The influence of context on hemispheric recruitment during metaphor processing

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Abstract

Although the left hemisphere's prominence in language is well established, less emphasis has been placed on possible roles for the right hemisphere. Behavioral, patient, and neuroimaging research suggests that the right hemisphere may be involved in processing figurative language. Additionally, research has demonstrated that context can modify language processes and facilitate comprehension. Here we investigated how figurativeness and context influenced brain activation, with a specific interest in right hemisphere function. Previous work in our lab indicated that novel stimuli engaged right inferior frontal gyrus and that both novel and familiar metaphors engaged right inferior frontal gyrus and right temporal pole. The Graded Salience Hypothesis (GSH) proposes that context may lessen integration demands, increase the salience of metaphors, and thereby reduce right hemisphere recruitment for metaphors. In the present study, functional Magnetic Resonance Imaging was used to investigate brain function while participants read literal and metaphoric sentences that were preceded by either a congruent or an incongruent literal sentence. Consistent with prior research, all sentences engaged traditional left hemisphere regions. Differences between metaphors and literal sentences were observed, but only in the left hemisphere. In contrast, a main effect of congruence was found in right inferior frontal gyrus, right temporal pole, and dorsal medial prefrontal cortex. Partially consistent with the GSH, our results highlight the strong influence of context on language, demonstrate the importance of the right hemisphere in discourse, and suggest that in a wider discourse context congruence has a greater influence on right hemisphere recruitment than figurativeness.

INTRODUCTION

Figurative language can provide a vivid and concise description of two seemingly dissimilar items (e.g., *The crocus is spring's messenger.*). Previous behavioral, clinical, and imaging research suggests that the right hemisphere is important in figurative language processing. However, there has been disagreement about whether figurativeness, per se, or other factors that may co-vary with metaphoric status, such as novelty and semantic integration demands, influence right hemisphere recruitment. The Graded Salience Hypothesis (GSH), proposes that comprehension is influenced by salience, with more salient words, phrases, and sentences being easier to process than less salient text and requiring less right hemisphere recruitment (Giora, 1997, 2003). One factor that influences salience is the amount of supporting context, with increasing supportive context facilitating comprehension, increasing salience, and reducing right hemisphere recruitment. However, research on discourse processing has highlighted the importance of the right hemisphere in a variety of experimental manipulations including processing topical violations (Caplan & Dapretto, 2001), causal inference generation and integration (Kuperberg, Lakshmanan, Caplan, &

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Holcomb, 2006; Mason & Just, 2004), and when manipulating semantic integration demands (Robertson et al., 2000; St. George, Kutas, Martinez, & Sereno, 1999). In the present study we manipulated figurativeness and contextual congruence to investigate the influence of these factors on right hemisphere recruitment.

While the GSH provides a general hypothesis about right hemisphere recruitment, the Coarse Coding Hypothesis (CCH) provides additional anatomical detail about hemispheric functions (Jung-Beeman, 2005). It proposes that the right hemisphere processes concepts more diffusely (i.e., coarse coding) while the left hemisphere has more focal activations, with posterior temporal cortex supporting semantic activation, anterior temporal cortex supporting semantic integration and inferior frontal cortex supporting semantic selection. An alternative hypothesis has been proposed by Federmeier and colleagues who suggest that while both hemispheres are sensitive to language and sentence-level processes, the right hemisphere focuses on integrative language functions while the left hemisphere focuses on predictive language functions (Federmeier, 2007). Although incompletely aligned, collectively these hypotheses provide several ideas about possible roles for the right hemisphere and potential regions of interest.

