Article:

Ferreira, Roberto A., Göbel, Silke M. orcid.org/0000-0001-8845-6026, Hymers, Mark et al. (1 more author) (2015) The neural correlates of semantic richness:Evidence from an fMRI study of word learning. Brain and Language. pp. 69-80. ISSN: 0093-934X

https://doi.org/10.1016/j.bandl.2015.02.005

The neural correlates of semantic richness: Evidence from an fMRI study of word learning

Roberto A. Ferreira[a,b] , Silke M. Göbel[a] , Mark Hymers[c], and Andrew W. Ellis[a]

[a]Department of Psychology, University of York, Heslington, York, YO10 5DD, UK

[b]Departamento de Lenguas, Facultad de Educacion, Universidad Católica de la Santísima Concepción, Alonso de Ribera 2850, Concepción, 4090541, Chile[1]

[c]York Neuroimaging Centre, University of York, Innovation Way, York, YO10, UK

Address correspondence to Roberto A. Ferreira, Facultad de Educación, Universidad Católica de la Santísima Concepción, Alonso de Ribera 2850, Concepción, 4090541, Chile.
Telephone: +56-41-2345629. Fax: +56-41-2345001. Email: rferreira@ucsc.cl

Running title: The neural correlates of semantic richness

---

[1] Present address.

Abstract

We investigated the neural correlates of concrete nouns with either many or few semantic features. A group of 21 participants underwent two days of training and were then asked to categorize 40 newly learned words and a set of matched familiar words as living or nonliving in an MRI scanner. Our results showed that the most reliable effects of semantic richness were located in the left angular gyrus (AG) and middle temporal gyrus (MTG), where activation was higher for semantically rich than poor words. Other areas showing the same pattern included bilateral precuneus and posterior cingulate gyrus. Our findings support the view that AG and anterior MTG, as part of the multimodal network, play a significant role in representing and integrating semantic features from different input modalities. We propose that activation in bilateral precuneus and posterior cingulate gyrus reflects interplay between AG and episodic memory systems during semantic retrieval.

Key words: word learning, semantic representation, semantic richness, semantic features, angular gyrus, middle temporal gyrus, fMRI.

1. Introduction

All familiar words known to a language user were once completely unfamiliar nonwords. Recent examples of these are terms such as *blog*, *twitter*, or *selfie*. As language users, we have learned the form and meaning of these words by means of complex learning mechanisms that are particularly active in childhood but remain dynamic and effective throughout adulthood (Bloom, 2000; Mayor & Plunkett, 2010; McMurray, Horst, & Samuelson, 2012). Along the different stages of learning, individuals acquire most of their vocabulary incidentally and with no explicit instruction (e.g., Mestres-Missé, Rodriguez-Fornells, & Münte, 2007; Nagy, Anderson, & Herman, 1987). This process seems to depend on a variety of factors, including the number of different contexts in which words are encountered (e.g., Bolger, Balass, Landen, & Perfetti, 2008; van Daalen-Kapteijns, Elshout-Mohr, & de Glopper, 2001) and the amount of semantic information with which the new vocabulary is associated during learning (Ferreira, 2011; McKay, Castles, Davis, & Savage, 2007). A sizeable number of behavioral studies employing familiar words as stimuli have shown that words with rich semantic representations show processing advantages in comparison with words that have poor semantics (e.g., Grondin, Lupker, & McRae, 2006; Pexman, Lupker, & Hino, 2002; Pexman, Holyk, & Monfils, 2003; Yap, Tan, Pexman, & Hargreaves, 2011). Despite this, semantic richness has never been manipulated in word learning studies. In addition, the neural mechanisms that support semantic processing and benefit from richer semantic representations remain elusive. The current study investigated the neural correlates of processing newly learned words and matched familiar words associated with many or few semantic features.

Several different measures have been used to investigate semantic richness. These include word concreteness (e.g., Kroll & Merves, 1986), the number of semantic features (e.g., Pexman, Holyk, & Monfils, 2003), the number of semantic associates (e.g., Buchanan, Westbury, & Burgess, 2001), and the number of semantic neighbors (e.g., Siakaluk, Buchanan, & Westbury, 2003), among others. These variables have been widely used in studies of familiar words, where semantic richness effects have been reported in word naming (e.g., Pexman et al., 2002), lexical decision (e.g., Borowsky & Masson, 1996; Buchanan et al., 2001; Kroll & Marves, 1986; Pexman et al., 2002), semantic categorization (e.g., Grondin et al., 2006; Pexman et al., 2002; Pexman et al., 2003), and free recall (e.g., Walker & Hulme, 1999). Despite the overwhelming evidence of a semantic richness effect in behavioural studies, we are aware of only one fMRI study that directly investigated the neural correlates of semantic richness. Pexman, Hargreaves, Edwards, Henry, and Goodyear (2007) looked at neural differences between words with high and low number of semantic associates (NSA). They found less activation for high-NSA than low-NSA words in a number of cortical regions, including the left inferior frontal gyrus, and the left inferior temporal gyrus. No areas showed significantly higher activation for high-NSA than low-NSA words. Pexman and colleagues suggested that increased activity for low-NSA words was due to the more effortful lexical and semantic processing required by words with few associations.

In the current study, we used a different measure of semantic richness (the number of semantic features) and a word learning approach in order to gain more control over the differences between the semantic representations of our stimuli. The number of semantic features has been a very influential variable for classical, prototype, and exemplar theories of word meaning (Medin & Schaffer, 1978; Minda & Smith, 2002; Smith & Medin, 1981). Within the cognitive psychology tradition, concept and categorization theories have also employed semantic features (e.g., Minsky, 1975; Norman & Rumelhart, 1975), as well as computational models of semantic representation (e.g., Cree, McNorgan, & McRae, 2006; McRae, de Sa, & Seidenberg, 1997; Vigliocco, Vinson, Lewis, & Garrett, 2004). Within cognitive neuroscience, features have been used to explain semantic deficits in a wide variety of populations (Garrard, Lambon Ralph, Patterson, Pratt, & Hodges, 2005; Rogers et al., 2004; Tyler, Moss, Durrant-Peatfield, & Levy, 2000), among other phenomena. Despite being a crucial variable for theories of word meaning, there is very little information about the neural mechanisms underlying featural representations and particularly how new features are bound together to become integrated in semantic memory.

Most word learning research, including neuroimaging studies, has taught participants new labels for familiar concepts and can be thought of as simulating second language learning (e.g., Bradley, King, & Hernandez, 2013; Breitenstein et al., 2005; Clements-Stephens et al., 2012; Mestres-Missé, Cámara, Rodriguez-Fornells, Rotte, & Münte, 2008; Mestres-Missé, Rodriguez-Fornells, & Münte, 2010; Raboyeau, Marcotte, Adrover-Roig, & Ansaldo, 2010). Our paradigm, in contrast, was designed to simulate word learning in a first language where a new word is usually associated with a new concept. The present study is one of only a small number that have attempted to simulate the acquisition of new vocabulary in adults' first language by teaching novel word-forms in association with real but novel meanings (Cornelissen et al., 2004; Grönholm, Rinne, Vorobyev, & Laine, 2005; Hultén, Vihla, Laine, & Salmelin, 2009; Takashima, Bakker, van Hell, Janzen, & McQueen, 2014). To the best of our knowledge, the current study is also the first to combine a comparison of familiar *vs*. newly learned words with a comparison of rich *vs*. poor words, and the only one to make those comparisons in the context of a semantic judgment task (living or nonliving). We are therefore uniquely positioned to evaluate the extent to which differences in activations generated by rich and poor words, and different activations generated by familiar and newly learned words, can be given a similar explanation.

Despite the sizeable number of neuroimaging studies of semantics, the neurobiological foundation of semantic memory is still poorly understood. On the one hand, there seem to be some brain regions that are modality-specific, being associated with the processing of either written or spoken words, and others that are multi-modal, being involved in the integration of information from multiple modality-specific areas (e.g., Binder & Desai, 2011; Damasio, 1989a, b; Patterson, Nestor, & Rogers, 2007). Damasio (1989a, b) proposed the theory of convergence zones in order to account for the brain's ability to integrate input from different modalities. He suggested that convergence zones are located at multiple neural levels and can bind information from different sensory inputs. They also provide feedback to multiple lower-level cortical regions modulating neural activity. Due to their relevance for the current work, we focus primarily on multimodal areas or convergence zones, including inferior parietal lobe and much of the temporal lobe. On the basis of a meta-analysis of 120 functional neuroimaging studies, Binder et al. (2009) identified several putative semantic areas, which lie primarily in the left temporal lobe and the left inferior parietal cortex (Binder & Desai, 2011; Vigneau et al., 2006). Within inferior parietal cortex, the most consistently activated area was the angular gyrus (AG). Binder et al. (2009) suggested that the AG plays a role in high-level integration of complex semantic information; for example, integrating the meanings of the component words in sentences or the component sentences in texts, or combining spatial and temporal information to create representations of event concepts (cf. Bemis & Pylkkanen, 2013; Binder & Desai, 2011). Activation of the AG has been reported to be stronger for words than nonwords (Carreiras, Mechelli, Estévez, & Price, 2007; Cattinelli, Borghese, Gallucci, & Paulesu, 2013; Davis & Gaskell, 2009; Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005) and stronger for concrete than abstract nouns (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Mestres-Missé, Münte, & Rodriguez-Fornells, 2008; Sabsevitz, Medler, Seidenberg, & Binder, 2005). Words have meanings in a way that nonwords do not, and concrete words have been argued to have richer, more detailed semantic representations (on average) than abstract words (Plaut & McClelland, 1993). AG activation would therefore appear to be a function of the amount of semantic information being processed.

