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The influence of sentence novelty and figurativeness on brain activity

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Abstract

The predominance of the left hemisphere in language comprehension and production is well established. More recently, the right hemisphere's contribution to language has been examined. Clinical, behavioral, and neuroimaging research support the right hemisphere's involvement in metaphor processing. But, there is disagreement about whether metaphors, in and of themselves, engage the right hemisphere or if other factors that vary between metaphors and literal language elicit right hemisphere engagement. It is important to disambiguate these issues to improve our basic knowledge of figurative language processing, to more precisely define how the right hemisphere supports language, and to facilitate our ability to understand and treat language impairments. Here we investigated the role of the right hemisphere in language comprehension with functional magnetic resonance imaging (fMRI) by manipulating familiarity in both literal and metaphoric sentences. In an event-related design, participants viewed English sentences that appeared every 4.5 to 9 seconds, and to which they made a pleasantness judgment. All sentences elicited activation in traditional language brain regions including left inferior frontal gyrus, left anterior inferior temporal and left posterior middle temporal gyri. Overall, metaphors and novel stimuli elicited activation in bilateral inferior frontal gyri and left temporal regions. Additionally, metaphors elicited greater activation than literal sentences in right temporal pole. Although our results are partially consistent with the graded salience hypothesis and the coarse coding hypothesis, the right hemisphere's sensitivity to familiar metaphors suggests that right hemisphere recruitment is most influenced by semantic integration demands.

Keywords

metaphor; novelty; language; semantics; laterality; hemispheric contribution

1. INTRODUCTION

Metaphors and other literary devices occur frequently, and contribute to the richness of language. They can provide a succinct, effective, and vivid description of an object, person, or event (e.g., "You are a window the sun shines through."). Metaphors differ from literal language in that they have both literal and figurative meanings. In addition to their dual

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meanings, metaphors may differ from literal text along other factors, such as novelty, ease of integration, and valence. Researchers have questioned whether the differences in processing metaphors are due to metaphors *per se* or to these other factors. Additionally, these same factors can vary within metaphors themselves. Conventional metaphors (e.g., ‘sweet dreams’), also known as frozen, familiar, or dead metaphors, may become instantiated in semantic memory much like the definition of a word because of their frequency of use. If this is the case, accessing and understanding such phrases may be similar to processing literal language. In contrast, processing novel metaphors requires integrating multiple disparate concepts dynamically. For example, in the metaphor “During the tedious meeting, her thoughts were a cool breeze.” the idea of refreshment and invigoration from ‘cool breeze’ must be integrated with the concept ‘her thoughts’. These two concepts may never have been associated prior to encountering that sentence. Thus, conventional and novel metaphors may engage different cognitive processes and may require different neural resources. However, differences in novelty are not restricted to figurative sentences alone. Literal sentences may also vary along this dimension. A remaining question for the field is how manipulations of novelty influence hemispheric recruitment when processing both figurative and literal sentences.

1.1 Hemispheric Differences in Language Processing

The importance of the left hemisphere in language processes has been thoroughly established through experimental manipulations (For a review see (Bookheimer, 2002)) and neurological observations (Bookheimer, 2002; Broca, 1861; Davis & Wada, 1978; Dejerine, 1891). More recently, there has been a growing appreciation for the role of the right hemisphere in language. One hypothesis that has been proposed regarding hemispheric differences in language processing is the Gradient Salience Hypothesis (GSH) (R. Giora, 1997, 1999, 2003). The GSH postulates that hemispheric recruitment is influenced by salience rather than by whether an item is literal or figurative. According to the GSH, several factors influence the degree of salience including frequency, familiarity, and the amount of context that is provided. For example, the dimension of frequency can be examined using polysemous words such as bark (canine sound or tree covering), in which the dominant, more frequently used, sense (canine sound) is proposed to be more salient than the subordinate, less frequently used, sense (tree covering). According to the GSH, highly salient words and phrases are easier to process, are activated before alternative, less salient interpretations, and primarily engage the left hemisphere. In contrast, less salient words and phrases require additional cognitive resources, are activated after more salient interpretations, and recruit additional neural resources from the right hemisphere.

While the GSH provides a rich psycholinguistic framework for understanding figurative language, it does not propose any specific neural mechanism. The Coarse Coding Hypothesis (CCH) (Beeman & Chiarello, 1998; Beeman et al., 1994; Chiarello, 1988; Jung-Beeman, 2005) provides additional mechanistic detail regarding the roles of the two hemispheres in understanding language. It proposes that both the right and left hemisphere are engaged in semantic activation, integration, and selection. The right hemisphere is involved in non-selective, widespread, semantic activation (i.e., coarse coding), while the left hemisphere supports more focused, context-relevant, semantic activation (i.e., fine coding). For example, returning to the previous example of the word ‘bark’, the CCH suggests that the right hemisphere would keep both senses of bark (canine sound and tree covering) active, while the left hemisphere would activate only the sense that was contextually congruent. This has relevance to literal and figurative language processing in that literal language, in particular when it contains familiar semantic relationships, should benefit from focal, context-relevant analyses (i.e., left hemisphere), while figurative

language, especially novel metaphoric language, benefits from the activation of many, loosely related concepts (i.e., right hemisphere).

Much of the evidence in support of the Coarse Coding Hypothesis has been derived from behavioral visual half field studies. However, electrophysiological evidence has provided evidence in support of another neural hypothesis regarding how the right and left hemisphere support language. Work by Federmeier and colleagues has suggested that the left hemisphere adopts a top-down, predictive approach in processing language, while the right hemisphere incorporates a bottom-up, integrative approach (Federmeier, 2007). Federmeier and colleagues conducted a series of studies in which participants read sentences that ended with either the most expected item, an unexpected word that came from the same category as the most expected word, or an equally unexpected word from a different semantic category (e.g., They wanted to make the hotel look more like a tropical resort. So, along the driveway, they planted rows of palms/pines/tulips.) (Federmeier & Kutas, 1999a, 1999b, 2002; Federmeier, McLennan, De Ochoa, & Kutas, 2002). In their visual half-field study they found an N400 reduction to words that were from the same semantic category as the expected sentence final word, but only in the left hemisphere (Federmeier & Kutas, 1999a). They hypothesized that this facilitation to an essentially implausible word was mediated by pre-activation of semantic features of the expected word. In the right hemisphere, the N400 responses to both violations were equivalent. This pattern of response suggests that unlike the left hemisphere, the right hemisphere does not have a predictive role, but rather integrates stimuli as they appear (Federmeier, 2007). Although these theoretical frameworks postulate different roles for the right hemisphere in language processing (salience, coarse coding, integration), each theory highlights the importance of the right hemisphere when processing unique or unexpected semantic relationships.