Neuroimaging research on metaphors has shown that metaphors elicited greater activation than literal stimuli in traditional left hemisphere brain regions, such as such as inferior frontal gyrus and left inferior and middle temporal gyri (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Diaz, Barrett, & Hogstrom, 2011; Mashal, Faust, Hendler, & Jung-Beeman, 2009; Rapp, Leube, Erb, Grodd, & Kircher, 2004, 2007; Schmidt & Seger, 2009). Additionally, many studies have also reported that sentential metaphors engaged right prefrontal regions such as right inferior frontal gyrus (Ahrens et al., 2007; Bottini et al., 1994; Diaz, Barrett, & Hogstrom, 2011; Schmidt & Seger, 2009; Stringaris et al., 2006) and right insula (Schmidt & Seger, 2009), and also right temporal areas such as right middle (Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Diaz, Barrett, & Hogstrom, 2011) and inferior temporal gyri (Ahrens et al., 2007; Eviatar & Just, 2006; Yang, Edens, Simpson, & Krawczyk, 2009). These results are consistent with clinical research that has shown that damage to the right hemisphere can impair comprehension of metaphors (Brownell, Simpson, Bihrle, Potter, & Gardner, 1990; Bryan, 1988; McIntyre, Pritchard, & Lombroso, 1976; Rinaldi, Marangolo, & Baldassarri, 2004; Winner & Gardner, 1977), jokes (Bihrle, Brownell, Powelson, & Gardner, 1986), idioms (Kempler, Van Lancker, Marchman, & Bates, 1999; Van Lancker & Kempler, 1987), and prosody (Tucker, Watson, & Heilman, 1977).

However, several fMRI studies have not supported right hemisphere involvement in metaphor comprehension (Lee & Dapretto, 2006; Mashal, Faust, Hendler, & Jung-Beeman, 2009; Rapp, Leube, Erb, Grodd, & Kircher, 2004, 2007). In some instances stimulus repetition may have reduced power and sensitivity (Rapp, Leube, Erb, Grodd, & Kircher, 2004, 2007). However, others have explained the absence of right hemisphere activation to sentential metaphors by suggesting that the right hemisphere is primarily sensitive to word associations, and less sensitive to context than the left hemisphere (Faust, Babkoff, & Kravetz, 1995; Faust, Bar-lev, & Chiarell, 2003; Faust, Kravetz, & Babkoff, 1993; Mashal, Faust, Hendler, & Jung-Beeman, 2009). While context may influence metaphor processing, results from several studies which used sentences as stimuli suggest that presenting metaphoric ideas in a sentential context does not prevent right hemisphere recruitment (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Eviatar & Just, 2006; Schmidt & Seger, 2009; Sotillo et al., 2005; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009).

However, one gap in the previous literature is that potential differences in stimulus characteristics between metaphors and literal sentences, such as novelty and context, have not been extensively examined. In a prior study, we manipulated stimulus novelty in both literal sentences and metaphors (Diaz, Barrett, & Hogstrom, 2011). We found significant main effects of novelty and figurativeness in right inferior frontal gyrus and an additional significant main effect of figurativeness in right anterior temporal pole. Partially consistent with the GSH, these results suggest that sentence novelty influenced right hemisphere recruitment. However, the sensitivity of the right hemisphere to relatively familiar metaphors suggested that the right hemisphere may also be sensitive to the increased semantic integration demands of metaphors. These results are consistent with one other study that examined familiarity in metaphors (Schmidt & Seger, 2009).

In addition to novelty, other factors, such as context may also influence right hemisphere recruitment. Prior research on discourse processing suggests that the right hemisphere is important in discourse comprehension. A recent meta-analysis indicated that coherent sentences and stories elicited greater activation than incoherent text in traditional left hemisphere language regions, but also in bilateral anterior temporal cortex, bilateral superior temporal sulcus, right ventral medial prefrontal cortex, and left dorsal medial prefrontal cortex (Ferstl, Neumann, Bogler, & von Cramon, 2008). Right hemisphere recruitment during discourse processing has been found with a variety of experimental manipulations including auditory sentence comprehension (Price, 2010), reading untitled compared to titled stories (St. George, Kutas, Martinez, & Sereno, 1999), processing topical violations relative to logical violations (Caplan & Dapretto, 2001), reading sentences with definite articles compared to sentences with indefinite articles (Robertson et al., 2000), during causal inference generation and integration (Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mason & Just, 2004), and while examining discourse coherence (Ferstl, Rinck, & von Cramon, 2005; Ferstl & von Cramon, 2001, 2002; Siebörger, Ferstl, & von Cramon, 2007).

