



The hierarchical organization of semantic memory: Executive function in the processing of superordinate concepts

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ABSTRACT

Research on the processing of objects at different hierarchical levels has suggested that understanding superordinate concepts (e.g. *fruit*), relative to basic level concepts (e.g. *apple*), requires greater semantic control demands. Yet, it is unclear which factors underlie this difference in executive processing. We built on previous research showing that superordinate concepts have less shared features among their members and therefore may involve higher semantic control requirements. To test this hypothesis, we developed an fMRI study in which we orthogonally manipulated feature sharedness (more shared vs. less shared) and concept level (superordinate vs. basic) in a sentence verification task. Sentences involving less shared features, relative to more shared features, significantly engaged the L lateral PFC. Importantly, sentences that included superordinate concepts, relative to those with basic level concepts, also revealed a stronger response in L lateral PFC, along with posterior temporal gyrus activation. There was also a significant interaction between feature sharedness and concept level in several PFC regions and L posterior temporal areas. The results suggest that relative to basic level concepts, processing superordinate concepts requires extra semantic control in L lateral PFC to coordinate information that is less shared by other members of the category level. These findings demonstrate that feature sharedness impacts the neural basis of semantic knowledge, and is a critical dimension in the processing of superordinate concepts.

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Introduction

In their seminal work on object categorization, Rosch and colleagues (Rosch, 1978; Rosch et al., 1976) showed that people are able to categorize objects at different hierarchical levels. For example, a *Labrador* may be called a *Labrador* (subordinate level), a *dog* (basic level) or an *animal* (superordinate level). This influential work prompted a large body of studies on the nature of superordinate and basic level concepts and, more recently, how they are processed in the brain.

Data from neuropsychological research suggest that categorizing objects at different levels of specificity requires different cognitive and neural processes. Patients with semantic dementia (SD), a progressive disorder characterized by atrophy of the bilateral anterior temporal lobes, exhibit a pattern of knowledge where general concepts are relatively spared compared to more specific ones (Hodges et al., 1994; Warrington, 1975). For instance, SD patients may

recognize a *zebra* as an *animal*, but cannot identify it as a *zebra*. Moreover, features that are highly shared by the members of the category (e.g. *has four legs*) are often preserved, but those that are less shared (e.g. *has stripes*) are lost (Bozeat et al., 2003; Laisney et al., 2011; Rogers and Patterson, 2007). The opposite pattern, i.e. better performance at basic than superordinate level processing, has also been observed, albeit less frequently (e.g. Crutch and Warrington, 2008; Humpreys and Forde, 2005; Jónsdóttir and Martin, 1996). This deficit has been observed in stroke aphasia that results from prefrontal and temporo-parietal damage, but rarely affects the anterior temporal lobes (Jefferies and Lambon Ralph, 2006). For example, Humpreys and Forde (2005) reported a patient who suffered bilateral damage to frontal, temporal, and occipital cortices, whose performance in a word-picture matching task was significantly better when the word denoted a basic than superordinate level concept. Crutch and Warrington (2008) documented a group of four patients with a left middle cerebral artery stroke that resulted in lesions to left frontal and/or left parietal regions. All patients showed inferior performance in the superordinate (e.g. *mammal*) compared to the basic condition (e.g. *dog*), but also less accurate performance in the basic level relative to the even more specific, subordinate level (e.g. *Dalmatian*). Taken together, the semantic deficits revealed by SD and stroke aphasia patients suggest that understanding concepts at different levels may require distinct mechanisms. While basic level processing seems to rely more on the anterior temporal lobe, superordinate

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processing has been distinctively associated with left frontal and temporo-parietal areas.

In line with the patient's data, neuroimaging studies with healthy volunteers have revealed distinct neural mechanisms underlying different levels of object processing. In an fMRI study, Tyler and colleagues (Tyler et al., 2004) reported that, while both basic and superordinate naming of objects involved posterior temporal regions, only basic level concepts recruited the anterior temporal cortex. In a similar vein, Rogers et al. (2005) found greater activation in the lateral temporal cortex when participants identified objects at specific levels (e.g. *dog* or *Labrador*) relative to a more general level (e.g. *animal*). Some studies have also shown that processing superordinate concepts, relative to basic level concepts, may require increased activation in prefrontal cortex (PFC). For instance, Tyler et al. (2004) have reported activation in the frontal gyrus for superordinate compared to basic level naming. Similarly, electrophysiological data have revealed that superordinate categorizations produce a larger frontal negativity relative to basic level categorizations indicating increased semantic processing (Tanaka et al., 1999). Several fMRI studies have linked the left PFC to controlled semantic retrieval (Badre et al., 2005; Domb et al., 1995; Dobbins and Wagner, 2005; Thompson-Schill et al., 2005; Wagner et al., 2001). Specifically, it has been proposed that the left lateral PFC mediates retrieval and/or selection of semantic information represented elsewhere in the brain, notably in anterior and inferior temporal regions (Dobbins and Wagner, 2005; Lambon Ralph et al., 2010; Wagner et al., 2001; Whitney et al., 2011). Under this view, the difficulty of stroke aphasia patients to recognize superordinate categories may reflect a disruption to processes that mediate and control semantic knowledge rather than a loss of knowledge per se (Crutch and Warrington, 2008; Humpreys and Forde, 2005; Jefferies and Lambon Ralph, 2006; Jefferies et al., 2008).

Although research thus far has identified the key frontal and temporal regions that are differentially recruited during object processing across concept levels, the nature of this difference remains largely unknown. Research using property norm data has provided detailed information about the featural organization of concepts and has been extensively used to evaluate the nature of semantic knowledge (Barsalou, 1993; McRae et al., 2005; Randall et al., 2004). A recent study conducted on basic level concepts and their respective superordinate categories has evaluated the degree of feature sharedness for each concept level, that is, the extent to which specific semantic features are common to all members of a concept level. The study showed that members of the superordinate level share less features than those of the basic level (Marques, 2007). While for basic level concepts, 42% of the features produced were rated as being shared by all members of that concept, for superordinate categories the number decreased to 17%. In contrast, the two concept levels had a similar proportion of distinctive features, i.e. features that are an exclusive property of a concept and allow people to distinguish among similar concepts. Thus, superordinate and basic level concepts tend to have an equal amount of distinguishing properties that are critical in differentiating among similar concepts. However, the superordinate level has less shared features among its members, making superordinate concepts less strongly related than basic level concepts (see Marques, 2007 for further details). These results are consistent with the hypothesis that extra semantic control, supported by L lateral PFC, may be necessary to coordinate information that is less shared by members of superordinate concepts. A similar proposal was put forth by Humpreys and Forde (2005) who argue that greater controlled processes in the frontal cortex are needed for superordinate categorization, since semantic features from a broader set of exemplars must be drawn together from memory. Also, Rogers and Patterson (2007) suggested that more general names apply across a much broader span of

concepts, and therefore category level naming gets less benefit from similarity among concepts than basic level naming.