Hemispheric function has also been examined experimentally by observing patients with brain damage. Individuals with brain damage to the right hemisphere often have difficulty understanding non-literal language, such as metaphors (Winner & Gardner, 1977) and jokes (Bihrlé, Brownell, Powelson, & Gardner, 1986), and show deficits in understanding prosody (Tucker, Watson, & Heilman, 1977). In a seminal study, patients with damage to the right or left hemisphere were asked to select pictures that corresponded to verbal metaphors (Winner & Gardner, 1977). Patients with right hemisphere damage (RHD), but not left hemisphere damage (LHD), had difficulty matching pictures to metaphors. This result was replicated using a similar picture-matching task (Bryan, 1988) and extended with a verbal-matching task (Rinaldi, Marangolo, & Baldassarri, 2004). Several other clinical studies have demonstrated that patients with RHD have difficulty understanding metaphors (Brownell, Simpson, Bihrlé, Potter, & Gardner, 1990) and interpreting metaphors (McIntyre, Pritchard, & Lombroso, 1976). In addition, a double dissociation between injured hemisphere and type of language has been reported. Patients with RHD had more difficulty processing idioms, while patients with LHD had more difficulty processing literal sentences (Kempler, Van Lancker, Marchman, & Bates, 1999; Van Lancker & Kempler, 1987). Giora and colleagues found that LHD patients had more difficulty explaining conventional metaphors (high salience) than RHD patients, while RHD patients were impaired in comprehending sarcasm (low salience) compared to LHD patients (Rachel Giora, Zaidel, Soroker, Batori, & Kashner, 2000). However, other studies have found that patients with either LHD or RHD were equally impaired in processing metaphors (Gagnon, Goulet, Giroux, & Joannette, 2003; Tompkins, 1990) and these deficits may be particularly apparent when controlled or strategic processes were involved. Specifically, unlike controls, LHD and RHD participants failed to adopt strategies during an auditory lexical decision task when the ISI between prime and target words was long (Tompkins, 1990). Patient research has also indicated right hemisphere involvement in making remote semantic associations (Joannette, Goulet, & Le dorze, 1988), processing subordinate meanings of words (Burgess & Cushman, 1990), and

suppressing contextually-inappropriate meanings of ambiguous words (Tompkins, Baumgaertner, Lehman, & Fossett, 1997).

fMRI studies have also supported the role of the right hemisphere in conceptual integration. St. George and colleagues examined discourse comprehension by presenting titled and untitled paragraphs (St George, Kutas, Martinez, & Sereno, 1999). The paragraphs were identical and were written such that the untitled condition involved activating and integrating multiple concepts in the absence of an overall framework. Greater activation in right middle temporal sulcus was found when participants read untitled paragraphs compared to titled paragraphs. Others have found right hemisphere involvement in processing unusual semantic relationships (Seiger, Desmond, Glover, & Gabrieli, 2000) and in drawing inferences (Mason & Just, 2004). In summary, behavioral, patient, and functional imaging research strongly support the right hemisphere's involvement in processing semantic information that requires accessing and integrating loosely related concepts.

1.2 The Functional Imaging of Metaphor Comprehension

Several studies have used imaging techniques to examine the neural substrates of metaphor processing in healthy young adults. In one of the earliest experiments, Bottini and colleagues examined brain activation during a metaphor comprehension task, a literal sentence comprehension task, and a lexical decision task (Bottini et al., 1994). In addition to traditional left hemisphere language regions, they found that metaphors recruited several additional regions in the right hemisphere including the prefrontal cortex, the middle temporal gyrus, the precuneus, and the posterior cingulate.

Other studies examining sentential metaphors have also found right hemisphere recruitment during metaphor processing (Ahrens et al., 2007; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Schmidt & Seger, In Press; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009). Comparing metaphors and literal sentences, several studies have found that metaphors elicit greater activation than literal sentences in right middle temporal gyrus (Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008), right inferior temporal gyrus (Ahrens et al., 2007; Eviatar & Just, 2006; Yang, Edens, Simpson, & Krawczyk, 2009), right inferior frontal gyrus (Ahrens et al., 2007; Bottini et al., 1994; Schmidt & Seger, In Press; Stringaris et al., 2006), and right insula (Schmidt & Seger, In Press). For example, in an experiment examining brain activation while participants read brief stories that ended with a metaphoric, ironic, or literal sentence (Eviatar & Just, 2006), metaphors elicited greater activation in left inferior frontal gyrus and bilateral inferior temporal gyri compared to literal and ironic sentences. A comparison of literal sentences, conventional metaphors, and anomalous metaphors in Mandarin Chinese revealed that both anomalous and conventional metaphors elicited greater activation in right inferior temporal gyrus compared to literal sentences (Ahrens et al., 2007). In addition, anomalous metaphors elicited greater activation compared to literal sentences in bilateral superior, middle, and inferior frontal gyri, and bilateral superior and middle temporal gyri. Source localization techniques, used in combination with electrophysiological data, found that differences between related and unrelated metaphoric sentences localized to the right middle and superior temporal gyri (Sotillo et al., 2005). However, others have failed to find electrophysiological differences between the hemispheres in processing low cloze literal and low cloze metaphoric sentence endings, suggesting that the two hemispheres processed metaphors similarly (Coulson & Van Petten, 2007).

Several investigations with sentences have also explored other factors that may influence hemispheric recruitment in metaphor processing. Schmidt and colleagues examined familiarity and difficulty by comparing literal sentences, familiar metaphors that were easy to understand, unfamiliar metaphors that were easy to understand, and unfamiliar metaphors

that were difficult to understand (Schmidt & Seger, In Press). Overall, metaphors elicited greater activation than literal sentences in right insula, right inferior frontal gyrus, and left temporal pole. In addition they found a general effect of difficulty in left inferior frontal gyrus in which difficult metaphors elicited greater activation than easy metaphors. Familiarity influenced activity in right inferior and middle frontal gyri. However, it was easy familiar metaphors that elicited greater activation than easy unfamiliar metaphors. Unfamiliar metaphors elicited greater activation than familiar metaphors, but not in regions primarily involved in language (e.g., left cingulate, left hippocampus). Yang and colleagues also compared novel and conventional metaphors in a valence and an imagery task (Yang, Edens, Simpson, & Krawczyk, 2009). When participants were asked to judge the valence of the sentence, novel metaphors elicited greater activation in right inferior frontal gyrus than both literal sentences and conventional metaphors. When participants were asked to create a mental image of each sentence, novel metaphors elicited greater activation in right inferior frontal gyrus and right inferior temporal gyrus when compared to literal sentences.