In the present study we examined the role of the right hemisphere in processing literal and metaphoric sentences presented in congruent and incongruent contexts. Prior research has suggested that metaphors, presented in isolation, engage the right hemisphere (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Diaz, Barrett, & Hogstrom, 2011; Eviatar & Just, 2006; Schmidt & Seger, 2009; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009). However, some theoretical accounts suggest that metaphor processing may be facilitated by supportive context and which may reduce right hemisphere involvement (Giora, 1997, 2003). Additionally, prior research on discourse suggests that coherent sentences will engage traditional left hemisphere regions, left DMPFC, and inferior frontal and temporal regions of the right hemisphere. The present experiment will provide additional insight into how the factors figurativeness and context congruence influence right hemisphere activation.

METHODS

Participants

Sixteen, right-handed, native English speaking, healthy young adults (mean age 24.8; age range 21-31; 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.

Stimuli

Stimuli consisted of pairs of grammatical English sentences that varied in their figurativeness and congruence. In each sentence pair, the first sentence was always literal, and the second sentence could be either metaphoric or literal. Within sentence pairs, sentences were either congruent or incongruent in meaning. This yielded four conditions of English sentence pairs: congruent literal sentences, incongruent literal sentences, congruent metaphoric sentences, and incongruent metaphoric sentences. Example sentences are presented in Table 1. 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 sentence pairs. Literal and metaphoric sentences were created from published sources and a previous study conducted in our lab (Diaz, Barrett, & Hogstrom, 2011; Katz, Paivio, & Marschark, 1985; Katz, Paivio, Marschark, & Clark, 1988). A behavioral pilot study was conducted with a separate group of participants (N=15) to assess sentence familiarity and comprehension, previously reported in (Diaz, Barrett, & Hogstrom, 2011). There were no significant differences in familiarity across sentence conditions. There was a significant main effect of comprehension between metaphors and literal sentences (t=6.08, df=158, p<.001). Metaphors were rated as slightly more difficult to comprehend compared to literal sentences (congruent literal = 6.12, incongruent literal = 6.04, congruent metaphor = 5.49, incongruent metaphor = 5.38, out of 7.0, higher values on the Likert scale indicated greater comprehension). Follow up pair-wise comparisons between conditions indicated that critical sentences from both metaphor conditions were slightly more difficult to comprehend than critical sentences from both literal conditions, although there were no significant differences in comprehension within literal or metaphoric conditions. Again, these ratings of comprehension were obtained for the presentation of the sentences in isolation (i.e., without the congruent or incongruent context) and in a separate group of individuals. 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. There were no significant differences in comprehension between critical congruent and critical incongruent sentences, again when critical sentences were presented in isolation. Additionally, a separate group of participants (N=10) assessed the congruence of the sentence pairs to ensure consistency with our classification of the sentence pairs. Overall there was a high degree of reliability in sentence classifications across participants (Fleiss' Kappa = .884). There were no significant differences in the concordance of the classification ratings across sentence categories (congruent literal = 97.2%, incongruent literal = 97.7%, congruent metaphors = 97.5%, incongruent metaphors = 96%). In addition, to account for any remaining variability in ratings during the fMRI experiment we incorporated a response based analysis strategy for the fMRI data as described in the analyses below. 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. The first sentence of each pair was 5-11 words in length, average length = 6.61 words. Critical sentences were 4 - 9 words in length, average length = 5.98 words. Nouns within the four English sentence conditions were matched for frequency (Coltheart, 1981; Kucera & Francis, 1967; Wilson, 1988b), and concreteness (Coltheart, 1981; Wilson, 1988b). Ratings of frequency and concreteness were obtained from the MRC psycholinguistic database (Coltheart, 1981). Additionally, to minimize the possibility of word-word priming, all sentences were screened to ensure that there were no associated words within the sentences. Strength of association between words was measured through the Edinburgh Associative Thesaurus and the University of South Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998; Wilson, 1988a). 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.

