeuroImage, 62*, 782–790.
Kalénine, S., Peyrin, C., Pichat, C., Segebarth, C., Bonthoux, F., & Baciu, M. (2009). The sensory-motor specificity of taxonomic and thematic conceptual relations: a behavioral and fMRI study. *NeuroImage, 44*, 1152–1162.
Kanske, P., & Kotz, S. A. (2007). Concreteness in emotional words: ERP evidence from a hemifield study. *Brain Research, 1148*, 138–148.
Kapur, N., Barker, S., Burrows, E. H., Ellison, D., Brice, J., Illis, L. S., et al. (1994). Herpes simplex encephalitis: long term magnetic resonance imaging and neuropsychological profile. *Journal of Neurology, Neurosurgery and Psychiatry, 57*, 1334–1342.
Katz, R. B., & Goodglass, H. (1990). Deep dyslexia: analysis of a rare form of repetition disorder. *Journal of Brain and Language, 39*, 153–185.
Kiehl, K. A., Liddle, P. F., Smith, A. M., Mendrek, A., Forster, B. B., & Hare, R. D. (1999). Neural pathways involved in the processing of concrete and abstract words. *Human Brain Mapping, 7*, 225–233.
Kounios, J., & Holcomb, P. J. (1994). Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. *Journal of Experimental Psychology: Learning, Memory and Cognition, 20*, 804–823.
Kousta, S. T., Vigliocco, G., Vinson, D. P., Andrews, M., & Del Campo, E. (2011). The representation of abstract words: why emotion matters. *Journal of Experimental Psychology: General, 140*, 14–34.
Kroll, J. F., & Merves, J. S. (1986). Lexical access for concrete and abstract words. *Journal of Experimental Psychology: Learning, Memory and Cognition, 12*, 92–107.
Kučera, H., & Francis, W. N. (1967). *Computational analysis of present day American English*. Providence: Brown University Press.
Kuperman, V., Stadthagen-Gonzalez, H., & Brysbaert, M. (2012). Age-of-acquisition ratings for 30 thousand English words. *Behavior Research Methods, 44*, 978–990.
Lambon Ralph, M. A., Graham, K. S., & Patterson, K. (1999). Is a picture worth a thousand words? Evidence from concept definitions by patients with semantic dementia. *Brain and Language, 70*, 309–335.
Loiselle, M., Rouleau, I., Nguyen, D. K., Dubeau, F., Macoir, J., Whatmough, C., et al. (2012). Comprehension of concrete and abstract words in patients with selective anterior temporal lobe resection and in patients with selective amygdalo-hippocampectomy. *Neuropsychologia, 50*, 630–639.
Macoir, J. (2009). Is a plum a memory problem? Longitudinal study of the reversal of concreteness effect in a patient with semantic dementia. *Neuropsychologia, 47*, 518–535.
Maguire, M. J., Hirsh-Pasek, K., & Michnick Golinkoff, R. (2006). A unified theory of word learning: putting verb acquisition in context. In K. Hirsh-Pasek, & R. Michnick Golinkoff (Eds.), *Action meets world: How children learn verbs* (pp. 364–391). Oxford University Press.
Martin, N., & Saffran, E. M. (1992). A computational account of deep dyslexia: evidence from a single case study. *Brain and Language, 43*, 240–274.
McCarthy, R. A., & Warrington, E. K. (1988). Evidence for modality-specific meaning systems in the brain. *Nature, 344*, 428–430.
Mestres-Missé, A., Münte, T. F., & Rodriguez-Fornells, A. (2009). Functional neuroanatomy of contextual acquisition of concrete and abstract words. *Journal of Cognitive Neuroscience, 2*, 2154–2217.
Mesulam, M. (1985). Patterns in behavioral neuroanatomy: association areas, the limbic system, and hemispheric specialization. In M. Mesulam (Ed.), *Principles of behavioral neurology* (pp. 1–70). Davis.
Mion, M., Patterson, K., Acosta-Cabronero, J., Pengas, G., Izquierdo-Garcia, D., Hong, Y. T., et al. (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain, 133*, 3256–3268.
Mirman, D., & Britt, A. E. (2014). What we talk about when we talk about access deficits. *Philosophical Transactions of the Royal Society B: Biological Sciences, 369*. http://dx.doi.org/10.1098/rstb.2012.0388.