Several other investigators have also examined novelty in metaphors using word pairs. An investigation of metaphor processing comparing literal word pairs, conventional metaphors (e.g., sweet dreams), novel metaphors (e.g., wisdom dust), and unrelated words found that novel metaphoric word pairs elicited greater activation than conventional metaphoric word pairs in right superior temporal sulcus, and right middle and inferior frontal gyri (Mashal, Faust, Hendler, & Jung-Beeman, 2007). A principal components analysis of the same data set found a right hemisphere homologue of Wernicke's area that was involved during the processing of novel, but not conventional metaphors (Mashal, Faust, & Hendler, 2005). A transcranial magnetic stimulation (TMS) investigation of word pairs found that TMS over right posterior superior temporal sulcus disrupted the processing of novel metaphors but not conventional metaphors or literal word pairs. TMS over left inferior frontal gyrus impaired literal and conventional metaphors but not novel metaphors (Pobric, Mashal, Faust, & Lavidor, 2008). Taken together these findings support a role for right prefrontal and temporal gyri in novel metaphor comprehension.

However, not everyone has found preferential right hemisphere recruitment for metaphors. In an event-related fMRI study comparing literal and metaphoric sentences in German (Rapp, Leube, Erb, Grodd, & Kircher, 2004, 2007), metaphors elicited greater activation than literal sentences in left inferior frontal, left inferior temporal, and left middle temporal gyri. However, they failed to find differences in laterality or a right hemisphere preference for metaphors. In another study examining metaphoric and literal Hebrew sentences, Mashal and colleagues found only left hemisphere activation for novel metaphoric sentences and literal sentences (Mashal, Faust, Hendler, & Jung-Beeman, 2009). However, a post-scan assessment suggested that participants may not have been aware of the metaphoric nature of some of the sentences. Likewise, Lee and Dapretto (2006) failed to find right hemisphere activity for metaphoric word triplets. Instead they reported differences between metaphors and literal stimuli in left inferior frontal gyrus, left middle temporal gyrus, and left inferior parietal gyrus (Lee & Dapretto, 2006). Stringaris and colleagues used event-related fMRI to compare brain activation elicited by metaphoric sentences, literal sentences, and anomalous sentences during which they found that the left inferior frontal gyrus and left thalamus were more active to metaphors and anomalous sentences than literal sentences (Stringaris, Medford, Giampietro, Brammer, & David, 2007). Although metaphors elicited activation in right temporal regions (BA 39), literal sentences and nonsense sentences also elicited activation in neighboring right temporal regions (BA 37).

It is possible that these discrepancies in results may be due to differences in characteristics of the stimuli. Familiarity is a dimension that should affect processing according to several theoretical frameworks (Federmeier, 2007; R. Giora, 1997; Jung-Beeman, 2005). Familiar

metaphors are likely to be encoded in the lexicon (i.e., salient), and have close semantic relationships that would not require or benefit from weak activation of loosely related semantic concepts (e.g., coarse coding or post-lexical integration of the right hemisphere). Likewise unfamiliar word pairs and sentences are likely to have different integration demands compared to familiar items. Some of the studies that did not find differential right hemisphere activation used metaphors that could have been familiar to participants (e.g., surgeons as butchers) (Stringaris, Medford, Giampietro, Brammer, & David, 2007) or were not rated for novelty (Rapp, Leube, Erb, Grodd, & Kircher, 2004, 2007). Additionally, several studies that failed to find differences between figurative and literal stimuli repeated sentence or word contexts across conditions (e.g., The lover's words are harp sounds/lies, Lee & Dapretto, 2006; Rapp et al., 2004, 2007; Stringaris et al., 2007).

An additional factor that may influence right hemisphere engagement is the context in which a word is presented. Some research has suggested that the two cerebral hemispheres may differ in their processing abilities, whereby the right hemisphere is primarily sensitive to word-level or lexical associations and less sensitive to context and message level information than the left hemisphere (Faust, Babkoff, & Kravetz, 1995; Faust, Bar-lev, & Chiarelli, 2003; Faust, Kravetz, & Babkoff, 1993). For example, behavioral studies using the visual half field (VHF) paradigm have found a larger magnitude of priming in the right visual half field/ left hemisphere (RVF/LH) compared to the left visual field/ right hemisphere (LVF/RH) when words were preceded by a syntactically and semantically valid sentence (Faust, Babkoff, & Kravetz, 1995; Faust, Bar-lev, & Chiarelli, 2003). Additionally, associatively primed words embedded in meaningless sentences yielded priming in the LVF/RH but not the RVF/LH (Faust, Barlev, & Chiarelli, 2003). These findings suggest that the left hemisphere is more sensitive to sentential context than the right hemisphere, and that the right hemisphere may be more sensitive to word level processes than the left hemisphere. However, electrophysiological investigations using the VHF paradigm have suggested that both hemispheres are sensitive to message level information (Coulson & Van Petten, 2007; Federmeier, 2007; Federmeier & Kutas, 1999a).

If the right hemisphere is biased toward lexically-mediated processes, then metaphoric word pairs may elicit more right hemisphere activation than sentential metaphors. Of four data sets that did not find right hemisphere or differential right hemisphere activation to metaphors, three involved sentential metaphors (Mashal et al., 2009; Rapp et al., 2004, 2007; Stringaris et al., 2007) and one incorporated word triplets (Lee & Dapretto, 2006). So although context may influence metaphor processing, presenting metaphoric ideas in a sentence context does not seem to prevent right hemisphere recruitment (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Schmidt & Seger, In Press; Sotillo et al., 2005; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009).

In the present experiment we used fMRI to examine the relationship between novelty and figurativeness and how these factors influence hemispheric recruitment. Previous research investigating metaphors suggests that the right hemisphere may be important for figurative language processing. However, it is unclear whether figurative language in and of itself underlies right hemisphere involvement, or if other factors, such as stimulus novelty may contribute to these findings. While some previous research has manipulated novelty within metaphors (Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007, 2009; Pobric, Mashal, Faust, & Lavidor, 2008; Schmidt & Seger, In Press; Yang, Edens, Simpson, & Krawczyk, 2009), prior work has failed to examine whether the right hemisphere is sensitive to manipulations of novelty in literal text. This comparison is critical to understanding how the right hemisphere supports figurativeness, novelty, or a combination of both factors in language.

2. METHODS

2.1 Participants

Sixteen right-handed, native English speaking, healthy young adults (mean age 23.8; age range 18-30; 8 male) participated in this study. All participants had normal or corrected to normal vision, and none had a history of neurological or psychological disorders. Each participant provided informed consent and was paid for his or her participation. All experimental procedures were approved by the Duke University Medical Center Institutional Review Board.