Several studies have argued that the degree of feature sharedness plays a central role in the processing of concepts (Garrard et al., 2001; McRae et al., 2005; Tyler and Moss, 2001). However, the specific hypothesis that superordinate concepts impose greater demands on L PFC regions due to their lower feature sharedness has not been directly tested. Prior studies have mainly focused on the ventral temporal stream, namely addressing the anterior vs. posterior temporal activation as a function of concept level and semantic similarity (e.g. Lambon Ralph et al., 2010; Moss et al., 2005b; Simmons and Barsalou, 2003; Tyler et al., 2004), but the specific role played by the lateral PFC in superordinate processing has not been investigated. To address this issue, we carried out an fMRI study using a sentence verification task, in which we orthogonally manipulated concept level (superordinate vs. basic) and feature sharedness (more shared vs. less shared).

We expect increased lateral PFC activation for processing features that are less shared by members of a category level, since they are associated with increased controlled semantic demands. Moreover, if the degree of feature sharedness modulates the processing of objects at different levels of specificity, then an increased lateral PFC response should be observed for superordinates relative to basic level concepts, due to lower feature sharedness among members of superordinate concepts. Thus, the critical prediction is that the different structure of superordinate and basic level concepts in terms of feature sharedness results in differential semantic control requirements in L lateral PFC. Finally, as a more stringent test for the role of left lateral PFC in processing concepts and features, we investigated the interaction between concept level and feature sharedness considering two hypotheses. One hypothesis is that L lateral PFC recruitment is greater for sentences that involve both superordinate concepts and less shared features, since this condition elicits maximal semantic control demands. Alternatively, it may be that L lateral PFC is recruited whenever superordinate concepts or less shared features are processed. In this case, one should observe PFC activation for all conditions, except when sentences involve basic concepts and more shared features, as in this case semantic control is relatively low and thus no frontal activity is expected.

Material and methods

Participants

Seventeen right-handed, healthy, native Portuguese speaking (18–25 years old, 16 females) participants were recruited for this study. All gave informed written consent to the experimental procedure, which was approved by the local committee.

Materials and procedure

The stimuli consisted of 240 written sentences, half of which were true statements, and the other half were false. There were four types of true sentences. Basic level sentences included a concept that denoted the unique name of an object followed by a semantic feature that could be either more shared (Basic-More condition, e.g. *The car has a steering wheel*) or less shared by the members of that concept (Basic-Less condition, e.g. *The piano is an antique*). Superordinate level sentences involved a more general concept denoting a semantic category followed by a highly shared feature (Superordinate-More condition, e.g. *The plant needs water*) or less shared feature (Superordinate-Less condition, e.g. *The clothes are made from wool*). Concepts and features were drawn from a database of 838 concept–feature pairs developed by Marques (2007) and Marques et al. (2008) (see Appendix A for more examples of the stimuli). A total of 17 basic level concepts and 15 superordinate concepts directly derived from the basic level were used. Each

Table 1
Descriptive statistics of stimuli characteristics.

	Concept log linguistic frequency	Feature production frequency	Proportion of non-sensory features	Feature distinctiveness	Feature sharedness	Sentence length (characters)
Basic-Less shared	2.2	20.9	0.6	3.9	3.9	28.0
Basic-More shared	2.3	21.4	0.6	4.1	6.6	26.6
Superordinate-Less shared	2.1	19.9	0.5	4.0	3.8	29.2
Superordinate-More shared	2.4	19.5	0.8	3.9	6.4	27.5
False-Basic	2.1	–	0.7	–	–	28.9
False-Superordinate	2.2	–	0.6	–	–	29.2

concept was presented in the more shared and less shared feature conditions (except 5 basic level concepts and 2 superordinate concepts that appeared in only one condition due to constraints in concept–feature pairing). Concepts in the four sentence conditions were matched for log linguistic frequency ($p > .1$; see Table 1). Basic level concepts were rated higher in concept imageability than superordinate concepts (mean = 6.4 for basic; mean = 6.0 for superordinate). Even though this difference is statistically significant ($p < .01$), it is important to note that both concept levels were considered highly imageable, being rated an average of 6 or more in a 7 point scale (Hoffman et al., 2010).

The semantic features included sensory, function and encyclopedic attributes of the concepts. The degree of feature sharedness was determined using the norms available from Marques (2007). In that study, a group of participants rated the degree to which a given feature was shared by all members of a specific superordinate or basic level concept using a 7 point scale. Features in the more shared condition were significantly more shared among the members of the concept than features in the less shared condition ($p < .001$ for both basic-level and superordinate sentences). There were no significant differences in feature sharedness between basic and superordinate sentences. Importantly, features in the four sentence conditions were matched for production frequency ($p > .3$), feature distinctiveness ($p > .5$) and proportion of non-sensory attributes ($p > .06$). Moreover, all sentences were also matched in length for number of characters ($p > .1$; see Table 1).

False statements, used as filler items, contained the same basic or superordinate level concepts as the true sentences, but the semantic feature presented was not a property of that concept (e.g. *The apple eats worms*; *The mammal has wings*). To ensure that participants attended to the sentences, the concept and feature in the false condition were related in meaning. True and false sentences were matched for number of characters, log linguistic frequency of the concept and proportion of non-sensory features ($p > .05$ in all cases; see Table 1). All materials were in Portuguese. Each sentence was presented on the screen for 3000 ms during which participants had to decide if the statement was true or false, by pressing the left index finger for true and the left middle finger for false. We included 60 baseline items to control for the visual and motor demands of the task. This corresponded to strings of plus signs (e.g. +++ +++++ ++ ++ +++) that appeared for 3000 ms and participants had to press the left index finger for each string. Successive trials were separated by a variable inter-stimulus interval (500, 1000 and 1500 ms in proportion of 4:2:1) in order to optimize statistical efficiency.

The items were pseudo-randomly organized into three sessions of 100 trials each (40 true sentences, 40 false sentences and 20 baseline trials), with session order counterbalanced across participants. Sentences involving the same concept were presented with an average of 54 trials interspersed in between to avoid word repetition effects. Each scanning session started with 1 min rest (i.e. low level baseline), during which subjects saw a blank screen and no response was required. Each session lasted approximately 8 min. Presentation and

timing of stimuli were controlled using EPrime software (www.psnet.com). We recorded both reaction times and accuracy during fMRI data acquisition.

MRI acquisition and imaging analysis

Scanning was conducted at Sociedade Portuguesa de Ressonância Magnética on a 3-Tesla Philips MR system (Philips Medical Systems, Best, NL) using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR = 2000 ms, 34 interleaved slices parallel to the AC-PC line, with isotropic voxels, 2 mm thick, interslice gap of 1 mm, 2 mm × 2 mm in-plane resolution, FOV = 23 cm × 23 cm, matrix size = 116 × 115). Acquisition covered the entire brain. Before functional data collection, five dummy volumes were discarded to allow for T1 equilibrium. High-resolution T1-weighted anatomical images were acquired for visualization.