Experimental Task

Each trial consisted of two sentences presented simultaneously on the screen. The first sentence was always a literal English sentence and the second sentence could be either literal or metaphoric. In addition to metaphor status, we also manipulated congruence between sentence pairs, such that the two sentences could be either semantically congruent or incongruent. This resulted in the second sentence being one of four types: a congruent literal sentence, an incongruent literal sentence, a congruent metaphoric sentence, or an incongruent metaphoric sentence. To ensure that participants were attentive to the stimuli during the fMRI session, participants were asked to read each sentence pair and judge each sentence pair as related, unrelated, or non-word sentences.

Each sentence pair was presented for 6 seconds with a variable inter-trial-interval, 1.5 to 19s in length. Each run began and ended with the presentation of a fixation cross, and a fixation cross was presented between each sentence pair. Trial order across conditions and inter-trial-interval were randomized and optimized using the optseq2 program (Greve, 2002). A randomized order of presentation and a variable inter-stimulus-interval were incorporated to minimize participant preparation and anticipation of stimuli. 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).

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 commisures 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 fSPGR pulse sequence (TR=7.384 ms; TE=2.988 ms; ti=450 ms; FOV=25.6 cm^2; flip angle=12°; voxel size= $1 \times 1 \times 2$mm; 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=25.6m^2; flip angle=60°; voxel size=$4 \times 4 \times 4$mm; 30 contiguous axial slices). Each of 8 runs consisted of the acquisition of a time series of 232 brain volumes (~6 minute runs). Four initial RF excitations were performed to achieve steady state equilibrium and were subsequently discarded.

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. Each participant's classification of the trials as congruent, incongruent, or nonword were incorporated into the functional analyses to ensure consistency between trial classification and each subject's individual ratings. Across conditions there were no differences in the average number of trials per condition.

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 (Beckman, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckman, Jenkinson, & Smith, 2004). Additionally, a repeated measures ANOVA was calculated to assess for main effects of figurativeness, discourse congruence, and the interaction between the two factors. All activations were cluster corrected according to Gaussian random fields (GRF) theory ($p < .01$) and results from higher level comparisons were masked by results from lower level analyses. Coordinates of the centroids of activation and their corresponding anatomical gyri were determined through the use of anatomical atlases. All reported coordinates are in MNI space and results are overlaid on the MNI template brain.

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 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. The results were masked by brain regions that were significant in the main FSL analyses. Thus the hemodynamic responses presented in the figures represent areas that were significant in both analyses.

RESULTS

Behavioral Results

Across valid English sentences, the conditions of greatest interest, there were no significant differences in response times $F(3,63) = 0.49$, $p=0.69$. Participants' average response time for the relatedness judgment was 3433.2 (SD=1297.3 ms); response times to individual conditions were as follows: congruent literal sentences = 4090.2 ms (SD=669.5 ms), incongruent literal sentences = 3836.1 ms (SD=599.7 ms), congruent metaphors = 4083.8 ms (SD=744.4), incongruent metaphors = 3977.7 ms (SD=689.5 ms), and nonword sentences = 1178.4 ms (SD= 450.7 ms). Nonword sentences were responded to significantly faster than the other conditions $F(4,79) = 62.7$, $p<.01$, but there were no significant differences in response times across the English sentence conditions $F(3,60) = .49$, $p=.69$. 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 5.1% of the data. There were no significant differences across any conditions in this error analysis $F(4,195) = 1.09$, $p=.36$. The response time data indicated that the participants were able to perform the task successfully. Moreover, the lack of differences in response times and accuracy across the English sentence conditions suggests that task difficulty was similar across these conditions.