2.2 Stimuli

Stimuli consisted of literal and metaphoric grammatical English sentences that varied in their novelty. This yielded four conditions of valid English sentences: familiar literal sentences, novel literal sentences, familiar metaphors, and novel metaphors. A fifth condition of nonword sentences was also included to control for brain activation to basic visual characteristics of the stimuli, letter level processing, and motor responses. Each of the five conditions contained 40 sentences (3 - 9 words in length, average length = 5.97). A behavioral pilot study was conducted with a separate group of participants (N=15) to select the stimuli for the fMRI study. Familiar and novel metaphors were collected from published sources (Katz, Paivio, & Marschark, 1985; Katz, Paivio, Marschark, & Clark, 1988), and the initial set was created using published ratings. Novelty was manipulated in literal sentences by using semantic feature and prototypicality ratings (McRae, Cree, Seidenberg, & McNorgan, 2005; McRae, Cree, Westmacott, & De Sa, 1999). From these ratings we selected the most and least prototypical exemplars from a category, and created an initial set of sentences. For example, a robin is a prototypical bird while an emu is less prototypical. A car is an example of a more prototypical vehicle, while an ambulance is an example of a less prototypical vehicle. Only one item from each category (e.g., bird or vehicle) was included in the final stimulus set. To control for syntactic complexity, all stimuli followed a noun-verb-noun sentence format. These initial set of stimuli were then rated by a separate group of individuals for familiarity, ease of comprehension, and positivity on 7 point Likert scales. There was a significant effect of Novelty ($t=11.01$, $df=158$, $p<.001$) when comparing novel and familiar stimuli. There was also a significant main effect of comprehension between metaphors and literal sentences ($t=11.01$, $df=158$, $p<.001$) and between novel and familiar sentences ($t=7.15$, $df=158$, $p<.001$). Metaphors were slightly more difficult to comprehend compared to literal sentences (average comprehension rating metaphors = 5.1, literal = 6.2 out of 7.0) and novel sentences were slightly more difficult to comprehend compared to familiar sentences (average comprehension rating novel = 5.2, familiar = 6.0 out of 7.0). Higher values on the Likert scale indicated greater comprehension. Although these significant differences were present in the materials, the overall comprehension ratings for all sentences were well above the midpoint of the measure, indicating that all sentences were understandable. Across sentence categories, sentences did not differ in their positivity ratings. These initial behavioral measures were also used to confirm that adequate reading time was allocated in the scanner.

Across all conditions, sentences were matched for length. Nouns within the four English sentence conditions were matched for frequency (Coltheart, 1981; Kucera & Francis, 1967; Wilson, 1988), and concreteness (Coltheart, 1981; Wilson, 1988). Ratings of frequency and concreteness were obtained from the MRC psycholinguistic database (Coltheart, 1981). Nonword letter strings were created using a random letter generator that randomly selected letters of the alphabet. No valid English words were embedded in any portion of the nonwords, and nonwords were not constrained to follow English phonology.

2.3 Experimental Task

Each run began and ended with the presentation of a fixation cross. To ensure that participants were attentive to the stimuli during the fMRI session, participants were asked to read each sentence and rate the valence of each sentence as positive, neutral, or negative. Participants were instructed to make their best assessment about the emotional connotation of each sentence. For example, the sentence '*The rumor was a disease.*' has a negative connotation whereas the sentence '*That bird is a robin.*' might be considered neutral. Each trial consisted of a single sentence drawn randomly from one of the five conditions: familiar literal sentences, novel literal sentences, familiar metaphors, novel metaphors, or nonword sentences. Each sentence was presented for 6 seconds and a fixation cross was presented between each sentence for a variable interval, 4.5 to 9 seconds in length. Randomized order of presentation and a variable inter-stimulus-interval were incorporated to minimize participant preparation and anticipation of subsequent stimuli. Trials were presented in ten, 4.5 minute runs. All stimuli were presented via LCD goggles (MRI Resonance Technologies, Los Angeles, CA, USA) using the CIGAL experimental control program (Voyvodic, 1999). Responses were recorded with a hand-held fiber optic response box (Current Designs, Philadelphia, PA, USA). An overview of the task is provided in Figure 1.

2.4 Acquisition of MRI Data

MRI scanning was completed on a 3.0 Tesla GE EXCITE HD whole-body 60 cm bore human scanner equipped with 40 mT/m gradients and a 150 T/m/s slew rate. An eight-channel head coil was used for Radio Frequency reception (General Electric, Milwaukee Wisconsin, USA). Sagittal T-1 weighted localizer images were acquired and used to define a volume for high order shimming. The anterior and posterior commissures were identified for slice selection and shimming. A semi-automated high-order shimming program was used to ensure global field homogeneity. High-resolution structural images were acquired using a 3D fast SPGR pulse sequence (TR=7.456ms; TE=3.016 ms; FOV=25.6 cm²; flip angle=12°; voxel size= 1 × 1 × 2mm; 60 contiguous slices). Functional images sensitive to blood oxygen level-dependent (BOLD) contrast were acquired using an inverse spiral pulse sequence (TR=1.5s; TE=30ms; FOV=25.6m²; flip angle=60°; voxel size=4 × 4 × 4mm; 30 contiguous axial slices). Each of 10 runs consisted of the acquisition of a time series of 182 brain volumes. Four initial RF excitations were performed to achieve steady state equilibrium, and were subsequently discarded.

2.5 Data Analysis

FSL was used to assess functional activations to each sentence condition. Preprocessing and first level analysis of each individual run for each participant were performed using FSL version 4.1.4 [Oxford Centre for Functional Magnetic Resonance Imaging of the Brain (FMRIB), Oxford University, U.K.] (Smith et al., 2004; Woolrich et al., 2009). Functional image data were motion-corrected, high-pass filtered, and spatially smoothed using a Gaussian kernel (FWHM= 8 mm) (Jenkinson, Bannister, Brady, & Smith, 2002; Jenkinson & Smith, 2001). No participant had a greater than 4mm movement in the X, Y, or Z dimension, and motion parameters were included in the overall FSL model. Pre-whitening or voxel-wise temporal autocorrelation was estimated and corrected using FMRIB's Improved Linear Model (FILM) (Woolrich, Ripley, Brady, & Smith, 2001). The skull and other coverings were stripped from the structural brain images using the FSL brain extraction tool (Smith, 2002). Functional images of each participant were co-registered to structural images in native space, and structural images were normalized to the Montreal Neurological Institute (MNI) standard brain. The same transformation matrices used for structural-to-standard transformations were then used for functional-to-standard space transformations of co-registered functional images. A double γ function was used to model the hemodynamic response for each trial in each run.