Preprocessing and statistical analysis of the data were performed using Statistical Parametric Mapping software (SPM5, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn MA, USA). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice collected, followed by rigid body motion correction across all sessions. Functional data were spatially normalized to a canonical echo-planar imaging template using a 12-parameter affine and nonlinear transformation, and then spatially smoothed with an 8 mm Gaussian kernel. We modeled the responses to each condition (Basic-More, Basic-Less, Superordinate-More, Superordinate-Less, False-Basic, False-Superordinate, and Control trials) separately.

Participants were treated as random effects. Data for each subject were modeled with the general linear model using the canonical hemodynamic response function (HRF). The least squares parameter estimates of the best-fitting canonical HRF for each condition of interest were used in pairwise contrasts and stored as a separate image for each subject. These images were then tested against the null hypothesis using one-tailed *t* tests. Activations were considered significant if they consisted of twenty or more contiguous resampled voxels (2 mm isotropic) and exceeded an alpha threshold of .001 for simple contrasts. Montreal Neurological Institute coordinates are reported. Beta values were obtained for the peak activations. These data were further analyzed using off-line statistical software.

Results

Behavioral data

Separate repeated measures ANOVA were conducted on the proportion of correct responses and response time (RT) data. As expected, participants were significantly more accurate in the baseline (mean = .99) than in the experimental conditions (mean for true sentences = .89; mean for false sentences = .91; $F(2, 297) =$

Table 2
Mean proportion (and standard deviation) of correct responses for each sentence condition.

	True		False
	Less shared	More shared	
Basic	.84 (.17)	.91 (.09)	.93 (.09)
Superordinate	.86 (.18)	.95 (.05)	.88 (.12)

14.7, $p < .001$). There were no significant differences in accuracy between true and false sentences ($t(238) = -.8$, $p > .1$). For true sentences, there was a main effect of feature sharedness, with significantly more accurate responses for sentences involving more shared features ($F(1, 116) = 10.1$, $p < .001$; see Table 2). There was no significant main effect of concept level ($F(1, 116) = 2.1$, $p > .1$) and no significant interaction between concept level and feature sharedness ($F(1, 116) = .1$, $p > .1$). As for false sentences, there was an effect of level of concept, with more accurate responses for superordinate than basic level sentences ($t(118) = 2.4$, $p = .01$; see Table 2).

Analysis of RTs was restricted to correct responses. Results showed significantly faster responses for the baseline (mean = 741 ms) relative to the experimental conditions (mean for true sentences = 1698 ms; mean for false sentences = 1718 ms; $F(2, 297) = 532.3$, $p < .001$), and no differences between true and false sentences ($t(238) = -.9$, $p > .1$). True sentences revealed a significant main effect of feature sharedness, which was associated with faster responses for sentences that involved more shared than less shared features ($F(1, 116) = 26.6$, $p < .001$; see Table 3). We found no main effect of level of concept ($F(1, 116) = .2$, $p > .1$) and no interaction between level of concept and feature sharedness ($F(1, 116) = .1$, $p > .1$). Regarding false sentences, there were no significant differences in RTs between sentences involving basic and superordinate concepts ($t(118) = -.6$, $p > .1$).

Overall, the behavioral analysis showed that, relative to more shared features, processing features that are less shared by the members of a concept is more demanding. Importantly, there were no significant differences in accuracy or RTs between true sentences involving basic and superordinate concepts, and no interaction between concept level and feature sharedness. Thus, any potential difference in neural responses for sentences involving concepts at different hierarchical levels cannot be attributed to general difficulty or time spent on task.

Functional imaging data

We first investigated the brain regions engaged during processing of written sentences, by comparing all sentences (true and false) against baseline (series of plus signs). Sentence processing was associated with an extensive left lateralized network, including L inferior temporal gyrus (ITG, BA 20), extending to L fusiform gyrus (BA 20, 37), and L middle temporal gyrus (MTG, BA 21). Activation was also

Table 3
Mean response time (and standard deviation) for correct responses in each sentence condition (in ms).

	True		False
	Less shared	More shared	
Basic	1782 (179)	1587 (174)	1705 (224)
Superordinate	1830 (173)	1591 (259)	1731 (191)

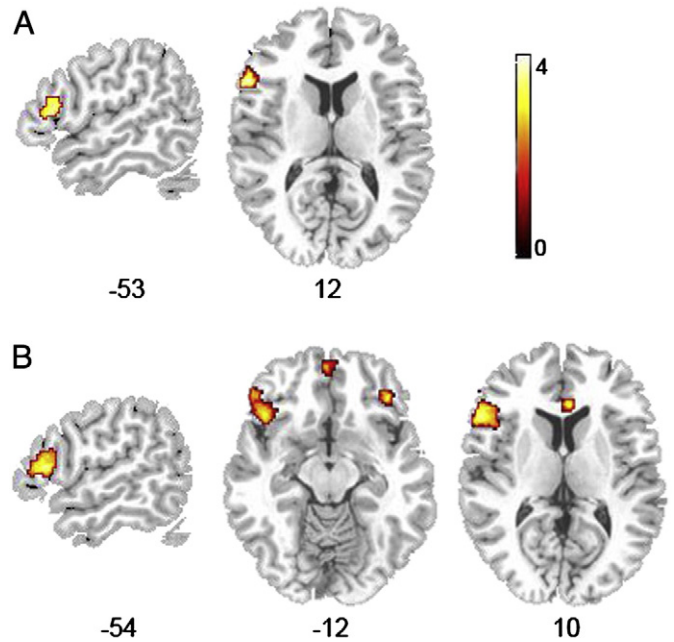


Fig. 1. (A) Cortical regions activated for less shared minus more shared features, combined for basic and superordinate sentences. (B) Cortical regions activated for less shared minus more shared features in the basic level condition. Activations were overlaid on a canonical brain and thresholded at $p = .005$, 32 voxels for display purposes.

found in L inferior frontal gyrus (IFG, BA 47, 45), and L precentral gyrus (BA 6). There was bilateral occipital (BA 18) activation which included the lingual gyrus (BA 19). Activation in these regions has been consistently reported in fMRI studies of semantic processing (Devlin et al., 2002; Marques et al., 2008; Martin and Chao, 2001; Thompson-Schill et al., 2005), suggesting that this experiment successfully tapped into the semantic processing system. Subsequent analyses focused on true sentences only, because in this condition we are able to control the extent to which a specific feature is shared by the members of superordinate and basic level concepts.

To explore the differential effects of feature sharedness, we contrasted activity for sentences involving less shared features with sentences containing more shared features, independently of concept level. We found increased activation in lateral inferior PFC (BA 44) for less relative to more shared features (Fig. 1A; Table 4). Similar activation was observed when we compared less and more shared features for the basic level condition (Fig. 1B; Table 4). However, for the superordinate condition, there were no activations above threshold for less relative to more shared features. The reverse contrast (more shared > less shared) identified significant activation in bilateral MTG (BA 37), extending to L STG (BA 22, 48), as well as R

Table 4
Regions demonstrating significant increases of response to less shared minus more shared features.