fMRI Activation

Consistent with previous fMRI results, when collapsing across conditions, valid English sentences elicited greater activation than nonword sentences in traditional language regions: bilateral inferior frontal gyri (Left: −54, 28, 2, Right: 34, 26, −6), bilateral insula (Left: −38, 20, 14; Right: 28, 20, −4), left dorsal medial prefrontal cortex (−10, 58, 24), and bilateral middle temporal gyri (Left: −60, −32, 2, Right: 50, −18, −8). The bilateral inferior frontal activations extended dorsally to middle frontal gyri and ventrally into anterior superior temporal gyri. The middle temporal gyrus activation in the left hemisphere extended from the temporal pole into angular gyrus, and also extended into portions of the superior and inferior temporal gyri. Also consistent with previous reports, English sentences elicited more activation in left hemisphere regions compared with their right hemisphere homologues. Outside of traditional language regions, we also observed activation to sentences in left motor cortex, bilateral occipital cortex, and subcortical regions.

Our primary comparisons of interest were the effects of sentence figurativeness and discourse congruence, and the interaction of the two. With regard to the main effect of figurativeness, our working hypothesis was that additional congruent context may decrease the integration demands of processing figurative language and therefore may reduce right hemisphere recruitment for metaphors. Overall metaphors elicited greater activation than literal sentences in language regions in the left hemisphere only. See Figure 1 and Table 2 for details. These regions included left inferior frontal gyrus, dorsal medial prefrontal gyrus (DMPFC), temporal pole/anterior middle temporal gyrus, and posterior middle temporal gyrus. Activation in left inferior frontal gyrus included the insula and extended inferiorly into the temporal pole. Activation in middle temporal gyrus consisted of a more anterior region which included the temporal pole and extended into superior temporal gyrus, and a more posterior region which extended into the angular gyrus. Metaphoric sentences also elicited more activation than literal sentences in non-language related regions including left cingulate gyrus and bilateral occipital cortex. There were no regions in which literal sentences elicited more activation than metaphors.

Our second main comparison of interest concerned the effects of discourse congruence, and how these may be related to the effects of figurativeness. A main effect of congruence (congruent > incongruent) revealed activations in bilateral inferior frontal gyrus, bilateral temporal pole, left middle temporal gyrus, angular gyrus, and left DMPFC. See Figure 2 and Table 2 for details. Activation in the left inferior frontal gyrus was extensive (BA 44, 45, 47) and included the insula (Figure 2). Activation in right inferior frontal gyrus included pars triangularis and pars orbitalis (BA 45, 47). Activation in the left middle temporal gyrus extended the length of the gyrus, into lateral inferior and superior temporal cortex, and included portions of the angular gyrus. Activation was also present in non-language related areas including right middle frontal gyrus, bilateral orbital frontal cortex, bilateral occipital gyri and the brain stem. There were very few regions where incongruent sentences elicited greater activation than congruent sentences. These regions included left post-central gyrus and two clusters of activation in left superior temporal gyrus. Examining the results of the two previous comparisons, congruent > incongruent and incongruent > congruent together, there appeared to be an anterior-posterior shift in DMPFC that was sensitive to discourse congruence (Figure 4). In a more anterior region in DMPFC, congruent trials were more active compared to incongruent trials. In a more posterior region, incongruent sentence pairs elicited greater activation than congruent sentence pairs. A summary of regions that differentiated congruent and incongruent discourse is presented in Table 2.

We conducted a repeated-measures ANVOA to assess the interaction between figurativeness and congruence. There were no regions in which the interaction was significant.

DISCUSSION

Recent research suggests that the right hemisphere, in addition to the left, contributes to language comprehension. Specifically, several studies have suggested that the right hemisphere may be involved in processing figurative language (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Diaz, Barrett, & Hogstrom, 2011; Eviatar & Just, 2006; Mashal, Faust, & Hendler, 2005; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Pobric, Mashal, Faust, & Lavidor, 2008; Schmidt & Seger, 2009; Sotillo et al., 2005; Stringaris et al., 2006; Yang, Edens, Simpson, & Krawczyk, 2009). However, some theoretical accounts of language, such as the Graded Salience Hypothesis (GSH), argue that factors other than figurativeness per se, may influence right hemisphere recruitment, and moreover that the addition of context may facilitate processing metaphors, which in turn may reduce right hemisphere involvement. However, other research suggests that processing discourse may also engage the right hemisphere (Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mason & Just, 2004; Robertson et al., 2000; St. George, Kutas, Martinez, & Sereno, 1999). The present study investigated how these two factors, figurativeness and discourse context, influence hemispheric recruitment.