Another area involved in semantic processing is the anterior temporal lobe (ATL), identified in Binder et al.'s (2009) meta-analysis as extending back from the left temporal pole to include the anterior middle temporal gyrus (MTG) and portions of the inferior temporal gyrus and anterior fusiform gyrus. Devlin et al. (2000) reported stronger activation of the left anterior MTG and temporal pole during semantic decisions to written words compared with visual classification of letter sequences (see also Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Scott, Leff, & Wise, 2003; Visser, Jefferies, & Ralph, 2009). Stronger ATL responses have also been reported to high than low frequency words (Majerus et al., 2005; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006) and to familiar words than nonwords (Davis & Gaskell, 2009; Majerus et al., 2005; Orfanidou, Marslen-Wilson, & Davis, 2006). Ellis, Burani, Izura, Bromiley, and Venneri (2006) found stronger activation of left ATL when participants were naming early acquired objects than when they were naming late acquired objects. Urooj et al. (2014) obtained a similar pattern with MEG. Ellis et al. (2006) and Urooj et al. (2014) argued that these effects arise at the ATL because early acquired concepts have richer semantic representations than late acquired concepts.

Binder et al. (2009) proposed that the left ATL is involved in integrating semantic information across different sensory modalities and in concept retrieval (cf. Bemis & Pylkkanen, 2013). Other researchers have proposed that the region functions as a 'semantic hub', drawing together visual, auditory, motor, functional and 'encyclopedic' knowledge about words and concepts to form high-level, amodal conceptual representations (Patterson et al., 2007; Rogers et al., 2006; Visser, Embleton, Jefferies, Parker, & Ralph, 2010).

The present study investigated the neural consequences of semantic richness across familiar and newly learned words. Our study provides novel insights into the brain mechanisms involved in acquiring the semantic information of new words, using the number of semantic features. Its results inform our understanding on the number of exposure participants require in order to acquire a novel word and its meaning, and the extent to which the representations of novel words learned in an experimental setting resemble those of familiar, real words. The novel words were trained during the two days immediately preceding the scanning session. Participants learned the spoken forms, written forms and meanings of the novel words. We manipulated semantic richness by teaching participants many or few features of the novel concepts. In the scanning task, participants were shown the newly learned words mixed with an equal number of familiar words. The familiar words were selected on the basis of previously-obtained norms as being words for which adults typically have rich or poor semantic representations. An attempt was made to match the novel and the familiar words on semantic richness. Half the novel and half the familiar words referred to living things while the other half referred to nonliving things. The participants' task in the scanner was to classify each word as it appeared as living or nonliving.

The study therefore allowed orthogonal comparisons of neural activation during a semantic classification task to familiar versus newly learned words and to semantically rich versus semantically poor words, as well as the interaction between familiarity and semantic richness. On the basis of previous studies (see Binder et al., 2009), we expected to see more activation to familiar than newly learned words, and to rich than poor words, in areas associated with semantic representation including the AG and left ATL. In contrast, the task of deciding whether a word denotes a living or a nonliving thing should be more difficult for newly learned words and words with poor semantic representations than for familiar words and words with rich semantic representations. We therefore expected activation in IFG to show the opposite pattern of activations in the contrast between familiar and novel words and the orthogonal contrast between rich and poor words. Bearing in mind that orthographic and phonological processing areas respond more strongly to unfamiliar than familiar words (e.g., Bruno, Zumberge, Manis, Lu, & Goldman, 2008; Cattinelli et al., 2013; Davis & Gaskell, 2009), we also expected that activation of the left posterior and mid fusiform gyrus during orthographic processing and activation of the posterior MTG and posterior IFG during phonological processing would be stronger to novel than familiar words.

2. Materials and methods

2.1 Participants

The participants were 21 students from the University of York (7 males, 15 females; mean age = 20.82 years; range 18-30). All were right handed (laterality index >80; Oldfield, 1971) native speakers of British English with normal or corrected-to-normal vision. One additional participant was enrolled in the study but subsequently excluded from the group analyses because of high error rates (3.2 SDs below the group mean for accuracy) on the fMRI task. The study was approved by the Research Ethics and Governance Committee of the York Neuroimaging Centre, University of York, UK. Participants gave informed consent and received either payment or course credit.

2.2 Stimuli

The 40 familiar words used in the experiment were selected from a larger set of 100 object names. In a separate semantic feature generation study, the 100 object names were divided into 5 sets of 20. Each set was presented to a different group of 20 student participants who were asked to list as many attributes and semantic features as they could for each object (cf. McRae, Cree, Seidenberg, & McNorgan, 2005; Vinson & Vigliocco, 2008). Features were selected for inclusion if they were generated by at least 4 of the 20 participants (see Table 2SM, for detail). Taxonomic features (e.g., animal, tool) were excluded from the final count because the superordinate category of a concept conveys different information from that of other types of features (function, parts, etc.) (McRae et al., 2005). Twenty words (10 living, 10 nonliving) were chosen with high numbers of semantic features (mean = 18.0, range = 14-24). A further 20 words (10 living, 10 nonliving) were chosen with low numbers of semantic features (mean = 9.6, range = 5-13). Examples of familiar words for which participants listed many features and have, therefore, rich semantic representations are *duck*, *gorilla, bath* and *piano*. Examples of familiar words with poorer semantic representations are *crow*, *otter, peg* and *cello*. Familiar words were matched on AoA, concreteness, orthographic neighborhood, letter length, bigram frequency, and word frequency (see Table 1). Independent t-tests were run across all variables and found no significant differences between rich and poor words ($p > 0.05$).

Forty novel words were then created. These were matched to the familiar words on initial letter, number of letters, number of orthographic neighbors and bigram frequency. Examples are *darp*, *epernald, ornel* and *parack*. Details of the matching of both word and nonword sets are shown in Table 1. Each novel word was then paired with a real but obscure concept (half living and half nonliving, covering the same range of semantic categories as the familiar words). For example, *darp* was paired with helmeted hornbill (a bird) while *parack* was paired with cimbalom (a musical instrument). Half of the novel words were assigned to a high semantic features set. These semantically rich novel words were trained in association with colored pictures of the associated objects (see Figure 1SM) and accompanied by sentences which identified a mean of 18.0 specific features per concept (range 14-24). The number of semantic features trained for the rich novel words therefore matched the number of semantic features generated in the normative study for rich familiar words. Examples of the training sentences are *A darp is ugly, has an ivory-like helmet, and a wrinkled throat*, *A darp can fly, is large, and has a long white tail*. The remaining 20 novel words were assigned to the low semantic features set. These semantically poor novel words were trained in association with pictures that had been slightly blurred using the Gaussian Blur filter in Photoshop CS3, with a radius ranging from 7 to 10 pixels. The resulting images conveyed basic visual features, including shape and color of the novel objects (see Figure 1SM). The poor novel words were accompanied in training by sentences which identified a mean of 9.6 semantic features (range 5-13), matched to the number of semantic features produced for the poor familiar words. The sentences used to train the semantic features of the novel words never included taxonomic features (e.g., animal, object) since they are of a different nature (see McRae et al., 2005) and can provide access to many more features. We also avoided the words ‘living’ or ‘nonliving’ since this judgment had to be inferred during the fMRI experiment from the information provided.

Table 1 about here

2.3 Procedure

The experiment took place over three days. On days 1 and 2, participants were trained on both the spoken and written forms of the novel words. The training was carried out in a quiet room in the Department of Psychology. The training session on each day lasted approximately one hour. Day 3 involved categorizing the familiar and the newly learned novel words in the MRI scanner. This was followed by a semantic feature generation task that was added in order to assess learning and retention of the semantic features of the novel words.

2.3.1 Training

Training on day 1 began with task 1 in which the spoken forms of the 20 novel words from either the rich or the poor set were presented twice through headphones. Each nonword was accompanied by a picture of the associated unfamiliar object. This was followed by task 2 in which the same items (rich or poor) were presented in both spoken and written form, accompanied once again by the associated pictures. Participants were instructed to study the picture and read / repeat the word. Participants were then shown slides which presented the novel words embedded within sentences that conveyed semantic features. More semantic features were provided for the rich than the poor items. This was followed by short questions which prompted the participants to recall one of the semantic features of each novel word and type the name of that feature as a response (e.g., *What is a parak made of?*). The correct answer (e.g., *It is made of wood*) was then displayed. Task 3 involved presenting the 20 pictures one at a time, accompanied by the written and spoken novel words, but without the feature sentences. Participants were instructed to type each novel word into a space below the picture. Task 4 was similar to task 3 except that the written form of the novel word did not accompany the picture and the spoken word. Participants were instructed to type the word in the space below the picture. When the participant pressed Enter, the correct form of the word was displayed above the picture so that they could compare the correct form with their attempt. After completing the four tasks with one set of novel words (rich or poor), participants were allowed a short break before repeating the entire procedure with the other set.