Region	BA	No voxels	Z-score	MNI coordinates		
				x	y	z
<i>Less shared > more shared</i>						
L inferior frontal gyrus	44	23	3.33	-60	20	12
<i>Basic-less shared > basic-more shared</i>						
L inferior frontal gyrus	45	97	4.07	-54	24	8
Anterior cingulate gyrus	24	20	3.87	4	30	10
L orbitofrontal gyrus	38	24	3.39	-44	24	-12

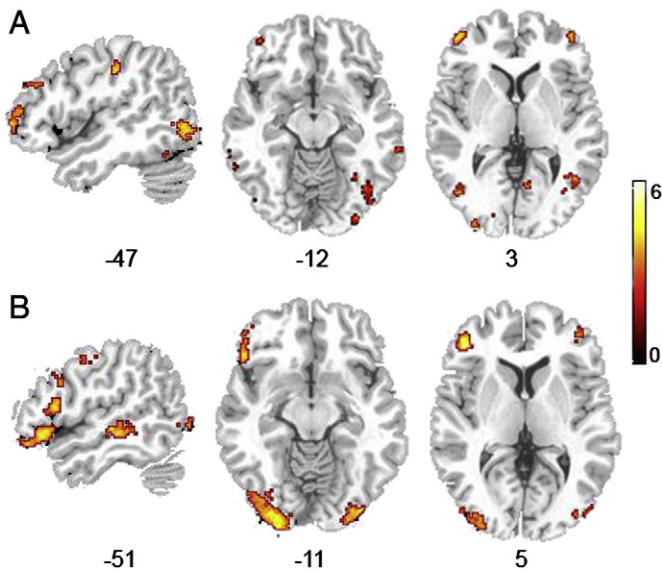


Fig. 2. (A) Cortical regions activated for superordinate relative to basic level, combined for more and less shared feature sentences. (B) Cortical regions activated for superordinate relative to basic level in the more shared feature condition. Activations were overlaid on a canonical brain and thresholded at $p = .001$, 20 voxels.

Table 5

Regions demonstrating significant increases of response to superordinate relative to basic level concepts.

Region	BA	No voxels	Z-score	MNI coordinates		
				x	y	z
<i>Superordinate > Basic</i>						
R supramarginal gyrus	2	1719	4.50	44	-38	36
L middle occipital gyrus	18	205	4.47	-34	-96	-2
R middle temporal gyrus	20	33	4.40	64	-36	-18
R posterior cingulate gyrus	23	245	4.37	8	-22	32
L middle frontal gyrus	46	122	4.36	-46	50	2
L postcentral gyrus	3	146	4.31	-46	-24	38
L inferior parietal cortex	40	256	4.13	-32	-58	40
R superior occipital gyrus	18	103	4.12	18	-92	18
R caudate	80	80	3.93	18	-6	20
L superior temporal gyrus	48	49	3.89	-62	-16	10
L middle occipital gyrus	37	86	3.88	-50	-74	-4
L middle temporal gyrus	21	68	3.88	-66	-44	-6
R precentral gyrus	6	69	3.87	54	2	36
L anterior cingulate gyrus	24	20	3.85	-6	6	38
R inferior frontal gyrus	45	43	3.85	40	42	6
R middle frontal gyrus	46	25	3.84	42	56	-6
L inferior frontal gyrus	45	93	3.67	-42	38	32
R inferior temporal gyrus	37	50	3.62	42	-66	-10
R superior temporal gyrus	22	23	3.61	56	-30	8
R middle occipital gyrus	19	38	3.58	36	-90	-4
R inferior occipital gyrus	18	22	3.54	32	-92	-14
L precentral gyrus	6	22	3.29	-58	8	26
<i>Superordinate-more shared > basic-more shared</i>						
L inferior frontal gyrus	45	130	4.71	-44	40	4
L inferior occipital gyrus	18	746	4.63	-28	-92	-14
L inferior frontal gyrus	44	103	4.51	-58	14	26
R inferior frontal gyrus	48	145	4.44	46	14	32
L inferior frontal gyrus	45	154	4.31	-54	18	8
L postcentral gyrus	6	47	4.25	-48	-8	46
R lingual gyrus	18	139	4.16	24	-94	-14
L middle temporal gyrus	21	140	4.13	-54	-34	0
L inferior frontal gyrus	47	177	4.13	-50	26	-8
R inferior parietal gyrus	7	323	4.09	32	-56	50
L middle occipital gyrus	19	42	4.03	44	-84	8
L precuneus	7	90	3.82	-4	-70	36
Anterior cingulate gyrus	24	25	3.64	0	30	10
R superior occipital gyrus	19	20	3.63	22	-88	22
R inferior frontal gyrus	47	22	3.59	38	44	8

supramarginal gyrus (BA 40), R rolandic operculum (BA 6, 48), R insula (BA 48) and R precentral gyrus (BA 6). There was also a significant cluster in R superior medial frontal gyrus (BA 10, 11) and cingulate gyrus (BA 23). Importantly, there were no significant clusters in any lateral PFC region. Consistently with the behavioral data, the neuroimaging analysis revealed that features that are less shared by the members of a concept require greater semantic control associated with increased lateral PFC activation.

To investigate the neural regions activated for different concept levels, we directly contrasted activity during processing of sentences involving superordinate and basic level concepts, independently of the degree of feature sharedness. The contrast of basic minus superordinate sentences showed no significant clusters of activation, even at a lower threshold of $p < .005$, 20 voxels. The reverse contrast of superordinate minus basic level engaged two regions of the lateral PFC, one located in anterior ventrolateral PFC (BA 47, 46) bilaterally, and another centered in L dorsolateral PFC (BA 46). There was also extensive activation in bilateral MTG (BA 20, 37), extending to L STG (BA 48) and R ITG (BA 20), bilateral inferior occipital gyrus (BA 18, 19), superior occipital (BA 18) and inferior parietal (BA 7, 40; Fig. 2A, Table 5). We also contrasted the two concept levels in the less and more shared feature conditions separately. We found that when the feature was highly shared by the members of the concept, there was significantly more activation in L ventrolateral PFC (BA 47, 45, 44) for superordinate concepts compared to basic ones (Fig. 2B, Table 5). Such activation was accompanied by recruitment of bilateral fusiform gyrus (BA 19), lingual gyrus (BA 18), inferior occipital gyrus (BA 18) and L MTG (BA 20, 21). In contrast, for sentences where the feature was less shared by the members of the concept, we found no differences in lateral PFC between superordinate and basic level concepts.