The first level analyses from the experimental runs of each participant were combined and a second level analysis was performed for each participant. These second level analyses were then combined across participants into a group level analysis using the FMRIB Local Analysis of Mixed Effects (FLAME 1 & 2) to identify voxels that were activated by each trial type ($p < .01$) (Beckman, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckman, Jenkinson, & Smith, 2004). The results from higher level comparisons were masked by results from lower level analyses. Activations were masked to exclude clusters smaller than 7 voxels in extent.

In addition to the analyses described above, the single trial peri-event averages for each trial and segment were measured at each voxel (Gadde & McCarthy, 2009). Percent signal change was determined by averaging the hemodynamic response elicited by each condition and segment and calculating the difference between baseline and peak points for each condition. These t-statistic peri-event waveforms were combined across participants using a random effects analysis, and the results were masked by brain regions which were significant in the main FSL analyses. Coordinates of the centroids of activation and their corresponding anatomical gyri were determined through the use of anatomical atlases (Lancaster et al., 2000; Talairach & Tournoux, 1988). All reported coordinates are in MNI space. Results are displayed overlaid on an individual participant's brain normalized to MNI space.

3. RESULTS

3.1 Behavioral Results

Participants' average accuracy for the pleasantness rating task was 93.5% ($SD=7.9\%$); accuracies across conditions were as follows: familiar literal sentences 94.1% ($SD=7.1\%$), novel literal sentences 93.7% ($SD=7.8\%$), familiar metaphors 95.0% ($SD=7.9\%$), novel metaphors 92.1% ($SD=8.4\%$), and nonword sentences 92.9% ($SD=10.5\%$). Across all 5 conditions, there were no significant differences in accuracy. Trials with no response and trials with response times less than 250 ms or greater than 3 standard deviations from the mean were treated as errors and removed from further analyses. This eliminated 2.1% of the data. Behavioral data from three participants was lost due to computer error.

The average response time (RT) for the pleasantness rating task was 2572 ms ($SD=847$ ms); response times across conditions were as follows: familiar literal sentences 2548 ms ($SD=680$ ms), novel literal sentences 2932 ms ($SD=763$ ms), familiar metaphors 2730 ms ($SD=710$ ms), novel metaphors 2973 ms ($SD=793$ ms), and nonword sentences 1678 ms ($SD=502$ ms). Nonword sentences were responded to significantly faster than the other conditions $F(4,79) = 8.61$, $p < .01$. However, across valid English sentence categories, the conditions of greatest interest, there were no significant differences in response times $F(3,63) = 1.13$, $p = 0.34$. The accuracy and response time data indicated that the participants were able to perform the task successfully. Moreover, the lack of differences in accuracy and response times across the English sentence conditions suggests that there were no differences in task difficulty across conditions.

3.2 fMRI Activation

We first report the results of the individual conditions (familiar literal sentences, novel literal sentences, familiar metaphors, and novel metaphors) compared to the nonword baseline condition. Collapsing across all sentence conditions revealed activation in classic left hemisphere language regions including: left inferior frontal gyrus, left anterior middle temporal gyrus, and left posterior middle temporal gyrus. We also observed subcortical activation (thalamus, bilateral caudate and midbrain) in the comparison between all

sentences and nonword sentences. Novel and familiar metaphors both elicited activation in bilateral inferior frontal gyri, left parahippocampal/ medial inferior temporal gyrus, left posterior middle temporal gyrus, and subcortical regions. The large cluster of activation located in left inferior frontal gyrus extended into the superior portion of the left temporal lobe for both novel and familiar metaphors. Additionally, novel metaphors elicited activation in right middle temporal gyrus and right temporal pole. Novel literal sentences elicited activation in left inferior frontal gyrus, right superior frontal gyrus, left parahippocampal/ medial inferior temporal gyrus, left posterior middle temporal gyrus, and subcortical regions. Familiar literal sentences elicited activation in left inferior frontal gyrus, left posterior middle temporal gyrus, and subcortical regions. A summary of the activations to individual conditions that were found in traditional language regions is presented in Table 2.

Of greatest interest were comparisons between metaphors and literal sentences, and between novel and familiar sentences (Figures 3 & 4). These comparisons showed that metaphors elicited greater activation than literal sentences in bilateral inferior frontal gyri, left medial superior frontal gyrus, left anterior inferior temporal gyrus, left anterior middle temporal gyrus, left posterior middle temporal gyrus, and right temporal pole. Literal stimuli elicited greater activation than metaphoric stimuli in right superior, medial frontal gyri. As noted above, there was a significant effect of figurativeness in right inferior frontal gyrus and right temporal pole. To examine these effects further, we conducted pair-wise comparisons of novel metaphors with novel literal sentences and familiar metaphors with familiar literal sentences. There were no significant differences between novel metaphors and novel literal sentences. However, familiar metaphors elicited significantly greater activation than familiar literal sentences in left inferior frontal gyrus (X, Y, Z: -56, 28, 2; max $z=4.31$; 1966 voxels), left inferior temporal gyrus (X, Y, Z: -62, -8, -18; max $z=3.33$; 142 voxels), and left middle temporal gyrus (X, Y, Z: -44, 2, -32; max $z=3.80$; 544 voxels).

Novel stimuli elicited greater activation than familiar stimuli in bilateral inferior frontal gyri, right middle frontal gyrus, left medial frontal gyrus, left parahippocampal gyrus/ medial inferior temporal gyrus, left posterior middle temporal gyrus, bilateral occipital gyri, and subcortical regions. There were no regions in which familiar stimuli elicited significantly greater activation than novel stimuli. As noted above, there was a significant effect of novelty in right inferior frontal gyrus. To examine these effects further, we conducted pair-wise comparisons between novel and familiar metaphors and novel and familiar literal sentences. There were no significant differences between novel and familiar metaphors, however novel literal sentences elicited greater activation than familiar literal sentences in left inferior frontal gyrus (X, Y, Z: -40, 18, -10; max $z=3.93$; 2235 voxels), left inferior temporal gyrus (X, Y, Z: -48, -4, -32; max $z=2.9$; 11 voxels), and left middle temporal gyrus (X, Y, Z: -58, -64, 4; max $z=3.36$; 326 voxels). A summary of the activations to metaphors and literal stimuli, and to novel and familiar stimuli that were found in traditional language regions is presented in Table 3.

4. DISCUSSION

The role of the right hemisphere in figurative language processing has been a recent topic of investigation. Metaphors, in particular novel metaphors, are hypothesized to require additional processing resources as comprehension requires integrating the commonalities of two semantically distinct concepts (e.g., tree trunks as straws). Several studies have suggested that the right hemisphere is involved in processing metaphors (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Pobric, Mashal, Faust, & Lavidor, 2008; Schmidt & Seger, In Press; Sotillo et al., 2005; Stringaris et al.,

2006; Yang, Edens, Simpson, & Krawczyk, 2009). However, other studies have yielded discrepant results (Lee & Dapretto, 2006; Mashal et al., 2009; Rapp et al., 2004, 2007; Stringaris et al., 2007). An unanswered question is how does sentence novelty influence right hemisphere recruitment in processing both figurative and literal language. Here we used functional MRI to examine the role of sentence figurativeness and novelty on patterns of brain activation.