On day 2, tasks 1 to 4 were repeated with only slight modifications. Those participants who were trained on day 1 on rich novel words followed by poor novel words received the two sets in the opposite order on day 2. The remaining participants who were trained on day 1 on poor novel words followed by rich novel words likewise received the two sets in the opposite order on day 2. Following the second presentation of task 4, a fifth task was given. Whereas the two versions of task 4 contained either the rich novel words or the poor novel words, task 5 required participants to type the names of *all* the objects in response to pictures only, with rich and poor items interleaved in a random order. In each trial, the correct name of the item was presented after the participants had entered their attempt.

By the end of day 2, participants had heard each novel word 6 times across the two training sessions, read it as an isolated written word 7 times and in sentence contexts 10 times, and had attempted to type it 4 times, making 27 exposures in total.

2.3.2 Scanning Task

On day 3, participants were tested in the York Neuroimaging Centre. Before scanning, participants were familiarized with the categorization task by completing 10 practice trials using additional familiar words. Once positioned in the scanner, participants performed the semantic categorization task on the 40 novel words and 40 familiar object names (which had not previously been exposed in the experiment). An event-related design was used, with the 80 experimental stimuli being presented in a random, interleaved order. Stimuli were back-projected onto a screen which could be viewed through an angled mirror positioned above the participant's head. Each trial began with a 500 msec fixation cross at the center of the screen, followed by a familiar or newly learned word presented for 2,500 msec in lower case 50-point Courier New font in white on a black background. Participants were instructed to classify each word as living or nonliving as quickly as possible by pressing one of two buttons on a response box held in their right hand. Half the participants pressed the button under their index finger for 'living' and the button under their middle finger for 'nonliving'. For the remaining participants, the designation of the two buttons was reversed. Following the presentation of each word, a blank screen appeared for an average of 2.5 secs (range 1.1 - 8.0 secs jittered across trials). The presentation of the stimuli and collection of reaction times was done using the Presentation software (version 12.0, www.neurobs.com).

All 80 stimulus words were presented once in a randomized, fully interleaved order. The 80 words were then presented again in a different order but within the same acquisition run. There were therefore 160 trials in total, 40 per experimental condition (familiar rich, familiar poor, novel rich, novel poor).

2.3.3 Feature Recall Task

After completing the scanning experiment, participants were taken to a different room where they were presented with the 40 novel words one at a time and were allowed a maximum of 1 minute to write down as much information as they could remember about each one in the form of a list of features or attributes. As an example, they were shown all features listed for the word *cheese* in the McRae et al. (2005) study.

2.3.4 MRI Data Acquisition

Whole-brain structural and functional images were acquired on a 3.0 Tesla MRI scanner (General Electric HDx Excite) using an 8-channel, 8-element phased-array head coil. Foam padding was used to keep participants' heads stable and minimize movement. Participants wore earplugs to reduce noise levels. fMRI data were acquired using a gradient single-shot echo planar imaging (EPI) sequence (TR = 3 sec, TE = 33.7 msec, flip angle = 90º, FOV = 26 x 26, matrix = 128 x 128, continuous slice thickness = 3.5 mm). In order to facilitate localization and co-registration of functional data to the structural image, a T1-weighted in-plane anatomical image was also acquired using a fluid attenuated inversion recovery (FLAIR) sequence (TR = 2.5 sec, TE = 9.94 msec, inversion time (TI) 1050 msec, acquisition matrix = 256 x 224, FOV = 288 mm, slice thickness = 3 mm). High-resolution T1-weighted structural images were acquired using an inversion recovery-prepared 3-D FSPGR (Fast Spoiled Gradient Echo) pulse sequence (TR = 8.03 msec, TE = 3.07 msec, TI = 450 msec, acquisition matrix = 256 x 256, Flip angle 20º, FOV = 290 mm, slice thickness = 1 mm).

2.4 fMRI Data Analysis

Functional imaging data were pre-processed and analyzed using version 5.98 of FEAT, the FMRI Expert Analysis Tool in FSL 4.1.8 (FMRIB, Oxford, UK; http://www.fmrib.ox.ac.uk/fsl). Trials were defined as extending from the presentation of the stimulus word (individualized onset times for each participant) to the moment when a push-button response was detected (cf. Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). The same trials were used in the fMRI analysis as in the RT analysis (i.e. correct responses only with RTs >300 msec and <2.5 SDs from the mean for each condition and presentation). The data were first pre-processed using MCFLIRT motion correction, slice-timing correction with Fourier-space time series phase-shifting, spatial smoothing (Gaussian, FWHM 8 mm) and high pass temporal filtering (Gaussian-weighted least-squares straight line fitting with sigma = 50 sec). Registration to high-resolution and standard space was carried out using FMRIB's linear registration tool FLIRT (Jenkinson & Smith, 2001; Jenkinson, Bannister, Brady, & Smith, 2002). First-level general linear model (FILM) time-series analysis was carried out using local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). The data from each participant's fMRI session were entered into a general linear model for event-related analysis with 4 event types derived from the factorial crossing of familiarity (familiar versus novel) and semantic richness (rich versus poor). Familiarity x semantic richness interactions (familiar-rich + novel-poor versus familiar-poor + novel-rich) were also modeled. Two regressors were added at the first level analysis to account for order of presentation and RT. The regressor for order of presentation was included due to the variance associated with the fact that RTs were generally faster to second than first presentations of the stimulus words. The regressor for RT accounted for possible domain-general effects due to performance differences in response time across conditions (participants responded faster to familiar than novel words and to rich than poor words).

Higher-level analyses were conducted across the 21 participants using FLAME Bayesian mixed-effects analysis (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004) in order to generate z-statistics based on the contrasts between the conditions presented above. FMRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by Z > 2.3 and a (corrected) cluster significance threshold of $p = .05$ (Forman, Cohen, Fitzgerald, Eddy, Mintun, & Noll, 1995; Worsley, 2001). Peaks of activation falling more than 8 mm apart are reported separately. When peaks were separated by less than 8 mm, only the highest peak is reported.

Two conjunction analyses were also performed in FSL following the method described in Nichols, Brett, Andersson, Wager, and Poline (2005). These were 1. the conjunction of familiar > novel and rich > poor, and 2. the conjunction of novel > familiar and poor > rich**.** Images were again cluster thresholded at $Z > 2.3$ and a cluster significance threshold of $p < .05$ was employed.

Areas of activation were labeled with the help of the Harvard-Oxford Cortical Structure Atlas and the Harvard-Oxford Subcortical Structure Atlas incorporated into FSL view (Oxford Centre for Functional MRI of the Brain (FMRIB) Software Library; www.fmrib.ox.ac.uk/fsl). All coordinates are in MNI space (Evans, Collins, & Milner, 1992).

3. Results

3.1 Behavioral Data

3.1.1 Semantic Categorization

The 21 participants contributed 3360 responses (80 stimuli presented twice each to 21 participants). Of those 3360 responses, just 113 (3.4%) were miscategorization errors while 8 (0.2%) were no-response errors. Outliers were defined as responses below 300 msec or more that 2.5 SDs above the mean (defined separately for each participant for first and second presentations of familiar and novel items). Fifty-three outliers (1.6% of responses) were deleted. A total of 174 responses (5.2%) were therefore removed from both the RT and fMRI analyses.

The behavioral results for the categorization task are shown in Table 2. Because each word was categorized twice, the effects on RT and accuracy were analyzed in a repeated measures ANOVA with factors of presentation (1st or 2nd), familiarity (familiar versus novel) and semantic richness (rich versus poor). Effect sizes were measured in terms of partial eta squared (η_p^2). Analysis of RTs for correct, trimmed responses found a significant 139 msec effect of presentation, $F(1, 20) = 104.63$, $p < .001$, $\eta_p^2 = .84$, with faster responses to second presentations than first presentations, a 175 msec effect of familiarity, $F(1, 20) = 63.08$, $p < .001$, $\eta_p^2 = .76$, with faster responses to familiar words than novel words, and a 52 msec effect of semantic richness, $F(1, 20) = 29.80$, $p < .01$, $\eta_p^2 = .60$, with faster responses to items with rich than poor meanings. The only significant interaction was between presentation and familiarity, $F(1, 20) = 45.98$, $p < .001$, $\eta_p^2 = .70$, where the difference in RTs between familiar and novel words was reduced for the second presentation compared with the first. The interaction between familiarity and richness did not approach significance, $F(1, 20) = 1.09$, $p = .31$, $\eta_p^2 = .08$, indicating that the effect of semantic richness on RTs was comparable for familiar and novel words.

Table 2 about here

Error rates were generally low. Analysis of error rates showed significant main effects of familiarity, $F(1, 20) = 13.17$, $p < .01$, $\eta_p^2 = .40$, with fewer categorization errors to familiar than to novel words, and semantic richness, $F(1, 20) = 7.92$, $p < .01$, $\eta_p^2 = .28$, with fewer errors to rich than poor items. The main effect of presentation order on error rates was not significant. The only significant interaction involved familiarity and semantic richness, $F(1, 20) = 4.58$, $p < .05$, $\eta_p^2 = .19$, reflecting the fact that the difference in error rates between rich and poor items was greater for novel than familiar words.