We also tested the interaction between feature sharedness and concept level. At the standard threshold of $p < .001$ there was no significant interaction in any lateral PFC region. However, when we lowered slightly the threshold to $p < .005$ (>20 voxels) we found a significant interaction in the L lateral PFC (BA 47), confirming the relationship between feature sharedness and concept level. Both Superordinate-Less and Basic-Less conditions showed significant activity in the L lateral PFC and these activations were not significantly different. However, when the features in the sentence were highly shared, only those sentences involving superordinate concepts activated this region. In addition to the L PFC, there was an interaction in the L superior temporal pole (BA 38), L MTG (BA 20, 21), bilateral SFG (BA 11), anterior cingulate (BA 24) and L caudate nucleus (Fig. 3 and Table 6).

Finally, to further examine the response pattern in left lateral PFC we inspected the signal change in this region, based on a peak activation found in the contrast comparing all sentences to baseline. We chose this contrast because it is unbiased relative to any feature or concept level effects. Moreover, it allowed us to contrast the lateral

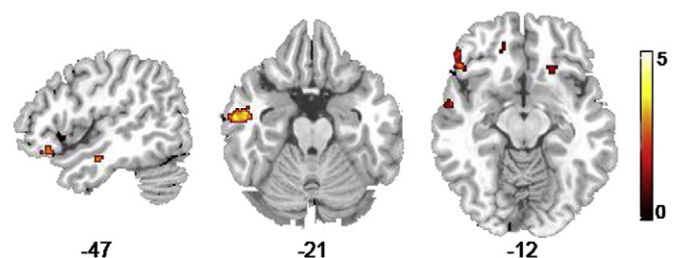


Fig. 3. Cortical regions activated for the interaction between feature sharedness and concept level. Activations were overlaid on a canonical brain and thresholded at $p = .005$, 20 voxels.

Table 6

Regions demonstrating a significant interaction between feature sharedness and concept level ($p < .005$, 20 voxels).

Region	BA	No voxels	Z-score	MNI coordinates		
				x	y	z
Anterior cingulate cortex	24	95	4.21	0	28	10
L middle temporal gyrus	21	153	3.93	-60	-12	-22
L superior frontal gyrus	11	29	3.46	-14	40	-16
R superior frontal gyrus	11	26	3.40	16	24	-16
L superior frontal gyrus	11	22	3.38	-4	56	-18
L superior temporal pole	38	48	3.31	-50	28	-16
L caudate	25	59	3.16	-10	18	6

PFC response with another region, the L ITG, that has been reliably linked with semantic processing in prior functional imaging literature (Binder et al., 2011; Lambon Ralph et al., 2010; Tyler et al., 2004; Visser et al., 2010), but for which we do not predict differential semantic control demands across category level or degree of feature sharedness. For each region, we extracted and compared the mean activity estimates for each condition (Superordinate-Less, Superordinate-More, Basic-Less, Basic-More) against the baseline (Fig. 4). A repeated measures ANOVA with the factors neural region (L lateral PFC vs. LITG), feature sharedness (less shared vs. more shared) and concept level (basic vs. superordinate) was conducted. The results yielded a significant main effect of region ($F(1, 16) = 5.3$, $p = .03$), reflecting the varying levels of response across the two regions. There was also a region by feature interaction ($F(1, 16) = 12.5$, $p = .002$), as less shared features were associated with greater activity in L lateral PFC than more shared features ($F(1, 16) = 5.1$, $p = .03$), but such difference did not occur in LITG ($F(1, 16) = .01$, $p > .1$). The interaction between neural region and concept level was also significant ($F(1, 16) = 5.9$, $p = .02$). Whereas in the L lateral PFC there was a marginal increase of activation for superordinate relative to basic level concepts ($F(1, 16) = 3.3$, $p = .08$), in the LITG the reverse trend was found (i.e. greater activation for basic; $F(1, 16) = 3.4$, $p = .08$). Overall, the results indicate that both superordinate categories and less shared features engage L lateral PFC, providing support for the claim that executive processes help direct and control semantic information that is less shared by the members of a concept.

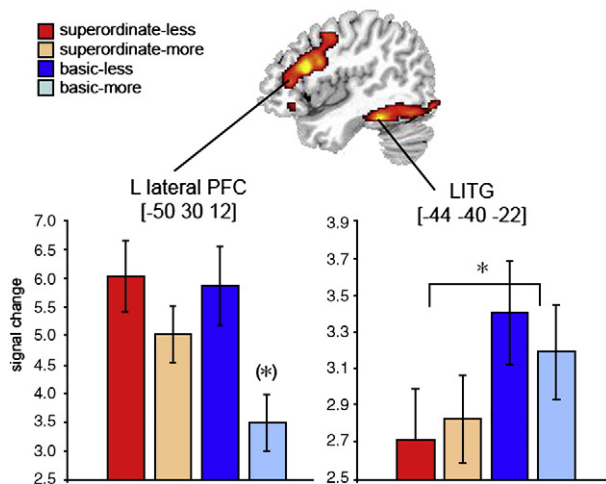


Fig. 4. Plots of the mean (and standard errors) of the parameter estimates extracted from the L lateral PFC and LITG.

Discussion

The goal of the current study was to investigate the nature of superordinate knowledge and clarify the contribution of the left PFC in processing superordinate concepts. We built on previous research that demonstrated that superordinate and basic levels of concepts are structurally distinguished with respect to the degree features are shared among their members (Marques, 2007). By manipulating concept level and feature sharedness, we examined the extent to which the lower degree of feature sharedness in superordinate concepts modulates the activation pattern in left PFC.

Sentences involving features that are less shared across concepts (regardless of concept level) revealed increased activation in left lateral PFC (BA 44). This region has been consistently associated with controlled semantic processing, with some studies suggesting that it is involved in controlled retrieval of semantic information (Badre et al., 2005; Dobbins and Wagner, 2005; Poldrack et al., 1999; Wagner et al., 2001) and others proposing its role in selection of task-relevant information among competing alternatives (Moss et al., 2005a; Thompson-Schill et al., 1999, 2005). In fMRI studies of word meaning retrieval, increased L lateral PFC response has been reported when the task involves recovery of information that is non-dominant or has low frequency, such as retrieving the subordinate meaning of an ambiguous word (Bedny et al., 2008; Rodd et al., 2005, 2010; Whitney et al., 2011). Similarly, in our study, this region was more strongly engaged when the features in the sentence were less shared by the members of the concept, reflecting higher semantic elaboration and/or selection demands (Dobbins and Wagner, 2005; Raposo et al., 2009; Thompson-Schill et al., 1999; Wagner et al., 2001). In contrast, when the sentence involved more shared features we observed extensive activation in temporal areas, such as bilateral MTG, L STG, and R supramarginal gyrus. Such activation may reflect a stronger representation of more shared features in the semantic network, since features that are common to many concepts are likely to be more strongly associated in memory (Randall et al., 2004; Rogers et al., 2004; Tyler et al., 2004). As expected, more feature sharedness facilitated performance both in terms of accuracy and RTs, an effect that has been reported in a variety of tasks, including feature verification (Cree et al., 2006; Randall et al., 2004), picture naming (Humphreys et al., 1988) and semantic decisions (Grondin et al., 2009).