4.1 Activation in Inferior Frontal Regions

In inferior frontal regions, the patterns of activation for metaphors and novel stimuli were similar. There was a main effect of figurativeness in which metaphors elicited more activation than literal sentences in bilateral inferior frontal gyri (IFG). Examination of the individual conditions against the nonword baseline indicated that both metaphoric conditions elicited bilateral activation in IFG, while both literal conditions elicited activation in left, but not right IFG. Although all four sentence conditions elicited significant activation in left IFG, pair-wise comparisons suggested both novelty and figurativeness modulated activity within this region. Novelty modulated the response of this region among literal sentences where novel literal sentences elicited greater activation than familiar literal sentences in left IFG. Similarly, sentence figurativeness modulated activation within familiar sentences where familiar metaphors elicited greater activation than familiar literal sentences in left IFG. These patterns of activation suggest that while all sentences engaged this region, both stimulus novelty and figurativeness further influenced activation in left prefrontal regions.

In right prefrontal regions, there were significant main effects of figurativeness and novelty: figurative sentences elicited more activation than literal sentences and novel sentences elicited greater activation than familiar sentences. Analyses of individual conditions against a nonword baseline showed that both novel and familiar metaphors elicited activation in right prefrontal regions, while both literal conditions did not. Moreover, pair-wise comparisons indicated no statistically significant differences between metaphoric conditions. These results suggest that all metaphors, even familiar ones, require additional processing resources that include right inferior frontal regions.

Although the results from the individual comparisons suggests that novel metaphors may underlie the main effect of novelty that was observed within right IFG, a pair-wise comparison showed no statistically significant differences between novel metaphors and novel literal sentences in right IFG. That is, within the right IFG novel sentences were processed to a similar extent regardless of the metaphoric or literal nature of the stimulus. These patterns of activation suggest that processing both figurative language and novel semantic relationships require additional resources, including right prefrontal regions.

Our results in inferior frontal regions are generally consistent with previous research on metaphor processing. Several studies have reported bilateral inferior frontal activation for metaphors (Ahrens et al., 2007; Bottini et al., 1994; Mashal, Faust, & Hendler, 2005; Mashal et al., 2007; Schmidt & Seger, In Press; Stringaris et al., 2006). Several studies have also found that novelty increased activation in right prefrontal regions among familiar and novel metaphoric word pairs (Mashal, Faust, & Hendler, 2005; Mashal et al., 2007) and between novel and familiar metaphoric sentences (Schmidt & Seger, In Press). Finally, a study using transcranial magnetic stimulation reported that stimulation of left IFG impaired literal stimuli and conventional metaphors but not novel metaphors suggesting that processing novel metaphors requires neural resources beyond left IFG, which may include right inferior frontal gyrus (Pobric et al., 2008).

In our study, both novel and familiar metaphors engaged right prefrontal regions, and among metaphors novelty did not modulate activation within right IFG. It is possible that all metaphors engaged participants in additional cognitive processes that included right prefrontal regions. Electrophysiological evidence has indicated that metaphoric stimuli may require additional integration even when other factors, such as cloze probability remain constant (Coulson & Van Petten, 2002; Coulson & Van Petten, 2007). Although Coulson and Van Petten did not find differences in how the hemispheres processed metaphors, they do report consistently larger N400 responses to metaphors. These results suggest that even when metaphors are as plausible as literal stimuli, they require additional cognitive resources. Our results also indicated that overall novelty increased activation in bilateral prefrontal regions compared to familiar stimuli and that among literal stimuli, novelty increased activation in left inferior frontal gyrus. These results indicate that novelty is an important semantic characteristic that can increase processing demands.

4.2 Activation in Temporal Regions

In addition to activation within prefrontal regions, we also observed effects of figurativeness and novelty in several temporal regions. Metaphors elicited greater activation than literal stimuli in left posterior and anterior middle temporal gyri (MTG) and right temporal pole. Moreover, in left MTG, familiar metaphors elicited greater activation than familiar literal sentences. Although significant differences between conditions were observed in left posterior MTG, each of the sentential conditions also elicited significant activation within this region. This suggests that this region is responding to general activation of semantic characteristics of the stimuli, and that this general response may also be sensitive to other factors such as novelty and figurativeness. Unlike activation in posterior regions, activation in left anterior MTG and right temporal pole was restricted to our comparison between metaphors and literal stimuli. We did not observe a significant main effect of novelty in anterior MTG or right temporal pole.

Although novel sentences did not elicit greater activation than literal sentences in right temporal regions, they did elicit activation in left posterior middle temporal gyrus and left parahippocampal/ inferior temporal gyrus. In left parahippocampal gyrus and left inferior temporal gyrus novel stimuli elicited greater activation than familiar stimuli. In addition, comparisons with the nonword condition indicated that all metaphors and novel literal sentences engaged left inferior temporal gyrus (Figure 2). Pair-wise comparisons indicated that novel literal sentences and familiar metaphors elicited greater activation in this region compared to familiar literal sentences. This pattern of activation in inferior and medial temporal regions suggests that this area was sensitive to both novelty and figurativeness. This region in particular, has been found to be sensitive to both conceptual and perceptual stimulus novelty [e.g., (Knight, 1996; O'Kane, Insler, & Wagner, 2005; Tulving, Markowitsch, Craik, Habib, & Houle, 1996)]. It is possible that activation in this region reflects the conceptual novelty of the sentences. Although we used relatively more and less familiar metaphors, we did not include many frozen or highly familiar metaphors. Post-hoc comparisons indicated that familiar metaphors were significantly more novel than familiar literal sentences (Tukey HSD, $p < .01$), although they were still less novel than novel literal sentences.