3.1.2 Feature Recall Task

Feature lists generated for the novel words after the scanning experiment were scored using the criteria employed by McRae et al. (2005). Participants recalled significantly more features for the novel words with rich semantics (mean = 6.0, SD = 1.4) than for the novel words with poor semantics (mean = 3.5, SD = 1.3), *t*(23) = 12.10, *p* < .001.

3.2 Neuroimaging Data

Whole-brain analysis was based on the same trials that were used in the analysis of RTs (i.e., trials where the stimuli were categorized correctly with RT outliers removed, which comprised 94.8% of all trials). BOLD responses were compared to familiar and novel words combined across rich and poor, and to rich and poor words combined across familiar and novel. The results are shown in Table 3 and Figure 1.

Both contrasts involving familiarity (familiar > novel and novel > familiar) produced significant clusters (Figure 1A). Greater activation to familiar than novel words was observed in the following regions: 1. the left occipito-temporo-parietal junction, including the superior lateral occipital cortex, the supramarginal gyrus, and the angular gyri, 2. the right occipito-temporal-parietal junction including the angular gyrus and the lateral occipital cortex, 3. left temporal cortex comprising inferior, middle, and superior temporal gyri, 4. left fronto-temporal cortex, which included frontal orbital cortex, IFG (pars triangularis), lateral frontal pole, and temporal pole, 5. right frontal and prefrontal cortices extending from frontal orbital cortex to IFG (pars triangularis, pars opercularis), 6. medial frontal and prefrontal cortices comprising bilateral superior frontal gyrus and left paracingulate gyrus, 7. bilateral precuneus and left posterior cingulate gyrus.

The converse pattern of greater activation to novel than familiar words was observed in 1. left ventral occipitotemporal (fusiform) cortex, 2. left medial inferior frontal pole and insular cortex, 3. right inferior insular and inferior frontal pole, 4. left parietal-occipital junction including parietal lobule, lateral occipital cortex, cuneus and extending into the left cerebellum.

The contrasts involving semantic richness revealed four major clusters showing stronger activation to rich than poor words. These were 1. the left AG and lateral occipital cortex, 2. left paracingulate gyri and frontal pole bilaterally, 3. bilateral precuneus and left posterior cingulate gyrus, 4. left temporal cortex including middle, superior, and inferior temporal gyri (Figure 1B). No significant clusters were observed showing stronger activation to poor than rich words.

An interaction between familiarity and semantic richness was found in one cluster located in bilateral cerebellum. This interaction reflected significantly higher activation for rich versus poor in novel words and no differences between these contrasts in familiar words.

In the conjunction analysis, the conjunction of familiar > novel and rich > poor revealed significant activations in the left AG / LOC, and left medial inferior prefrontal cortex extending into the right paracingulate gyrus (Fig. 1C and Table 3). The conjunction of novel > familiar and poor > rich found no significant activations.

Figure 1 and Table 3 about here

4. Discussion

Participants made an average of only 3.4% categorization errors in the scanner, demonstrating that the novel words had been well learned during the previous two days and that the familiar words that were interspersed with them were known to the participants. Participants were, however, faster to classify familiar than novel words, and rich than poor words. The effect of familiarity on categorization RTs was about three times larger than the effect of semantic richness and mirrors the faster semantic categorization of high than low frequency words reported by Taft and van Graan (1998). The faster categorization of rich than poor words, albeit with a smaller effect size, replicates similar behavioral findings by Pexman et al. (2003) and Yap et al. (2011). We note that the words 'living' and 'nonliving' were never used in the training of the novel words and that a range of different types of living and nonliving objects were used (e.g., birds, mammals, fish and insects for living things and clothing, tools and household objects for nonliving). Participants therefore had to retrieve what they knew about the meanings of the novel words in order to make their judgments.

Classifying familiar words generated more activation than classifying newly learned words in several parts of the semantic processing network identified by Binder et al. (2009). These included the left ATL / MTG and bilateral angular gyri, medial prefrontal cortex and precuneus / posterior cingulate gyri bilaterally. Other regions showed the opposite pattern of stronger responses to novel than familiar words and corresponded roughly to non-semantic areas of the reading network (Dehaene, 2010), including left occipital and ventral occipito-temporal regions, and bilateral anterior insula.

Reliable effects of semantic richness were observed in left AG, left anterior MTG, bilateral precuneus / posterior cingulate gyri, and left paracingulate gyrus, with stronger activation to rich than poor words. The left AG was also highlighted in the conjunction of familiar *vs*. novel and rich *vs*. poor words. No regions were found to show significantly stronger activation to poor than rich words. The only interaction found was located in bilateral cerebellum and it is explained by higher activation for rich *vs*. poor in novel words (see Table 3). Overall, our results replicated the findings of previous word *vs*. novel word studies (e.g., Davis & Gaskell, 2009; Orfanidou et al., 2006), and are compatible with the proposal that participants had less detailed semantic representations for novel than familiar words, and for poor than newly learned words. This was particularly clear in the left AG, which was activated in the conjunction (familiar > novel and rich > poor) analysis but showed no interaction effect, implying that semantic richness affected both familiar and newly learned words in this region. This fits in well with previous evidence since the left AG has been consistently activated in studies of semantic contrasts, including words *vs*. nonwords, semantic *vs*. phonological tasks, and meaningful *vs*. meaningless stimuli (see Binder et al., 2009, for review). Similar patterns of activation have also been reported by Orfanidou et al. (2006) in a comparison of words and nonwords in auditory lexical decision and by Davis and Gaskell (2009) in their meta-analysis covering several different auditory word processing tasks.

Regarding familiar word contrasts, Graves, Desai, Humphries, Seidenberg, and Binder, (2010) reported stronger bilateral AG responses to high than low frequency words using reading aloud. They also found enhanced activity for high *vs*. low imageability words in bilateral AG while Binder et al. (2005) and Sabsevitz et al. (2005) found stronger bilateral AG activation to concrete / high imageability nouns than to abstract / low imageability nouns (in lexical decision and semantic categorization, respectively). Binder et al. (2009) and Binder and Desai (2011) proposed that the AG plays a role in integrating high-level information, including integrating conceptual information with the spatial and temporal information necessary to define and represent coherent events (Ferstl, Rinck, & von Cramon, 2005; Ferstl & von Cramon, 2007). In the present experiment, the AG's role may have been to integrate the meanings of words and concepts being classified as living or nonliving. Familiar and rich words provide more semantic information to integrate with the context than do novel and poor words, so AG activation is correspondingly greater and may require the involvement of left (for rich *vs*. poor) and also right hemisphere resources, in the case of familiar *vs*. novel contrasts. We suggest that unlike the bilateral familiarity effect, semantic richness appears to modulate activity primarily in the left AG.

Beside the argument for a semantic hypothesis, we cannot ignore the possibility that increased activity for familiar > novel and rich > poor in AG might also reflect episodic memory processing since more access to semantic information will necessarily give rise to more event knowledge. This fits in well with previous interpretations since AG, as a general-domain area, stores abstract representations of concepts and event knowledge (Binder & Desai, 2011). Regarding episodic memory, Humphreys and Lambon Ralph (in press) discussed two alternative episodic views for AG activation, one in which the AG's role would be a temporal store of episodic information and another in which AG is the basis of a long-term multimodal episodic store. Our result probably fits best the second view since we also postulate a similar semantic interpretation. It is worth clarifying that it is beyond the scope of this study to discuss in depth which episodic view can best explain our findings.

The second region where we expected to find more activation for rich *vs*. poor words was the left ATL since this area is thought to be concerned with integrating semantic information across different sensory modalities (Patterson et al., 2007). The familiar *vs*. novel contrast produced a reliable effect in left ATL, including anterior temporal pole and MTG, whereas the comparison between rich *vs*. poor showed a similar pattern, but activation only reached significance within left MTG (see Table 3). Overall, these results are consistent with other studies, which have reported stronger left ATL responses to words than nonwords (Davis and Gaskell 2009; Majerus et al. 2005; Orfanidou et al. 2006), high than low frequency words (Prabhakaran et al. 2006) and early than late acquired words (Ellis et al., 2006; Urooj et al., 2014). Like Pexman et al. (2007), we were unable to observe stronger anterior temporal pole activation to rich than poor words. If left ATL activation is a function of the amount of detail present in semantic representations, then some measure of semantic richness *should* affect activation along the entire region. We suspect that lack of a significant effect of richness at the left anterior temporal pole in the present study may be due to a combination of the smaller effect size for richness compared with familiarity that was revealed in the RT data and the known difficulty of obtaining strong signals from the most anterior part of ATL using fMRI (Visser et al., 2010). The significant activation for rich *vs*. poor found in left MTG was located within the boundaries of one of the areas Binder and Desai (2011) called convergence zones. In their view, semantic memory consists of both modality-specific and supramodal representations. The latter are supported by convergence zones located in inferior parietal and temporal association cortex (mainly a large portion of MTG extending into ITG). Binder et al.