More importantly, sentences involving superordinate concepts (regardless of degree of feature sharedness) also recruited the left lateral PFC as compared to sentences involving basic level concepts. Activation was observed in two regions, one in more ventrolateral PFC bilaterally (BA 47), and the other in an L dorsolateral (BA 46) region. Both areas have been linked to executive control, with ventrolateral PFC being associated with controlled semantic analysis and/or selection demands, and dorsolateral portions mediating monitoring and evaluation of information (Badre and Wagner, 2004; Dobbins et al., 2002). Solid evidence from a prior property norm study has shown that superordinate concepts have less shared features among their members in comparison to basic level concepts (Marques, 2007). Here, we argue that due to their lower feature sharedness, processing superordinate concepts requires increasing executive demands in L lateral PFC in order to coordinate information that is less shared. This proposal converges with data from stroke aphasic patients, who exhibit impaired regulation of semantic control following prefrontal lesion. For example, the patients show strong phonemic cueing effects (i.e. performance improves considerably when phonemic cues are presented) suggesting that semantic knowledge is largely intact, but the patients are unable to retrieve the name without cues that help guide and direct towards the correct response (Jefferies and Lambon Ralph, 2006; Jefferies et al., 2008). Along the same line, Humpreys and Forde (2005) and Crutch and Warrington (2008) have argued that

the poor performance reported on superordinate comprehension tasks reflects a problem in guiding and regulating knowledge retrieval, since semantic control requirements are higher when processing superordinate concepts than basic level names.

Activation in the left lateral PFC for superordinate concepts was not accompanied by increasing demands in terms of RTs and accuracy. This result may seem contradictory to past work which has shown that people are generally faster and more accurate to process items at the basic than superordinate levels (Murphy and Smith, 1982; Rosch, 1975; Rogers and Patterson, 2007). However, such basic level advantage is highly dependent on the task and the experimental characteristics of the stimuli, which may explain the lack of behavioral differences in the current study as well as the fact that many other studies failed to replicate this effect (e.g. Lloyd-Jones and Humphreys, 1997; Macé et al., 2009; Mack et al., 2009; Moss et al., 2005b; Potter and Faulconer, 1975; Rogers and Patterson, 2007; VanRullen and Thorpe, 2001). For instance, Rogers and Patterson (2007) showed that when participants are forced to respond under time pressure, the usual basic advantage reverses, with accuracy for superordinate level items being higher than for basic level items. Here, we propose that when critical variables such as feature sharedness are matched between different concepts, the basic level advantage may disappear.

Although increased PFC activity was found for all superordinate sentences (collapsed across more and less shared features), it was particularly evident when the feature presented was more shared across category level members. This is because in the less shared feature condition, L lateral PFC was recruited for both superordinate and basic concepts due to the increasing semantic demands associated with processing less shared features. In contrast, when the feature in the sentence was highly shared, then differences in PFC emerged between superordinates and basic concepts, due to the lower feature sharedness among members of superordinate concepts (Marques, 2007). This result was further supported by the significant interaction observed in this region between feature sharedness and concept level. Overall, left lateral PFC recruitment was mediated by the level of feature sharedness, as determined by the type of feature (i.e. less shared) or the concept level (i.e. superordinate) presented in the sentence.

Along with left lateral PFC, superordinate concepts revealed activation in bilateral MTG, L STG and R ITG. These regions are an integral part of the semantic processing network, having been linked to the storage of semantic knowledge (Kuperberg et al., 2008; Marques et al., 2008; Noppeney et al., 2004; Thompson-Schill et al., 1997; Tyler et al., 2004; Wagner et al., 2001). Interestingly, the interaction between feature sharedness and concept specificity also activated various regions, including the L lateral PFC and the L temporal pole. Such co-activation of frontal and temporal regions is consistent with the view that control and representational demands interact. Specifically, it has been proposed that L lateral PFC helps semantic processing, via top-down mechanisms that aid semantic retrieval from more posterior temporal regions in a goal directed manner (Badre et al., 2005; Bar et al., 2006; Dobbins and Wagner, 2005; Ghuman et al., 2008; Miller and D'Esposito, 2005; Miller et al., 2002; Tomita et al., 1996).

The contrast of basic level sentences minus superordinate sentences showed no significant activation even when we lowered the threshold. Nevertheless, when we compared the signal change for the four sentence conditions in the L lateral PFC and in a region of the L inferior temporal area we found a significant region by concept level interaction, revealing that the activation patterns in the inferior frontal and inferior temporal regions are distinct. While the frontal region was recruited when semantic control demands increase (i.e. in superordinate condition), the L inferior temporal area was more strongly engaged for basic level concepts, pointing to the view that this region is involved in finer-grained representation of concepts (Clarke et al., 2011; Lambon Ralph et al., 2010;

Moss et al., 2005b; Patterson et al., 2007; Tyler et al., 2004; Visser et al., 2010). This raises the interesting hypothesis that superordinate concepts may be represented in a sparser and more abstract manner than basic level concepts, which could in turn explain the observed neural differences. Indeed, Hoffman et al. (2010) have suggested that abstract words involve greater lateral PFC activation because they require higher executive regulation than concrete words. The results of our behavioral pretests partially support this interpretation, as superordinate concepts had a lower imageability rating, and therefore may be considered more abstract than basic level concepts. However, as noted above, both basic and superordinate concepts had a high imageability rating, with an average value of 6.4 for basic concepts and 6.0 for superordinates (in a 7 point scale). Given the high imageability level of the words used, it is unlikely that the neural differences found between superordinate and basic level concepts are related to the processing of abstract concepts. Nevertheless, an interesting goal for future research involves establishing how the degree of imageability impacts the neural activation of superordinate and basic level concepts. It will be important to directly contrast the effect of concept imageability and feature sharedness to better understand how different factors modulate the neural basis of processing objects at different hierarchical levels.

Taken together, our results suggest that the degree of feature sharedness impacts the neural organization of semantic knowledge, in particular the processing of superordinate concepts. Although previous data are in accord with this perspective (Grondin et al., 2009; McRae et al., 2005; Randall et al., 2004; Rogers et al., 2004; Rosch, 1978), the relationship between feature sharedness and concept level had only been assessed indirectly. For instance, in most studies feature knowledge at superordinate level is inferred from features reported at basic level, in which case the specific features reported and the weight of such features is most likely distorted when translated to the respective superordinate category (Ashcraft, 1978; Marques, 2007; Rogers et al., 2004). Moreover, many studies conflate feature sharedness and feature distinctiveness in a single dimension (Garrard et al., 2001; McRae et al., 2005). Although related, they correspond to different dimensions, and this is particularly relevant when contrasting superordinate and basic level concepts (Marques, 2007). Feature sharedness refers to the degree to which specific semantic features are shared by all members of a concept (e.g. "has four legs" is shared by all dogs, but not by all animals). Feature distinctiveness refers to the degree to which specific features are an exclusive property of a concept, allowing people to discriminate among similar concepts (e.g. "has a mane" is an exclusive property of both lions and animals, at their respective concept levels). Here, we overcame these confounds by using a database for features directly listed for superordinate and basic level concepts and that includes separate ratings for feature sharedness and feature distinctiveness, among other dimensions (Marques, 2007). The results provide clear evidence that feature sharedness impacts the neural correlates of concepts at different hierarchical levels with the lower degree of feature sharedness among superordinate, compared to basic-level, concepts increasing the recruitment of L lateral PFC.