In general our results are consistent with several previous studies that suggest metaphors elicit greater activation in right temporal regions (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Pobric, Mashal, Faust, & Lavidor, 2008; Yang, Edens, Simpson, & Krawczyk, 2009). Although we did not find significant main effects of figurativeness or novelty in right superior temporal sulcus (rSTS), one condition, novel metaphors, elicited activation in a neighboring region: right posterior middle temporal

gyrus. Several studies using fMRI and transcranial magnetic stimulation have reported rSTS involvement in processing novel metaphors (Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Pobric, Mashal, Faust, & Lavidor, 2008). Others have shown right superior temporal gyrus recruitment for novel ironic sentences (Eviatar & Just, 2006). At least one other study using literal and metaphoric sentences did not report activation in rSTS or any other right temporal region (Mashal, Faust, Hendler, & Jung-Beeman, 2009). In that study, the authors attributed the lack of right hemisphere involvement to the use of sentences as the experimental stimuli. Prior studies by Mashal and colleagues that found activation in the rSTS incorporated word pairs (Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007), while their more recent work used sentences (Mashal, Faust, Hendler, & Jung-Beeman, 2009). Although context may influence metaphor processing, use of sentences does not seem to preclude right hemisphere activation (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Schmidt & Seger, In Press; Sotillo et al., 2005; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009) and several other studies have shown right hemisphere involvement in discourse and sentence processing in general (e.g., (St George, Kutas, Martinez, & Sereno, 1999)). Moreover, in the present experiment, which incorporated sentences, we observed activation in the right hemisphere.

One additional consideration is whether task difficulty influenced the patterns of results seen here. Prior research that has examined difficulty found a main effect of difficulty in left inferior frontal gyrus. While we found differences in activation across several comparisons in left IFG, the absence of differences in accuracy and response time among the four grammatical English sentence conditions suggests that there were not substantial differences in difficulty.

4.3 Integration of Results with Theoretical Frameworks

Our results are partially consistent with the Graded Salience Hypothesis, which suggests that right hemisphere recruitment is influenced by the salience of a stimulus (R. Giora, 1997). We found that overall novel stimuli engaged right prefrontal regions more than familiar sentences. However, all metaphors also engaged right IFG and pair-wise analyses did not show any differences between novel and familiar metaphors. These results suggest that both familiar and novel metaphors engaged the right IFG to a similar extent. Neither literal sentence condition engaged the right hemisphere and differences between literal sentences were restricted to the left hemisphere.

The coarse coding hypothesis (CCH) proposes additional details about the function of anatomical regions, and again, our results are partially consistent with this theoretical framework (Jung-Beeman, 2005). The CCH suggests that bilateral posterior temporal regions are involved in semantic activation, bilateral anterior temporal regions are involved in semantic integration and bilateral prefrontal regions are involved in semantic selection. Critically, right hemisphere resources should be recruited when integrating or selecting among loosely related concepts. In our experimental design, novel sentences contained semantic concepts that were weakly related. Therefore, we would expect greater right hemisphere activation to novel, but not familiar stimuli.

All of our sentential conditions elicited some activation in left posterior MTG and left IFG. Our results also indicated that both sentence novelty and metaphor status modulated activation in these regions, suggesting that novel stimuli and metaphors engaged additional neural resources when processed. Because lexical characteristics such as word frequency were controlled for across sentence categories, it is unlikely that either region is responding to purely lexical features. Rather, the pattern of results suggests sensitivity to semantic features. Our results are generally consistent with the role that the CCH proposes for

posterior lateral temporal regions: semantic activation (Jung-Beeman, 2005). However, we also observed the same pattern of activation within left inferior frontal regions, which the CCH proposes is involved in semantic selection. Our experiment did not specifically manipulate selection demands, and therefore is not ideally suited to disambiguate semantic activation from semantic selection.

Inconsistent with the CCH, we did not observe any effects of novelty in right temporal regions. Although we saw a significant effect of novelty in right IFG, we also observed a main effect of figurativeness in right IFG and right temporal pole. Individual comparisons indicated that both metaphoric conditions, but neither literal sentence condition elicited activation in right IFG. These results suggest that some stimuli that may have closer semantic relationships (familiar metaphors) engaged the right hemisphere, while some stimuli with distant semantic relationships (novel literal sentences) did not. In the current experiment, we used familiarity as a proxy for semantic relatedness and these two stimulus dimensions may not correlate completely. Moreover, our familiar metaphors were not the most familiar or ‘frozen’ metaphors. Therefore, it is possible that our familiar metaphors still activated loosely related concepts to some extent.

Alternatively, it is possible that because metaphors require integration of non-literal aspects of words, they would engage participants in more elaborate semantic integration processes. Some research has suggested that metaphors require additional integration demands, even when equated along other dimensions such as sentential constraint (Coulson & Van Petten, 2002; Coulson & Van Petten, 2007). Likewise, sentences that contain novel semantic relationships would also require relatively more semantic integration compared to sentences that contain familiar semantic relationships. Examined from this framework, our results are consistent with the right hemisphere’s involvement in semantic integration (Federmeier, 2007). Overall, conditions with the highest semantic integration demands engaged right hemisphere resources (novel stimuli overall, and familiar and novel metaphors individually).

4.4 Conclusions

The present fMRI study demonstrated that both novelty and figurativeness influenced recruitment of the right hemisphere. In right inferior frontal regions, metaphors elicited greater activation than literal stimuli, and novel sentences elicited greater activation than literal sentences. In addition, metaphors elicited greater activation than literal sentences in right temporal pole. In the left hemisphere, all sentences elicited activation in posterior middle temporal gyrus and inferior frontal gyrus. However, both figurativeness and novelty modulated activity within these regions. These results are partially consistent with the Graded Salience Hypothesis and the Coarse Coding Hypothesis in that sentences with novel semantic relationships engaged right inferior frontal gyrus more than familiar stimuli. Both hypotheses predict greater recruitment of right hemisphere resources when processing stimuli with distant semantic relationships. However, we also found right hemisphere activation to familiar metaphors in both inferior frontal and temporal regions, which is contrary to the predictions of the Graded Salience and Coarse Coding Hypotheses. While it is possible that our familiar metaphors still engaged semantically distant items, these results are also consistent with the right hemisphere’s involvement in semantic integration. It may be that metaphors, even ones that are relatively familiar, still require additional integrative strategies beyond those required for literal language.

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Figure 1. Experimental Design. Participants viewed literal, metaphoric, and nonword sentences (duration=6s). Sentences occurred every 4.5 to 9 seconds, and a fixation cross was presented between sentences. Participants assessed each sentence for its valence.

Figure 2. Activation in Parahippocampal Gyrus and Inferior Temporal Gyrus. Regions in which novel literal sentences (blue), novel metaphors (green), and familiar metaphors (purple) elicited significant activation in left parahippocampal gyrus / medial inferior temporal regions ($p < .01$, cluster thresholded).

Figure 3.