The first aim of this experiment was to investigate the effects of figurativeness, and how these may be influenced by context congruence. Previous imaging research has demonstrated that sentential metaphors elicit activation in right inferior frontal regions (Ahrens et al., 2007; Bottini et al., 1994; Diaz, Barrett, & Hogstrom, 2011; Schmidt & Seger, 2009; Stringaris et al., 2006) and right temporal gyri (Ahrens et al., 2007; Bottini et al., 1994; Chen, Widick, & Chatterjee, 2008; Diaz, Barrett, & Hogstrom, 2011; Eviatar & Just, 2006; Yang, Edens, Simpson, & Krawczyk, 2009). Moreover, even relatively familiar metaphors, and familiar metaphors with low processing demands, have been found to engage the right hemisphere (Diaz, Barrett, & Hogstrom, 2011; Eviatar & Just, 2006; Schmidt & Seger, 2009). These findings suggest that while novelty influenced right hemisphere recruitment, the right hemisphere may be involved in processing any metaphor. Based on the GSH, we hypothesized that additional context may decrease the integration demands of processing figurative language and therefore may reduce differences within the right hemisphere between metaphors and literal sentences. Our results were partially consistent with this. Although metaphors elicited greater activation than literal sentences, this occurred exclusively in left hemisphere regions: inferior frontal gyrus, dorsal medial prefrontal gyrus, temporal pole, middle temporal gyrus, and angular gyrus. At first glance these results are consistent with the GSH, however, unexpectedly and inconsistent with the GSH, we did not find a significant interaction between figurativeness and context congruence. That is, both congruent and incongruent context reduced differences between literal and metaphoric sentences in the right hemisphere. One possible influence on this result is the context that we provided. Because the first sentence of the discourse context was always literal, this may have reduced our ability to discern activation to the metaphors. However, one other study that examined figurative language in a larger context also provided literal context and found effects within the right hemisphere. Eviatar and Just compared coherent stories that ended with an ironic, metaphoric, or literal ending (Eviatar & Just, 2006). Metaphors engaged left inferior frontal gyrus and bilateral inferior temporal gyrus to a greater extent than literal or ironic sentences. Our results within the left hemisphere are consistent with these results. However, we did not see effects of figurativeness in the right hemisphere. One factor that may contribute to this discrepancy is that the present study included both congruent and incongruent discourse contexts while the former included only congruent contexts. However, a restricted analysis of only congruent trials also revealed effects of figurativeness in the left hemisphere only.

The second aim of the experiment was to examine the effects of discourse congruence in figurative and literal language. Main effects of congruence (congruent > incongruent) were found bilaterally in inferior frontal gyrus and temporal pole, and in left middle temporal gyrus and left dorsal medial frontal gyrus. Importantly, these effects of congruence were similar for metaphors and literal sentences. The pattern of results observed in the right hemisphere is consistent with prior research on discourse processing. Activation in right inferior frontal gyrus has been reported when processing more coherent discourse compared to less coherent discourse (Robertson et al., 2000), when processing topical violations compared to logical violations (Caplan & Dapretto, 2001), and when making causal inferences (Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006; Mason & Just, 2004).