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Appendix A

Examples of stimuli in all sentence conditions (English translation).

	True		False
	Less shared	More shared	
Basic	The apple can be bitter. The rose may be yellow. The pistol is used by policemen. The chair is made of metal.	The snake lays eggs. The apple has a peel. The hammer has a handle. The trousers cover the legs.	The snake may fly. The lettuce eats salad. The piano plays the keyboard. The trousers are made from wood.
Superordinate	The insect is black. The mammal may live in the sea. The gun is used to hunt. The musical instrument is large.	The plant has roots. The mammal breathes. The tool is useful. The vehicle is used to travel.	The fruit has bones. The reptile has two tails. The vehicle drives the road. The furniture cleans the table.

References

- Ashcraft, M., 1978. Property norms for typical and atypical items from 17 categories: a description and discussion. *Mem. Cognit.* 6, 227–232.
- Badre, D., Wagner, A.D., 2004. Selection, integration, and conflict monitoring: assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron* 41, 473–487.
- Badre, D., Poldrack, R.A., Pare-Blagoev, E.J., Insler, R.Z., Wagner, A.D., 2005. Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron* 47, 907–918.
- Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., Hämäläinen, M.S., Marinkovic, K., Schacter, D.L., Rosen, B.R., Halgren, E., 2006. Top-down facilitation of visual recognition. *Proc. Natl. Acad. Sci. U.S.A.* 103, 449–454.
- Barsalou, L.W., 1993. Flexibility, structure and linguistic vagary in concepts: manifestations of a compositional system of perceptual symbols. In: Collins, A.C., Gathercole, S.E., Conway, M.A., Morris, P.E.M. (Eds.), *Theories of Memory*. Lawrence Erlbaum Associates Ltd, Hove, UK, pp. 29–101.
- Bedny, M., McGill, M., Thompson-Schill, S.L., 2008. Semantic adaptation and competition during word comprehension. *Cereb. Cortex* 18, 2574–2585.
- Binder, J.R., Gross, W.L., Allendorfer, J.B., Bonilha, L., Chapin, J., Edwards, J.C., Grabowski, T.J., Langfitt, J.T., Loring, D.W., Lowe, M.J., Koenig, K., Morgan, P.S., Ojemann, J.G., Rorden, C., Szafarski, J.P., Tivarus, M.E., Weaver, K.E., 2011. Mapping anterior temporal lobe language areas with fMRI: a multicenter normative study. *Neuroimage* 54, 1465–1475.
- Bozeat, S., Lambon Ralph, M.A., Graham, K.S., Patterson, K., Wilkin, H., Rowland, J., Rogers, T.T., Hodges, J.R., 2003. A duck with four legs: investigating the structure of conceptual knowledge using picture drawing in semantic dementia. *Cogn. Neuropsychol.* 20, 27–47.
- Clarke, A., Taylor, K.L., Tyler, L.K., 2011. The evolution of meaning: Spatio-temporal dynamics of visual object recognition. *J. Cogn. Neurosci.* 23, 1887–1899.
- Cree, G.S., McNorgan, C., McRae, K., 2006. Distinctive features hold a privileged status in the computation of word meaning: implications for theories of semantic memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 32, 643–658.
- Crutch, S.J., Warrington, E.K., 2008. Contrasting patterns of comprehension for superordinate, basic-level, and subordinate names in semantic dementia and aphasic stroke patients. *Cogn. Neuropsychol.* 25, 582–600.
- 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. *J. Neurosci.* 15, 5870–5878.
- Devlin, J.T., Russell, R.P., Davis, M.H., Price, C.J., Moss, H.E., Fadili, M.J., Tyler, L.K., 2002. Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia* 40, 54–75.
- Dobbins, I.G., Wagner, A.D., 2005. Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cereb. Cortex* 15, 1768–1778.
- Dobbins, I.G., Foley, H., Schacter, D.L., Wagner, A.D., 2002. Executive control during episodic retrieval: multiple prefrontal processes subserve source memory. *Neuron* 35, 989–996.
- Garrard, P., Lambon Ralph, M.A., Hodges, J.R., Patterson, K., 2001. Prototypicality, distinctiveness, and intercorrelations: analyses of the semantic attributes of living and nonliving concepts. *Cogn. Neuropsychol.* 18, 125–174.
- Ghuman, A.S., Bar, M., Dobbins, I.G., Schnyer, D.M., 2008. The effects of priming on frontal-temporal communication. *Proc. Natl. Acad. Sci. U.S.A.* 105, 8405–8409.
- Grondin, R., Lupker, S.J., McRae, K., 2009. Shared features dominate semantic richness effects for concrete concepts. *J. Mem. Lang.* 60, 1–19.
- Hodges, J.R., Patterson, K., Tyler, L.K., 1994. Loss of semantic memory: implications for the modularity of mind. *Cogn. Neuropsychol.* 11, 505–542.
- Hoffman, P., Jefferies, E., Lambon Ralph, M.A., 2010. Ventrolateral prefrontal cortex plays an executive regulation role in comprehension of abstract words: convergent neuropsychological and repetitive TMS evidence. *J. Neurosci.* 30, 15450–15456.
- Humphreys, G.W., Riddoch, M.J., Quinlan, P.T., 1988. Cascade processes in picture identification. *Cogn. Neuropsychol.* 5, 67–103.
- Humphreys, G.W., Forde, E.M.E., 2005. Naming a giraffe but not an animal: base-level but not superordinate naming in a patient with impaired semantics. *Cogn. Neuropsychol.* 22, 539–558.
- Jefferies, E., Lambon Ralph, M.A., 2006. Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. *Brain* 129, 2132–2147.
- Jefferies, E., Patterson, K., Lambon Ralph, M.A., 2008. Deficits of knowledge versus executive control in semantic cognition: insights from cued naming. *Neuropsychologia* 46, 649–658.
- Jónsdóttir, M.K., Martin, R.C., 1996. Superordinate vs. basic level knowledge in aphasia: a case study. *J. Neurolinguistics* 9, 261–287.
- Kuperberg, G.R., Sitnikova, T., Lakshmanan, B.M., 2008. Neuroanatomical distinctions within the semantic system during sentence comprehension: evidence from functional Magnetic Resonance Imaging. *Neuroimage* 40, 367–388.
- Laisney, M., Giffard, B., Belliard, S., de la Sayette, V., Desgranges, B., Eustache, F., 2011. When the zebra loses its stripes: semantic priming in early Alzheimer's disease and semantic dementia. *Cortex* 47, 35–46.
- Lambon Ralph, M.A., Sage, K., Jones, R.W., Mayberry, E.J., 2010. Coherent concepts are computed in the anterior temporal lobes. *Proc. Natl. Acad. Sci. U.S.A.* 107, 2717–2722.
- Lloyd-Jones, T.J., Humphreys, G.W., 1997. Categorizing chairs and naming pears: category differences in object processing as a function of task and priming. *Mem. Cogn.* 25, 606–624.
- Macé, M.J., Joubert, O.R., Nespoulous, J.L., Fabre-Thorpe, M., 2009. The time-course of visual categorizations: you spot the animal faster than the bird. *PLoS One* 17, e5927.
- Mack, M.L., Wong, A.C.-N., Gauthier, I., Tanaka, J.W., Palmeri, T.J., 2009. Time-course of visual object categorization: fastest does not necessarily mean first. *Vision Res.* 49, 1961–1968.
- Marques, J.F., 2007. The general/specific breakdown of semantic memory and the nature of superordinate knowledge: insights from superordinate and basic-level feature norms. *Cogn. Neuropsychol.* 24, 879–903.
- Marques, J.F., Canessa, N., Siri, S., Catricalà, E., Cappa, S., 2008. Conceptual knowledge in the brain: fMRI evidence for a featural organization. *Brain Res.* 1194, 90–99.
- Martin, A., Chao, L.L., 2001. Semantic memory and the brain: structure and processes. *Curr. Opin. Neurobiol.* 11, 194–201.
- McRae, K., Cree, G.S., Seidenberg, M.S., McNorman, C., 2005. Semantic feature production norms for a large set of living and nonliving things. *Behav. Res. Methods* 37, 547–559.
- Miller, B.T., D'Esposito, M., 2005. Searching for “the top” in top-down control. *Neuron* 48, 535–538.
- Miller, E.K., Freedman, D.J., Wallis, J.D., 2002. The prefrontal cortex: categories, concepts and cognition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357, 1123–1136.
- Moss, H.E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., Tyler, L.K., 2005a. Selecting among competing alternatives: selection and retrieval in the left inferior frontal gyrus. *Cereb. Cortex* 15, 1723–1735.
- Moss, H.E., Rodd, J.M., Stamatakis, E.A., Bright, P., Tyler, L.K., 2005b. Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cereb. Cortex* 15, 616–627.
- Murphy, G.L., Smith, E.E., 1982. Basic-level superiority in picture categorization. *J. Verb. Learn. Verb. Behav.* 21, 1–20.
- Noppeney, U., Phillips, J.A., Price, C., 2004. The neural areas that control the retrieval and selection of semantics. *Neuropsychologia* 42, 1269–1280.
- Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the brain. *Nat. Rev. Neurosci.* 8, 976–988.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D.E., 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage* 10, 15–35.
- Potter, M.C., Faulconer, B.A., 1975. Time to understand pictures and words. *Science* 253, 437–438.
- Randall, B., Moss, H.E., Rodd, J.M., Greer, M., Tyler, L.K., 2004. Distinctiveness and correlation in conceptual structure: behavioral and computational studies. *J. Exp. Psychol. Learn. Mem. Cogn.* 30, 393–406.
- Raposo, A., Han, S., Dobbins, I.G., 2009. Ventrolateral prefrontal cortex and self-initiation of semantic elaboration during memory retrieval. *Neuropsychologia* 47, 2261–2271.
- Rodd, J.M., Davis, M.H., Johnsrude, I.S., 2005. The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cereb. Cortex* 15, 1261–1269.