(2009) found reliable activation throughout left temporal and parietal ‘heteromodal’ cortex. Interestingly, these areas correlate highly with the location of regions implicated in semantic dementia and semantic impairment due to temporal and parietal vascular lesions.

Another network of brain regions, including the bilateral paracingulate gyrus and medial prefrontal cortex, was highlighted across familiar *vs*. novel, rich *vs*. poor, and in the conjunction analysis. Binder et al. (2009) distinguished a ventromedial prefrontal region that includes medial orbital prefrontal cortex and the anterior cingulate from a more dorsal medial prefrontal region. They suggested that the ventromedial prefrontal region is involved in processing the affective significance of concepts while the more dorsal region is associated with self-guided, goal-directed retrieval of semantic information. Binder and Desai (2011) suggested that the more dorsal region may mediate between the ventromedial area and lateral prefrontal areas involved in activation, selection and maintenance of semantic representations and in decision making. The division between Binder et al.'s two medial prefrontal semantic systems is not apparent in our results which show only a single, larger area of bilateral activation, across familiar *vs*. novel words, but with left lateralization in the paracingulate gyrus for rich *vs*. poor, and the medial prefrontal region of the network in the conjunction analysis. If there are indeed two distinct medial prefrontal semantic systems, then our combined results indicate that both are more strongly activated by semantically rich than semantically poor words. If those areas were concerned in the present experiment with processing the affective significance of words and retrieving those semantic features that are relevant to the goal of classifying words as denoting living or nonliving things, it would seem reasonable to propose that semantically poor words will have less emotional significance than semantically rich words, and will activate fewer features relevant to the task of categorizing them as living or nonliving.

The final set of areas that also showed increased activity for familiar *vs*. novel and rich *vs*. poor was the cluster extending from bilateral precuneus to left posterior cingulate gyrus. We note that Mestres-Missé et al. (2010) found greater activation to new words presented in a 2-sentence context *vs*. a 1-sentence context in approximately the same regions, while Binder et al. (2005) and Sabsevitz et al. (2005) found more posterior cingulate and precuneus activation to concrete than abstract nouns bilaterally. Graves et al. (2010) found positive correlations between imageability and left posterior cingulate gyrus, as well as word frequency and bilateral posterior cingulate activation. The common finding between our study and those of Binder et al. (2005), Mestres-Missé et al. (2010) and Sabsevitz et al. (2005) is that the association of stimuli with more meaning results in more activation in posterior cingulate gyrus and the precuneus. Binder et al. (2009) noted that this region has been associated with a variety of functions including episodic and visuospatial memory, emotion processing and visual imagery. They reported that posterior cingulate and adjacent cortex has strong reciprocal connections with the hippocampal complex and suggested that the posterior cingulate acts as an interface between semantic retrieval and episodic encoding systems. If so, this bilateral response may be linked in the present experiment to the bilateral activation of the angular gyri. If the angular gyri are involved in defining and representing events by associating semantic features with spatial and temporal information, the posterior cingulate may be involved in helping to convert those event representations into permanent memories – in this case memories of categorizing a mixture of familiar and newly learned words while in a scanner, creating associations to the stimulus words to accompany the featural semantics (cf. Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Noppeney & Price, 2003). That said, we would not want to rule out an involvement of visual imagery in this response. Novel rich words were trained in conjunction with clear images of the associated unfamiliar objects while novel poor words were trained in conjunction with rather blurred images. If participants tried to conjure up visual images of associated objects when categorizing their written names as living or nonliving, areas involved in retrieving visual images could be more strongly activated by rich than poor meanings and by familiar than novel words. Those visual images could then form part of the same multimodal event memories that bind together featural semantics with the wider context in which words are experienced and processed.

The only area that showed a familiarity x semantic richness interaction was the cerebellum (see Table 3). Activation was higher for rich *vs*. poor only across novel words. Other word learning studies have also reported higher activation in the right cerebellum, for novel words presented in 2-sentence contexts *vs*. 1-sentence context (Mestres-Missé et al., 2008b; Mestres-Missé et al., 2010). As in our study, the cerebellum seems to be more active when more information is presented in association with the novel words. Hence, it is possible that this region has a role in learning since it shows higher activation when binding together a higher number of features or processing richer contextual information, as in Mestres-Missé et al.'s studies.

Overall, the results presented above have partially met our predictions since words with higher number of features produced higher activation in left AG and within left MTG – the two supramodal areas depicted by Binder and Desai (2011). The fact that no semantic richness effect was found in left anterior temporal pole, either due to lack of statistical power or signal loss, does not allow us to support a fundamental role of ATL in the integration of semantic features into concepts. Our results do not fit the 'semantic-plus-hub' view of semantic processing introduced by Patterson et al. (2007) since this approach attributes a central role to ATL as a multimodal area.

From the three most influential models of semantic processing, our findings are best accommodated by the neuroanatomical model of semantic processing of Binder and Desai (2011). This model proposes the existence of several multimodal areas without a prominent role for ATL. We found increased activity for rich *vs*. poor words along the MTG and left AG, within two of the regions that the above authors postulate as convergence zones (inferior parietal and temporal association cortex). Unlike Binder and Desai's model, the 'hub and spoke' model of Patterson et al. (2007) and the convergence zone model of Damasio (1989a,

b) both support the view that the anterior temporal pole represents the highest level in the hierarchy of convergence zones. Our findings did not show reliable activation in this region for the comparison rich *vs*. poor, which suggests that ATL might not play a fundamental role in the processing of more semantic features or the integration of more features into new concepts. Unlike ATL, the AG was the most strongly activated area for the comparison rich *vs*. poor supporting a role for increasingly richer semantic representations in this region. Binder and Desai (2011) argued that the inferior parietal cortex is located at a crossroad between different input modalities including visual, spatial, somatosensory, and auditory processing streams. The crucial location of this region and the evidence from a number of human functional imaging studies links it to high-level heteromodal semantic processing. The rational for our study is that words with high number of features generate the spread of more information from modal areas into convergence zones like inferior parietal and temporal cortex. In the process of learning new words with many or few features, the same pattern seems to be observed. As participants bind more features together for a particular concept, activation in the above heteromodal regions seems to increase due to progressively richer / more abstract semantic representations.

5. Conclusions

We report a word learning study that had participants learn new concepts and words with either rich or poor semantic representations. The study shows how the brain responds to the challenge of processing, comprehending and making semantic decisions to familiar and newly learned words with rich and poor meaning. In line with previous neuroimaging studies of semantics, we found that both familiar and newly learned words with many semantic features (rich meaning) showed increased activity primarily in the AG, and to a lesser extend, in anterior MTG, two areas associated with the integration of information from different input modalities. Along with the AG and MTG, the precuneus and posterior cingulate gyrus showed the same pattern, which we interpreted as reflecting an interface between semantic retrieval (driven by AG) and episodic encoding systems. Our findings are best accommodated by the neuroanatomical model of semantic processing of Binder and Desai (2011) since concepts that have or acquire more semantic features produce a heightened response in heteromodal regions, within left inferior parietal and temporal cortex.

Acknowledgments

This work was supported by the Chilean Government through the Comisión Nacional de Investigación Científica y Tecnológica (Becas CONICYT) and the Fondo Nacional de Desarrollo Científico y Tecnológico (CONICYT-FONDECYT 11130678).

We thank Anastasia Roschupkina for assistance with running participants. We also thank Fernando Cuetos, Ed Silson and members of the York Psycholinguistics Research Group for comments on this work.

References

Balota, D. A., Yap, M. J., Hutchison, K. A., Cortese, M. J., Kessler, B., Loftis, B., … Treiman, R. (2007). The English lexicon project. *Behavior Research Methods*, *39*(3), 445–459.

Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2003). General multilevel linear modeling for group analysis in FMRI. *Neuroimage*, *20*(2), 1052–1063.

Bemis, D. K., & Pylkkanen, L. (2013). Combination across domains: An MEG Investigation into the relationship between mathematical, pictorial, and linguistic processing. *Frontiers in Psychology*, *3, 583*.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*(11), 527–536.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796.

Binder, J. R., Medler, D. A., Desai, R., Conant, L. L., & Liebenthal, E. (2005). Some neurophysiological constraints on models of word naming. *NeuroImage*, *27*(3), 677–693.

Binney, R. J., Embleton, K. V., Jefferies, E., Parker, G. J. ., & Ralph, M. A. . (2010). The ventral and inferolateral aspects of the anterior temporal lobe are crucial in semantic memory: evidence from a novel direct comparison of distortion-corrected fMRI, rTMS, and semantic dementia. *Cerebral Cortex*, *20*(11), 2728–2738.

Bloom, P. (2000). *How children learn the meanings of words: Learning, development and conceptual change*. Cambridge (MA): MIT Press.

Bolger, D. J., Balass, M., Landen, E., & Perfetti, C. A. (2008). Context variation and definitions in learning the meanings of words: An instance-based learning approach. *Discourse Processes*, *45*(2), 122–159.

Borowsky, R., & Masson, M. E. . (1996). Semantic ambiguity effects in word identification. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *22*(1), 63.