We also found effects of discourse congruence in bilateral anterior temporal pole. Activation in bilateral anterior temporal pole has been consistently reported in sentence processing (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Ferstl & von Cramon, 2001, 2002; Humphries, Binder, Medler, & Liebenthal, 2006; Xu, Kemeny, Park, Frattali, & Braun, 2005) and a recent meta-analysis cited this region as one of several important for discourse processing (Ferstl, Neumann, Bogler, & von Cramon, 2008). Additionally, prior research supports a role for anterior temporal cortex in semantic memory (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Rogers et al., 2006; Tyler et al., 2004; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Visser, Jefferies, & Lambon Ralph, 2010), and involvement of anterior temporal regions in semantic memory is consistent with clinical research on semantic dementia, in which progressive atrophy of the temporal lobe is associated with increasing semantic impairments (Hodges & Patterson, 1996; Hodges, Patterson, Oxbury, & Funnell, 1992; Mummery et al., 1999; Snowden, Goulding, & Neary, 1989). Although, the exact function of this region has been debated (for a review see: (Simmons & Martin, 2009)), some have suggested that bilateral anterior temporal regions may be involved in modality independent semantic processing (Lambon Ralph, Pobric, & Jefferies, 2008; Patterson, Nestor, & Rogers, 2007; Pobric, Jefferies, & Lambon Ralph, 2007, 2010; Pobric, Lambon Ralph, & Jefferies, 2009; Rogers et al., 2006; Rogers et al., 2004; Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010). Combining bilateral anterior temporal lobe's involvement in semantic memory and also sentence processing, some have suggested that this region may be ideally suited for propositionalization or creating a larger abstract semantic representation from individual words (Ferstl, Neumann, Bogler, & von Cramon, 2008).

Our results also highlight the importance of dorsal medial prefrontal cortex (DMPFC) in processing coherent discourse. Prior research has shown involvement of left DMPFC in discourse coherence in written (Ferstl, Rinck, & von Cramon, 2005; Ferstl & von Cramon, 2001; Siebörger, Ferstl, & von Cramon, 2007) and auditory (Ferstl & von Cramon, 2002) modalities, in text comprehension (Ferstl, Neumann, Bogler, & von Cramon, 2008), and in making causal inferences in discourse (Kuperberg, Lakshmanan, Caplan, & Holcomb, 2006). Additionally, DMPFC recruitment may also be influenced by individual differences in task performance. Ferstl and colleagues found that poor performers engaged DMPFC more while processing text with inconsistencies, while better performers engaged DMPFC more while processing consistent text (Ferstl, Rinck, & von Cramon, 2005). In the present experiment we observed a spatial relationship between congruent and incongruent trials in medial prefrontal regions. An anterior medial prefrontal region responded more strongly to congruent sentence pairs compared to incongruent sentence pairs, and a posterior region responded more strongly to incongruent sentence pairs compared to congruent sentence pairs (Figure 3). Overall, these findings suggest that DMPFC is involved in several aspects of building a discourse model and that this region may also be sensitive to individual differences.

Our experiment was designed to test a specific hypothesis of the Graded Salience Hypothesis (i.e., reduced right hemisphere recruitment for metaphors in supportive context), and our results were partially consistent with this hypothesis. Although we failed to find a significant interaction between congruence and figurativeness as expected, there were no differences in right hemisphere activation to metaphors and literal sentences. An additional detail of this result is that differences between metaphors and literal sentences persisted in several left hemisphere regions including inferior frontal gyrus, DMPFC, and temporal regions. These results are consistent with prior research comparing figurative and literal language, and could speak to two possible conclusions. First, although stimuli were matched in terms of novelty and concreteness, words in a metaphoric context may still present increased processing demands. Second, although our results clearly indicate a role for the right hemisphere in discourse comprehension, it is possible that the left hemisphere is still more sensitive to language constraints.

Comparing our two main effects, figurativeness and context congruence, the effects of context congruence were substantially larger than effects of figurativeness. This may signify a difference in the relative importance of these factors in discourse comprehension. One perhaps counterintuitive result is that congruent context elicited greater activation than incongruent context. If context facilitates comprehension then why should congruent context elicit greater activation than incongruent context? One possible explanation is that discourse comprehension engages a number of additional cognitive processes such as narrative building and semantic integration across sentences. This interpretation is also consistent with our response time data in that participants responded to congruent and incongruent sentences similarly. The typical finding is that 'yes' responses are faster (which would be congruent trials in this case). But if congruent sentences engaged participants in additional cognitive processes, this may partially explain the relatively prolonged latencies for the congruent sentences.