Activation in Inferior Frontal Gyri. Left: Regions in which metaphors elicited greater activation than literal sentences (blue) and in which literal sentences elicited greater activation than metaphors (red, $p < .01$, cluster thresholded). Metaphors elicited greater activation than literal sentences in bilateral inferior frontal gyri, and left medial superior frontal gyrus. Greater activation to literal sentences compared to metaphors can be seen in right medial superior frontal gyrus. Hemodynamic responses from the cluster in left inferior frontal gyrus (IFG) are shown below. All sentences elicited a significant hemodynamic response in left IFG; however, this response was significantly larger for metaphors. Right: Regions in which novel sentences elicited greater activation than familiar sentences (green) and in which familiar sentences elicited greater activation than novel sentences (purple). Novel sentences elicited activation in bilateral inferior frontal gyrus, and left medial frontal gyrus. There were no regions in which familiar sentences elicited greater activation than novel sentences. Hemodynamic responses from the cluster in left IFG are shown below. All sentences elicited a significant hemodynamic response in left IFG; however, this response was significantly larger for novel sentences compared to familiar sentences.

Figure 4.

Activation in Lateral Temporal Gyri. Left: Regions in which metaphors elicited greater activation than literal sentences (blue) can be seen in anterior regions of middle temporal gyrus and left inferior frontal gyrus ($p < .01$, cluster thresholded). Hemodynamic responses (HDRs) from the cluster in left anterior middle temporal gyrus are shown. Metaphors elicited significantly larger hemodynamic responses in this region compared to literal sentences. Right: Regions in which novel sentences elicited greater activation than familiar sentences (green) can be seen in posterior middle temporal gyrus and left inferior frontal gyrus. Hemodynamic responses from the cluster in left posterior middle temporal gyrus are shown. Although both novel and familiar sentences elicited a hemodynamic response in this region; HDRs were larger for novel stimuli.

Table 1**Sentence Characteristics**

Sentence length, Frequency, Concreteness, and Ratings are provided for the four sentence types. Word frequencies are from (Kucera & Francis, 1967), and concreteness ratings are from the MRC database (Wilson, 1988). Novelty, positivity, and comprehension ratings range from 1 to 7, where lower values indicate lower novelty, positivity, and comprehension. There was a significant effect of novelty where novel sentences were rated as more novel than familiar sentences. There was also a significant effect of comprehension where literal sentences had a higher comprehension rating than metaphors, and familiar sentences had a higher comprehension rating than novel sentences. Overall, all sentences were rated above the midpoint of the scale indicating a high level of comprehension overall

	Novel Metaphors	Familiar Metaphors	Novel Literal	Familiar Literal
Length	5.5 (1.3)	5.5 (1.3)	5.9 (1.1)	5.9 (.9)
Frequency- Noun 1	78.4 (102.5)	100.9 (99.09)	136.6 (175.3)	91.7 (130.1)
Frequency - Noun 2	30.3 (86.2)	40.7 (59.5)	15.0 (20.0)	41.0 (45.9)
Concreteness - Noun 1	478.0 (128.5)	497.7 (121.8)	508.0 (108.4)	523.5 (95.7)
Concreteness - Noun 2	572.1 (80.1)	568.4 (57.9)	590.8 (37.0)	596.8 (31.8)
Novelty *	5.3 (0.2)	3.1 (0.5)	3.3 (.02)	1.9 (0.1)
Positivity	3.6 (1.2)	3.9 (1.4)	3.8 (0.5)	4.0 (0.3)
Comprehension **	4.5 (0.4)	5.7 (0.4)	6.0 (0.4)	6.4 (0.4)

* Significant main effect of novelty comparing novel and familiar sentences.

** Significant main effect of comprehension between literal sentences and metaphors, and between familiar and novel sentences.

MNI Coordinates, maximum Z values, and number of active voxels for the centers of activation that were found in traditional language regions. Clusters are shown for areas in which each of the four sentential conditions elicited significantly more activation than the nonword condition

Table 2

Region	Hemi- sphere	BA	X	Y	Z	Max Z	# Voxels
Novel Metaphors							
Inferior Frontal Gyrus	Left	10, 11, 45, 46, 47	-48	28	-8	4.15	3254
	Right	45	64	22	2	3.07	53
Parahippocampal Gyrus/ITG	Left	20	-34	-20	-26	3.61	139
Posterior Middle Temporal Gyrus	Left	21	-72	-46	0	3.18	260
	Right	21	64	6	-18	2.85	9
Temporal Pole	Right	38	44	10	-20	3.24	41
Familiar Metaphors							
Inferior Frontal Gyrus	Left	45, 47	-52	30	0	3.81	1734
	Right	45	62	32	2	3.37	90
Parahippocampal Gyrus/ ITG	Left	20	-32	-14	-28	3.26	114
Posterior Middle Temporal Gyrus	Left	21	-54	-44	-6	2.49	25
Novel Literal Sentences							
Inferior Frontal Gyrus	Left	44	-62	16	14	3.65	1054
Parahippocampal Gyrus/ ITG	Left	36	-36	-16	-26	3.26	136
Posterior Middle Temporal Gyrus	Left	21	-56	-30	-4	2.42	17
Familiar Literal Sentences							
Inferior Frontal Gyrus	Left	44, 45	-64	18	14	3.57	223
	Left	47, 38	-40	16	-20	3.27	90
	Left	47	-52	34	-20	2.73	8
Posterior Middle Temporal Gyrus	Left	21	-66	-32	-14	2.45	8
ITG - Inferior Temporal Gyrus							

MNI Coordinates, maximum Z values, and number of active voxels for the centers of activation in traditional language regions. Clusters are shown for areas in which metaphors elicited greater activation than literal stimuli, and in which novel sentences elicited greater activation than familiar sentences. There were no clusters of activation in traditional language regions for the familiar > novel comparison, and there were no regions in which literal sentences elicited greater activation than metaphors

Table 3

Region	Hemi- sphere	BA	X	Y	Z	Max Z	# Voxels
Metaphor > Literal							
Inferior Frontal Gyrus	Left	11, 38, 45, 47	-44	30	-6	4.53	3339
	Right	45, 47	58	26	10	3.32	152
Anterior Middle Temporal Gyrus	Left	20	-62	-8	-26	3.24	55
Posterior Middle Temporal Gyrus	Left	22	-64	-34	-4	2.53	16
	Left	21	-72	-34	-4	3.21	12
	Left	21	-58	-48	-2	2.57	8
Temporal Pole	Right	38	46	6	-18	2.62	7
Novel > Familiar							
Inferior Frontal Gyrus	Left	45, 47, 36, 38, 6	-54	20	-8	4.46	2484
	Left		-28	2	30	3.09	8
	Right	45	60	30	4	3.01	15
	Right	45	60	22	14	2.62	7
	Right	47	44	20	-6	2.76	8
Parahippocampal Gyrus/ ITG	Left	36	-28	-20	-26	2.98	112
Posterior Middle Temporal Gyrus	Left	21, 22	-62	-50	8	3.36	273
	Left	21, 22	-70	-28	-6	2.73	21
ITG - Inferior Temporal Gyrus	Left	37	-66	-54	-8	3.07	39