- Rodd, J.M., Longe, O.A., Randall, B., Tyler, L.K., 2010. The functional organisation of the fronto-temporal language system: evidence from syntactic and semantic ambiguity. *Neuropsychologia* 48, 1324–1335.
- Rogers, T.T., Patterson, K., 2007. Object categorization: reversals and explanations of the basic-level advantage. *J. Exp. Psychol. Gen.* 136, 451–469.
- Rogers, T.T., Lambon Ralph, M.A., Garrard, P., Bozeat, S., McClelland, J.L., Hodges, J.R., Patterson, K., 2004. Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol. Rev.* 111, 205–235.
- Rogers, T.T., Hocking, J., Mechelli, A., Patterson, K., Price, C., 2005. Fusiform activation to animals is driven by the process, not the stimulus. *J. Cogn. Neurosci.* 17, 434–445.
- Rosch, E., 1975. Cognitive representations of semantic categories. *J. Exp. Psychol. Gen.* 104, 192–233.
- Rosch, E., 1978. Principles of categorization. In: Rosch, E., Lloyd, B.B. (Eds.), *Cognition and Categorization*. Erlbaum, Hillsdale, NJ.
- Rosch, E., Mervis, C.B., Gray, W.D., Johnson, D.M., Boyes-Brahem, P., 1976. Basic objects in natural categories. *Cogn. Psychol.* 8, 382–439.
- Simmons, W.K., Barsalou, L.W., 2003. The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cogn. Neuropsychol.* 20, 451–486.
- Tanaka, J., Luu, P., Weisbrod, M., Kiefer, M., 1999. Tracking the time course of object categorization using event-related potentials. *Neuroreport* 10, 829–835.
- Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. U.S.A.* 94, 14792–14797.
- Thompson-Schill, S.L., D'Esposito, M., Kan, I.P., 1999. Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron* 23, 513–522.
- Thompson-Schill, S.L., Bedny, M., Goldberg, R.F., 2005. The frontal lobes and the regulation of mental activity. *Curr. Opin. Neurobiol.* 15, 219–224.
- Tomita, H., Ohbayashi, M., Nakahara, K., Hasegawa, I., Miyashita, Y., 1996. Top-down signal from prefrontal cortex in executive control of memory retrieval. *Nature* 401, 699–703.
- Tyler, L.K., Moss, H.E., 2001. Towards a distributed account of conceptual knowledge. *Trends Cogn. Sci.* 5, 244–252.
- Tyler, L.K., Stamatakis, E.A., Bright, P., Acres, K., Abdallah, S., Rodd, J.M., Moss, H.E., 2004. Processing objects at different levels of specificity. *J. Cogn. Neurosci.* 16, 351–362.
- VanRullen, R., Thorpe, S.J., 2001. Is it a bird? Is it a plane? Ultra-rapid visual categorisation of natural and artificial objects. *Perception* 30, 655–668.
- Visser, M., Jefferies, E., Lambon Ralph, M.A., 2010. Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *J. Cogn. Neurosci.* 22, 1083–1094.
- Wagner, A.D., Pare-Blagoev, E.J., Clark, J., Poldrack, R.A., 2001. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31, 329–338.
- Warrington, E.K., 1975. The selective impairment of semantic memory. *Q. J. Exp. Psychol.* 27, 635–657.
- Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M.A., Jefferies, E., 2011. The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cereb. Cortex* 21, 1066–1075.