Mirman, D., Chen, Q., Zhang, Y., Wang, Z., Faseyitan, O., Coslett, H. B., et al. (2015). Neural organization of spoken language revealed by lesion-symptom mapping. *Nature Communications*. http://dx.doi.org/10.1038/ncomms7762.
Mirman, D., & Graziano, K. M. (2012). Damage to temporo-parietal cortex decreases incidental activation of thematic relations during spoken word recognition. *Neuropsychologia, 50*, 1990–1997.
Mirman, D., Zhang, Y., Wang, Z., Branch Coslett, H., & Schwartz, M. F. (2015). The ins and outs of meaning: behavioral and neuroanatomical dissociation of semantically-driven word retrieval and multimodal semantic recognition in aphasia. *Neuropsychologia*. http://dx.doi.org/10.1016/j.neuropsychologia.2015.02.014.
Moseley, R., Carota, F., Hauk, O., Mohr, B., & Pulvermüller, F. (2012). A role for the motor system in binding abstract emotional meaning. *Cerebral Cortex, 22*, 1634–1647.
Nittono, H., Suehiro, M., & Hori, T. (2002). Word imageability and N400 in an incidental memory paradigm. *International Journal of Psychophysiology, 44*, 219–229.
Noppeney, U., & Price, C. J. (2003). Functional imaging of the semantic system: retrieval of sensory-experienced and verbally learned knowledge. *Brain and Language, 84*, 120–133.
Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *NeuroImage, 22*, 164–170.
Ohlsson, S., & Lehtinen, E. (1997). Abstraction and the acquisition of complex ideas. *International Journal of Educational Research, 27*, 37–48.
Paivio, A. (1991). Dual coding theory: retrospect and current status. *Canadian Journal of Psychology, 45*, 255–287.
Papagno, C., Capasso, R., & Miceli, G. (2009). Reversed concreteness effect for nouns in a subject with semantic dementia. *Neuropsychologia, 47*, 1138–1148.
Papagno, C., Fogliata, A., Catricalà, E., & Miniussi, C. (2009). The lexical processing of abstract and concrete nouns. *Brain Research, 1263*, 78–86.
Papagno, C., Martello, G., & Mattavelli, G. (2013). The neural correlates of abstract and concrete words: evidence from brain damaged patients. *Brain Sciences, 3*, 1229–1243.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? the representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*, 976–987.
Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of verbal working memory. *Nature, 362*, 342–345.
Perani, D., Cappa, S. F., Schnur, T., Tettamanti, M., Collina, S., Rosa, M. M., et al. (1999). The neural correlates of verb and noun processing: a PET study. *Brain, 122*, 2337–2344.
Pexman, P. M., Hargreaves, I. S., Edwards, J. D., Henry, L. C., & Goodyear, B. G. (2007). Neural correlates of concreteness in semantic organization. *Journal of Cognitive Neuroscience, 19*, 1407–1419.
Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage, 10*, 15–35.
Pulvermüller, F. (2013). Meaning and the brain: the neurosemantics of referential, interactive, and combinatorial knowledge. *Journal of Neurolinguistics, 25*, 423–459.
Race, D. S., Ochfeld, E., Leigh, R., & Hillis, A. E. (2012). Lesion analysis of cortical regions associated with nonreversable and reversable yes/no questions. *Neuropsychologia, 50*, 1946–1953.
Ramachandran, V. S., & Hubbard, E. M. (2003). The phenomenology of synaethesia. *Journal of Consciousness Studies, 10*, 49–57.
Renoult, L., Brodeur, M. B., & Debruille, J. B. (2010). Semantic processing of highly repeated concepts presented in single-word trials: electrophysiological and behavioral correlates. *Biological Psychology, 84*, 206–220.
Rogers, T. T., Lambon Ralph, M. A., Gerrard, P., Bozeat, S., McClelland, J. L., & Hodges, J. R. (2004). Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychological Review, 111*, 205–235.
Ross, L. A., & Olson, I. R. (2010). Social cognition and the anterior temporal lobes. *NeuroImage, 49*, 3452–3462.
Rubin, D. C. (1980). 51 properties of 125 words: a unit analyses of verbal behavior. *Journal of Verbal Learning and Verbal Behavior, 19*, 736–755.
Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *NeuroImage, 27*, 188–200.
Saffran, E. M., & Martin, N. (1990). Neuropsychological evidence for lexical involvement in short-term memory. In G. Vallar, & T. Shallice (Eds.), *Neuropsychological impairments of short-term memory* (pp. 145–166). Cambridge: Cambridge University Press.
Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: the role of the temporo-parietal junction in "theory of mind." *NeuroImage, 19*, 1835–1842.
Schwanenflugel, P. J., Akin, C., & Luh, W. M. (1992). Context availability and the recall of abstract and concrete words. *Memory & Cognition, 20*, 96–104.
Schwartz, M. F., Brecher, A. R., Whyte, J., & Klein, M. G. (2005). A patient registry for cognitive rehabilitation research: a strategy for balancing patients' privacy rights with researchers' need for access. *Archives of Physical Medicine and Rehabilitation, 86*, 1807–1814.
Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., et al. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *PNAS, 108*, 8520–8524.
Shallice, T., & Cooper, R. (2013). Is there a semantic system for abstract words? *Frontiers in Human Neuroscience, 7*(175), 1–10.
Sirigu, A., Duhamel, J. R., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. *Brain, 114*, 2555–2573.
Skipper, L. M., & Olson, I. R. (2014). Semantic memory: distinct neural representations for abstractness and valence. *Brain and Language, 130*, 1–10.
Skipper, L. M., Ross, L. A., & Olson, I. R. (2011). Sensory and semantic category subdivisions within the anterior temporal lobes. *Neuropsychologia, 49*, 3419–3429.
Tettamanti, M., Manenti, R., Della Rosa, A. P., Falini, A., Perani, D., Cappa, S. F., et al. (2008). Negation and the brain: modulating action representations. *NeuroImage, 43*, 358–367.
Thotharthiri, M., Kimberg, D. Y., & Schwartz, M. F. (2012). The neural basis of reversible sentence comprehension: evidence from voxel-based lesion-symptom mapping. *Journal of Cognitive Neuroscience, 24*, 212–222.
Tolentino, L. C., & Tokowicz, N. (2009). Are pumpkins better than heaven? an ERP investigation of order effects in the concrete-word advantage. *Brain and Language, 110*, 12–22.
Tsai, P., Yu, B. H., Lee, C., Tzeng, O. J., Hung, D. L., & Wu, D. H. (2009). An event-related potential study of the concreteness effect between Chinese nouns and verbs. *Brain Research, 1253*, 149–160.
Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analysis. *Frontiers in Systems Neuroscience, 5*(1), 1–20.
Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., et al. (2006). Neuronal correlates of theory of mind and empathy: a functional magnetic resonance imaging study in a nonverbal task. *NeuroImage, 29*, 90–98.
Wallentin, M., Østergaard, S., Lund, T. E., Østergaard, L., & Roepstorff, A. (2005). Concrete spatial language: see what I mean? *Brain and Language, 92*, 221–223.
Wang, J., Conder, J. A., Blitzer, D. N., & Shinkareva, S. V. (2010). Neural representation of abstract and concrete concepts: a meta-analysis of neuroimaging studies. *Human Brain Mapping, 21*, 1459–1468.
Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology, 27*, 635–657.
Warrington, E. K. (1981). Concrete word dyslexia. *British Journal of Psychology, 72*, 175–196.
Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain, 107*, 829–853.
West, W. C., & Holcomb, P. J. (2000). Processing of concrete and abstract words: an electrophysiological investigation. *Journal of Cognitive Neuroscience, 12*, 1024–1037.
Whaley, C. P. (1978). Word-nonword classification times. *Journal of Verbal Learning and Verbal Behavior, 17*, 143–154.
Wise, R. J. S., Howard, D., Mummery, C. J., Fletcher, P., Leff, A., Büchel, C., et al. (2000). Noun imageability and the temporal lobes. *Neuropsychologia, 38*, 985–994.
Xu, J., Kemeny, S., Park, G., Frattali, C., & Braun, A. (2005). Language in context: emergent features of word, sentence, and narrative comprehension. *NeuroImage, 25*, 1002–1015.
Yi, H., Moore, P., & Grossman, P. (2007). Reversal of the concreteness effect in patients with semantic dementia. *Neuropsychology, 21*, 9–19.
Zhang, Q., Guo, C., Ding, J., & Wang, Z. (2006). Concreteness effects in the processing of Chinese words. *Brain and Language, 96*, 59–68.
de Zubicaray, G. I., Hansen, S., & McMahon, K. L. (2013). Differential processing of thematic and categorical conceptual relations in spoken word production. *Journal of Experimental Psychology: General, 142*, 131–142.