Bradley, K. A. L., King, K. E., & Hernandez, A. E. (2013). Language experience differentiates prefrontal and subcortical activation of the cognitive control network in novel word learning. *NeuroImage*, *67*, 101–110.

Breitenstein, C., Jansen, A., Deppe, M., Foerster, A. F., Sommer, J., Wolbers, T., & Knecht, S. (2005). Hippocampus activity differentiates good from poor learners of a novel lexicon. *Neuroimage*, *25*(3), 958–968.

Bruno, J. L., Zumberge, A., Manis, F. R., Lu, Z. L., & Goldman, J. G. (2008). Sensitivity to orthographic familiarity in the occipito-temporal region. *Neuroimage*, *39*(4), 1988–2001.

Brysbaert, M., & New, B. (2009). Moving beyond Kucera and Francis: a critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods*, *41*(4), 977–990.

Brysbaert, M., Warriner, A. B., & Kuperman, V. (2014). Concreteness ratings for 40 thousand generally known English word lemmas. *Behavior Research Methods*, *46*(3), 904–911.

Buchanan, L., Westbury, C., & Burgess, C. (2001). Characterizing semantic space: Neighborhood effects in word recognition. *Psychonomic Bulletin & Review*, *8*(3), 531–544.

Cappa, S. F., Perani, D., Schnur, T., Tettamanti, M., & Fazio, F. (1998). The effects of semantic category and knowledge type on lexical-semantic access: a PET study. *NeuroImage*, *8*(4), 350–359.

Carreiras, M., Mechelli, A., Estévez, A., & Price, C. J. (2007). Brain activation for lexical decision and reading aloud: Two sides of the same coin? *Journal of Cognitive Neuroscience*, *19*(3), 433–444.

Cattinelli, I., Borghese, N. A., Gallucci, M., & Paulesu, E. (2013). Reading the reading brain: A new meta-analysis of functional imaging data on reading. *Journal of Neurolinguistics*, *26*(1), 214–238.

Clements-Stephens, A. M., Materek, A. D., Eason, S. H., Scarborough, H. S., Pugh, K. R., Rimrodt, S., … Cutting, L. E. (2012). Neural circuitry associated with two different approaches to novel word learning. *Developmental Cognitive Neuroscience*, *2*(Suppl 1), S99–S113.

Cornelissen, K., Laine, M., Renvall, K., Saarinen, T., Martin, N., & Salmelin, R. (2004). Learning new names for new objects: cortical effects as measured by magnetoencephalography. *Brain and Language*, *89*(3), 617–622.

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. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*(4), 643–658.

Damasio, A. R. (1989a). The Brain Binds Entities and Events by Multiregional Activation from Convergence Zones. *Neural Computation*, *1*(1), 123–132.

Damasio, A. R. (1989b). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, *33*(1–2), 25–62.

Davis, M. H., & Gaskell, M. G. (2009). A complementary systems account of word learning: neural and behavioural evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1536), 3773–3800.

Dehaene, S. (2010). *Reading in the Brain: The New Science of How We Read* (Reprint edition.). New York: Penguin Books.

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Wilson, J., Moss, H. E., … Tyler, L. K. (2000). Susceptibility-induced loss of signal: comparing PET and fMRI on a semantic task. *NeuroImage*, *11*(6 Pt 1), 589–600.

Ellis, A. W., Burani, C., Izura, C., Bromiley, A., & Venneri, A. (2006). Traces of vocabulary acquisition in the brain: Evidence from covert object naming. *Neuroimage*, *33*(3), 958–968.

Evans, A. C., Collins, D. L., & Milner, B. (1992). An MRI-based stereotactic atlas from 250 young normal subjects. *Society for Neuroscience Abstracts, 18*, 408.

Ferreira, R. A. (2011, September 14). Learning the meaning of new words: Behavioural and neuroimaging evidence. Retrieved July 18, 2012, from http://etheses.whiterose.ac.uk/1735/

Ferstl, E. C., & von Cramon, D. Y. (2007). Time, space and emotion: fMRI reveals content-specific activation during text comprehension. *Neuroscience Letters*, *427*(3), 159–164.

Ferstl, E. C., Rinck, M., & von Cramon, D. Y. (2005). Emotional and temporal aspects of situation model processing during text comprehension: an event-related fMRI study. *Journal of Cognitive Neuroscience*, *17*(5), 724–739.

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magnetic Resonance in Medicine: Official Journal of the Society of Magnetic Resonance in Medicine / Society of Magnetic Resonance in Medicine*, *33*(5), 636–647.

Garrard, P., Lambon Ralph, M. A., Patterson, K., Pratt, K. H., & Hodges, J. R. (2005). Semantic feature knowledge and picture naming in dementia of Alzheimer’s type: A new approach. *Brain and Language*, *93*(1), 79–94.

Graves, W. W., Desai, R., Humphries, C., Seidenberg, M. S., & Binder, J. R. (2010). Neural systems for reading aloud: a multiparametric approach. *Cerebral Cortex*, *20*(8), 1799–1815.

Grinband, J., Wager, T. D., Lindquist, M., Ferrera, V. P., & Hirsch, J. (2008). Detection of time-varying signals in event-related fMRI designs. *NeuroImage*, *43*(3), 509–520.

Grondin, R., Lupker, S. J., & McRae, K. (2006). Shared features dominate the number-of-features effect. In *Proceedings of the 28th annual meeting of the Cognitive Science Society* (pp. 1400–1405).

Grönholm, P., Rinne, J. O., Vorobyev, V., & Laine, M. (2005). Naming of newly learned objects: a PET activation study. *Brain Research*. *Cognitive Brain Research*, *25*(1), 359–371.

Hultén, A., Vihla, M., Laine, M., & Salmelin, R. (2009). Accessing newly learned names and meanings in the native language. *Human Brain Mapping*, *30*(3), 976–989.

Humphreys, G. F., & Lambon Ralph, M. A. (in press). Fusion and Fission of Cognitive Functions in the Human Parietal Cortex. *Cerebral Cortex*.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*(2), 143–156.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*(2), 825–841.

Kroll, J. F., & Merves, J. S. (1986). Lexical access for concrete and abstract words. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *12*(1), 92–107.

Kuperman, V., Stadthagen-Gonzalez, H., & Brysbaert, M. (2012). Age-of-acquisition ratings for 30,000 English words. *Behavior Research Methods*, *44*(4), 978–990.

Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behavior Research Methods, Instruments, & Computers*, *28*(2), 203–208.

Majerus, S., Van der Linden, M., Collette, F., Laureys, S., Poncelet, M., Degueldre, C., … Salmon, E. (2005). Modulation of brain activity during phonological familiarization. *Brain and Language*, *92*(3), 320–331.

Mayor, J., & Plunkett, K. (2010). A neurocomputational account of taxonomic responding and fast mapping in early word learning. *Psychological Review*, *117*(1), 1–31.

McKay, A., Castles, A., Davis, C., & Savage, G. (2007). The impact of progressive semantic loss on reading aloud. *Cognitive Neuropsychology*, *24*(2), 162–186.

McMurray, B., Horst, J. S., & Samuelson, L. K. (2012). Word learning emerges from the interaction of online referent selection and slow associative learning. *Psychological Review*, *119*(4), 831–877.

McRae, K., Cree, G. S., Seidenberg, M. S., & McNorgan, C. (2005). Semantic feature production norms for a large set of living and nonliving things. *Behavior Research Methods*, *37*(4), 547–559.

McRae, K., de Sa, V. R., & Seidenberg, M. S. (1997). On the nature and scope of featural representations of word meaning. *Journal of Experimental Psychology: General*, *126*(2), 99–130.

Medin, D. L., & Schaffer, M. M. (1978). Context theory of classification learning. *Psychological Review*, *85*(3), 207–238.

Mestres-Missé, A., Cámara, E., Rodriguez-Fornells, A., Rotte, M., & Münte, T. F. (2008a). Functional neuroanatomy of meaning acquisition from context. *Journal of Cognitive Neuroscience*, *20*(12), 2153–2166.

Mestres-Missé, A., Münte, T. F., & Rodriguez-Fornells, A. (2008b). Functional Neuroanatomy of Contextual Acquisition of Concrete and Abstract Words. *Journal of Cognitive Neuroscience*, *21*(11), 2154–2171.

Mestres-Missé, A., Rodriguez-Fornells, A., & Münte, T. F. (2007). Watching the brain during meaning acquisition. *Cerebral Cortex, 17*(8), 1858–1866.

Mestres-Missé, A., Rodriguez-Fornells, A., & Münte, T. F. (2010). Neural differences in the mapping of verb and noun concepts onto novel words. *NeuroImage*, *49*(3), 2826–2835.

Minda, J. P., & Smith, D. J. (2002). Comparing prototype-based and exemplar-based accounts of category learning and attentional allocation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(2), 275–292.

Minsky, M. (1975). A framework for representing knowledge. In P. H. Winston (Ed.), *The psychology of computer vision* (pp. 211–277). New York: McGraw-Hill.

Nagy, W. E., Anderson, R. C., & Herman, P. A. (1987). Learning Word Meanings From Context During Normal Reading. *American Educational Research Journal*, *24*(2), 237–270.

Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, *25*(3), 653–660.

Noppeney, U., & Price, C. J. (2003). Functional imaging of the semantic system: retrieval of sensory-experienced and verbally learned knowledge. *Brain and Language*, *84*(1), 120–133.

Norman, D. A., & Rumelhart, D. E. (1975). *Explorations in cognition*. San Francisco: Freeman.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Orfanidou, E., Marslen-Wilson, W. D., & Davis, M. H. (2006). Neural response suppression predicts repetition priming of spoken words and pseudowords. *Journal of Cognitive Neuroscience*, *18*(8), 1237–1252.

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*(12), 976–987.

Pexman, P. M., Hargreaves, I. S., Edwards, J. D., Henry, L. C., & Goodyear, B. G. (2007). The Neural Consequences of Semantic Richness When More Comes to Mind, Less Activation Is Observed. *Psychological Science*, *18*(5), 401–406.

Pexman, P. M., Holyk, G. G., & Monfils, M. H. (2003). Number-of-features effects and semantic processing. *Memory & Cognition*, *31*(6), 842–855.

Pexman, P., Lupker, S., & Hino, Y. (2002). The impact of feedback semantics in visual word recognition: Number-of-features effects in lexical decision and naming tasks. *Psychonomic Bulletin & Review*, *9*(3), 542–549.

Plaut, D. C., & McClelland, J. L. (1993). Generalization with componential attractors: Word and nonword reading in an attractor network. In *Proceedings of the 15th annual conference of the Cognitive Science Society* (pp. 824–829).

Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchison, E., & Britton, B. (2006). An event-related fMRI investigation of phonological-lexical competition. *Neuropsychologia*, *44*(12), 2209–2221.

Raboyeau, G., Marcotte, K., Adrover-Roig, D., & Ansaldo, A. I. (2010). Brain activation and lexical learning: the impact of learning phase and word type. *NeuroImage*, *49*(3), 2850–2861.

Rogers, T. T., Hocking, J., Noppeney, U., Mechelli, A., Gorno-Tempini, M. L., Patterson, K., & Price, C. J. (2006). Anterior temporal cortex and semantic memory: reconciling findings from neuropsychology and functional imaging. *Cognitive, Affective & Behavioral Neuroscience*, *6*(3), 201–213.

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. *Psychological Review*, *111*(1), 205–235.

Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *NeuroImage*, *27*(1), 188–200.

Scott, S. K., Leff, A. P., & Wise, R. J. S. (2003). Going beyond the information given: a neural system supporting semantic interpretation. *NeuroImage*, *19*(3), 870–876.

Siakaluk, P. D., Buchanan, L., & Westbury, C. (2003). The effect of semantic distance in yes/no and go/no-go semantic categorization tasks. *Memory & Cognition*, *31*(1), 100–113.

Smith, E. E., & Medin, D. (1981). *Categories and Concepts*. Cambridge, Mass: Harvard University Press.

Taft, M., & van Graan, F. (1998). Lack of Phonological Mediation in a Semantic Categorization Task. *Journal of Memory and Language*, *38*(2), 203–224.

Takashima, A., Bakker, I., van Hell, J. G., Janzen, G., & McQueen, J. M. (2014). Richness of information about novel words influences how episodic and semantic memory networks interact during lexicalization. *NeuroImage*, *84*, 265–278.

The British National Corpus, version 3 (BNC XML Edition). (2007). Distributed by Oxford University Computing Services on behalf of the BNC Consortium. URL: http://www.natcorp.ox.ac.uk/.

Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R., & Levy, J. P. (2000). Conceptual Structure and the Structure of Concepts: A Distributed Account of Category-Specific Deficits. *Brain and Language*, *75*(2), 195–231.

Urooj, U., Cornelissen, P. L., Simpson, M. I. G., Wheat, K. L., Woods, W., Barca, L., & Ellis, A. W. (2014). Interactions between visual and semantic processing during object recognition revealed by modulatory effects of age of acquisition. *NeuroImage*, *87*, 252–264.

Van Daalen-Kapteijns, M., Elshout-Mohr, M., & de Glopper, K. (2001). Deriving the Meaning of Unknown Words From Multiple Contexts. *Language Learning*, *51*(1), 145–181.

Vigliocco, G., Vinson, D. P., Lewis, W., & Garrett, M. F. (2004). Representing the meanings of object and action words: The featural and unitary semantic space hypothesis. *Cognitive Psychology*, *48*(4), 422–488.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., … Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, *30*(4), 1414–1432.

Vigneau, M., Jobard, G., Mazoyer, B., & Tzourio-Mazoyer, N. (2005). Word and non-word reading: What role for the Visual Word Form Area? *NeuroImage*, *27*(3), 694–705.

Vinson, D. P., & Vigliocco, G. (2008). Semantic feature production norms for a large set of objects and events. *Behavior Research Methods*, *40*(1), 183–190.

Visser, M., Embleton, K. V., Jefferies, E., Parker, G. J., & Ralph, M. A. L. (2010). The inferior, anterior temporal lobes and semantic memory clarified: novel evidence from distortion-corrected fMRI. *Neuropsychologia*, *48*(6), 1689–1696.

Visser, M., Jefferies, E., & Ralph, M. L. (2009). Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience*, *22*(6), 1083–1094.

Walker, I., & Hulme, C. (1999). Concrete words are easier to recall than abstract words: Evidence for a semantic contribution to short-term serial recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*(5), 1256–1271.

Woolrich, M. W., Behrens, T. E. J., Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2004). Multilevel linear modelling for FMRI group analysis using Bayesian inference. *NeuroImage*, *21*(4), 1732–1747.

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage*, *14*(6), 1370–1386.

Worsley, K. J. (2001). Statistical analysis of activation images. *Functional MRI: An Introduction to Methods*, *14*, 251–270.

Yap, M. J., Tan, S. E., Pexman, P. M., & Hargreaves, I. S. (2011). Is more always better? Effects of semantic richness on lexical decision, speeded pronunciation, and semantic classification. *Psychonomic Bulletin & Review*, *18*(4), 742–750.

Tables

Table 1. Details of the matching of the sets of experimental stimuli.

		Number of semantic features	Age of acquisition	Concreteness	Orthographic neighborhood size	Letter length	Log mean bigram frequency	Word frequency		
								log BNC	HAL	log SWF
Familiar rich	mean	18.0	6.3	4.8	3.9	5.3	3.19	6.3	7.9	2.6
	sd	2.5	2.5	0.2	4.8	1.5		1.2	1.3	0.5
	range	14-24	3.2-11.5	4.5-5-0	0-16	3-8	2.53-3.37	4-8	5-9	2-3
Familiar poor	mean	9.6	7.1	4.8	3.0	5.6	3.25	5.9	7.4	2.3
	sd	2.4	2.1	0.2	3.8	1.4		1.5	1.1	0.5
	range	5-13	3.6-11.0	4.3-5.0	0-16	3-9	2.79-3.48	3-9	6-10	2-3
Novel rich	mean	18.0	–	–	3.4	5.3	3.25	–	–	–
	sd	2.5	–	–	4.8	1.5		–	–	–
	range	14-24	–	–	0-16	3-8	2.63-3.41	–	–	–
Novel poor	mean	9.6	–	–	2.9	5.6	3.24	–	–	–
	sd	2.4	–	–	4.8	1.4		–	–	–

range	5-13	–		0-16	3-9	2.72-3.42	–	–	–

Orthographic neighborhood size and mean bigram frequency were taken from the English Lexicon Project (Balota et al., 2007). Age of Acquisition (Kuperman et al., 2012), Concreteness (Brysbaert et al., 2014), BNC = British National Corpus (The British National Corpus, 2007), HAL = Hyperspace Analogy to Language (Lund & Burgess, 1996), SWF = Subtitle Word Frequency (Brysbaert & New, 2009).

Table 2. Mean RTs in msec (with SDs) and error rates in the semantic categorization task as a function of presentation order, familiarity and semantic richness.

	Presentation 1		Presentation 2	
	Familiar	**Novel**	**Familiar**	**Novel**
Rich semantics				
Mean RT	852	1073	781	888
SD	132	161	123	128
% errors	1.4	5.2	3.3	4.3
Poor semantics				
Mean RT	895	1155	820	930
SD	130	159	126	158
% errors	3.1	9.0	4.0	9.8

Table 3. MNI Coordinates for Peak Voxels Showing Increased Activity for Familiar *vs*. Novel Words and Rich *vs*. Poor words; familiarity x semantic richness interactions, and the Conjunction of Familiar *vs*. Novel and Rich *vs*. Poor.

Activation loci	*Cluster size (voxels)*	*Z*	*Coordinates (MNI)* *x*	*y*	*z*
Familiar > novel words					
Left occipito-temporo-parietal junction	3459				
L. superior LOC		4.99	-56	-62	20
L. supramarginal gyrus		4.70	-58	-52	26
L. inferior AG		4.56	-44	-60	16
L. superior AG		4.51	-48	-56	30
L. lateral inferior AG		4.49	-56	-58	12
Right occipito-temporo-parietal junction	3638				
R. inferior AG		4.95	60	-54	16
R. superior LOC		4.59	56	-66	16
Left temporal cortex	1534				
L. anterior inferior temporal gyrus		4.08	-50	-10	-28
L. anterior MTG		3.99	-60	-16	-20
L. superior temporal gyrus		3.85	-62	-22	-6
L. posterior middle temporal gyrus		3.82	-62	-26	-8
Left fronto-temporal cortex	1261				
L. lateral frontal orbital cortex		5.01	-48	24	-14
L. medial frontal orbital cortex		4.37	-34	18	-18
L. IFG (pars triangularis)		3.90	-54	22	14

L. lateral posterior frontal pole		3.85	-42	38	-18
L. anterior temporal pole		3.71	-38	14	-22
Right frontal cortex / prefrontal cortex	450				
R. inferior frontal orbital cortex		4.12	44	24	-18
R. superior frontal orbital cortex		4.01	48	28	-8
R. IFG (pars triangularis)		3.53	50	28	0
R. IFG (pars opercularis)		3.25	54	18	14
R. IFG (superior pars triangularis)		3.25	52	24	10
Medial frontal cortex / prefrontal cortex	6677				
L. anterior superior frontal gyrus		5.12	-6	46	40
L. paracingulate gyrus		4.98	-4	52	20
R. superior frontal gyrus		4.77	4	50	32
L. posterior superior frontal gyrus		4.60	-10	30	56
L. medial anterior superior frontal pole		4.56	-14	50	34
Precuneus / Left posterior cingulate gyrus	1119				
L. precuneus / posterior cingulate gyrus		4.13	-6	-58	30
L. superior precuneus		3.85	-2	-58	42
R. superior precuneus		3.78	10	-60	40
B. Precuneus		3.76	0	-60	36
Novel > familiar words					
Left ventral occipitotemporal (fusiform) cortex	858				
L. temporal occipital fusiform cortex		4.32	-42	-62	-16
L. posterior inferior temporal gyrus		4.08	-48	-54	-22
L. occipital fusiform gyrus		3.91	-46	-70	-16
L. inferior LOC		3.34	-42	-68	-8

Left frontal pole / insular cortex	559				
L. anterior inferior frontal pole		3.89	-22	60	0
L. insular cortex		3.52	-30	20	-2
Right insular cortex / frontal cortex	972				
R. insular cortex		3.66	32	16	-2
R. posterior inferior frontal pole		3.36	26	42	-12
Left parietal-occipital junction / cerebellum	4006				
L. superior parietal lobule		5.52	-34	-56	40
L. posterior medial LOC		4.74	-28	-70	44
L. cerebellum		3.85	-6	-78	-28
L. cuneus		3.75	-12	-74	34
L. anterior medial LOC		3.73	-30	-60	50
Rich > poor					
Left AG / LOC	1520				
L. superior AG		3.85	-52	-56	28
L. inferior AG		3.49	-48	-58	16
L. superior LOC		3.34	-54	-64	26
L. lateral inferior AG		3.22	-64	-50	12
Left paracingulate gyrus / bilateral frontal pole	1694				
L. inferior paracingulate gyrus		3.32	-4	46	-2
R. medial anterior inferior frontal pole		3.31	2	56	2
L. superior paracingulate gyrus		3.24	-10	42	14
L. medial anterior inferior frontal pole		3.22	-8	60	-8
Precuneus/ left posterior cingulate gyrus	2232				
L. inferior precuneus		3.96	-8	-56	22

L. posterior cingulate gyrus		3.89	-4	-46	30
L. superior precuneus		3.62	-6	-60	32
R. superior precuneus		3.46	2	-58	36
Left temporal cortex	491				
L. anterior MTG		3.4	-56	-12	-20
L. posterior MTG		3.13	-52	-28	-6
L. superior temporal gyrus		3.09	-56	-28	-4
L. inferior temporal gyrus		3.04	-52	-10	-28
Familiarity x semantic richness interaction					
Cerebellum	555				
R. Cerebellum (Crus II)		3.52	8	-74	-30
L. Cerebellum (Crus II)		3.07	-2	-70	-30
R. Cerebellum (Crus I)		3.06	32	-88	-24
Conjunction familiar > novel and rich > poor					
Left occipito-temporo-parietal junction	577				
L. anterior AG		3.43	-50	-56	18
L. posterior superior AG		3.25	-52	-62	18
L. posterior inferior AG		3.25	-54	-64	-26
L. superior LOC		2.93	-46	-66	28
L. inferior LOC		2.93	-40	-64	18
L. medial prefrontal cortex / R. paracingulate	647				
R. anterior inferior paracingulate		3.18	2	54	4
L. medial inferior prefrontal cortex		3.12	-8	54	-6
R. anterior superior paracingulate		2.96	6	48	18

Note: L. left; R. right; AG, angular gyrus; MTG, middle temporal gyrus; IFG, inferior frontal gyrus; LOC, lateral occipital cortex.

Figure

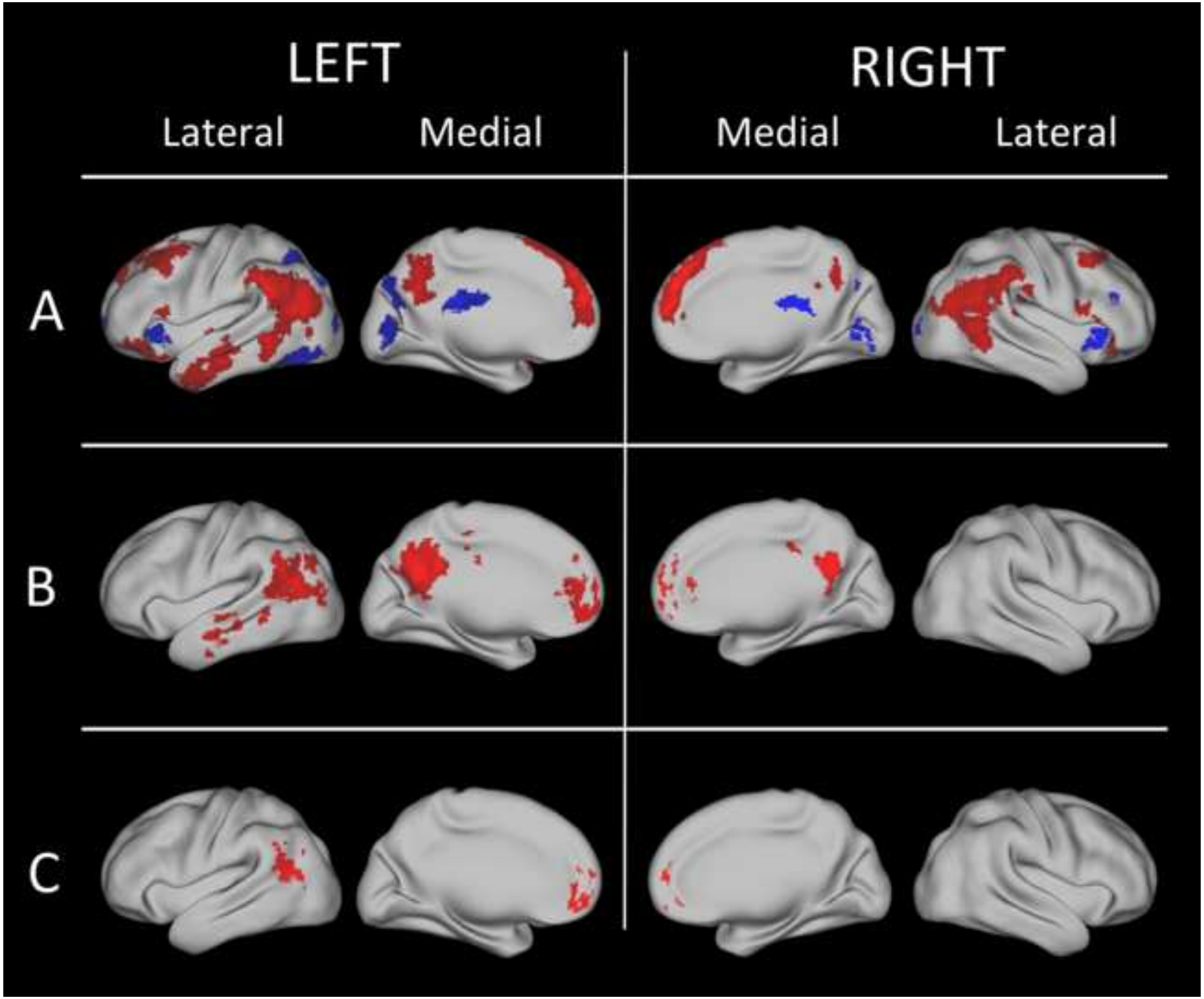

Figure 1 legend

Figure 1. Whole brain analysis. A). Activations to familiar and novel words, collapsed across words with rich and poor semantic representations at $Z > 2.3$. Familiar > novel shown in red; novel > familiar in blue. B). Activations to rich and poor words, collapsed across familiar and unfamiliar at $Z > 2.3$. Rich > poor shown in red. C). Conjunction of familiar vs. novel and rich vs. poor at $Z > 2.3$. Familiar > novel *and* rich > poor shown in red.