Although the present experiment was not explicitly designed to disambiguate other models of hemispheric function, the results have some general implications for models that suggest the right hemisphere is involved in coarser coding compared with the left (Jung-Beeman, 2005) or biased toward integrative rather than predictive functions (Federmeier, 2007). In the right hemisphere, we only saw an effect of context congruence. Processing congruent context is likely to engage participants in building a narrative, making inferences between sentences, and increased semantic integration. However, we cannot make more precise claims about component processes of discourse processing because the present experiment did not include conditions that would bias processing toward different types of processing.

Conclusions

In the present study, we investigated how figurativeness and context congruence influence brain activation. The strongest effects we observed were for congruent context: processing coherent discourse compared to incoherent discourse, regardless of the figurative or literal aspect of the text, engaged the right inferior frontal gyrus and right temporal pole. In relation to this and prior studies (Diaz, Barrett, & Hogstrom, 2011), discourse had a much larger effect than novelty or figurativeness. Although we expected an interaction between discourse congruence and figurativeness, this effect was not significant. These results highlight the strong influence of context on language processing, the importance of the right hemisphere in building a narrative, and suggest that in a wider discourse context, congruence has a much stronger role in right hemisphere recruitment than figurativeness.

Acknowledgments

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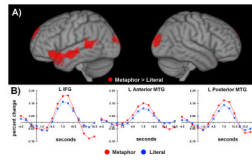
Figure 1.
Activation to metaphors and literal sentences. A. Regions in which metaphors elicited significantly greater activation than literal sentences (red). All displayed activations are thresholded, p<.01, GRF cluster corrected. There were no regions in which literal sentences elicited significantly more activation than metaphors. B. Hemodynamic responses to metaphors (red) and literal sentences (blue) from the clusters of activation in left inferior frontal gyrus (IFG, left), left anterior middle temporal gyrus (MTG, middle), and left posterior middle temporal gyrus (right).
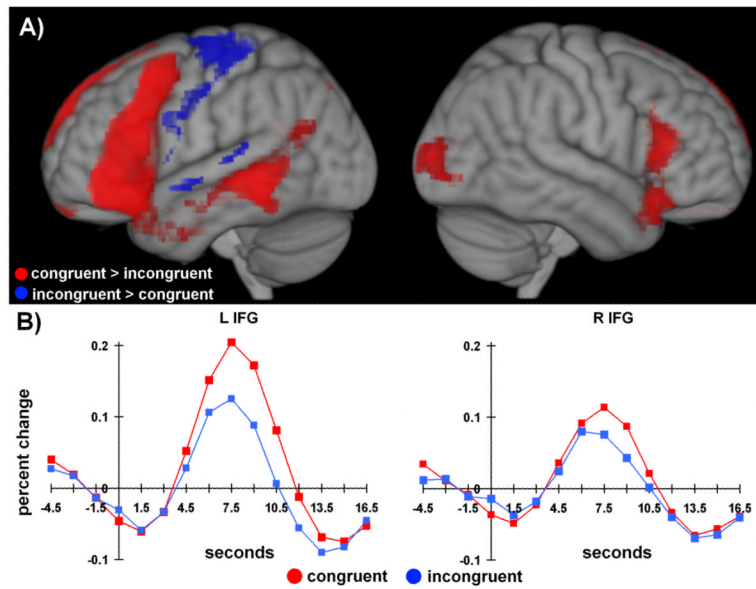
Figure 2.
Activation to congruent and incongruent sentences. A. Regions in which congruent sentences elicited significantly greater activation than incongruent sentences (red), and regions in which incongruent sentences elicited significantly greater activation than congruent sentences (blue). All displayed activations are thresholded, p<.01, GRF cluster corrected. B. Hemodynamic responses to congruent sentences (red) and incongruent sentences (blue) in left inferior frontal gyrus (left) and right inferior frontal gyrus (right).
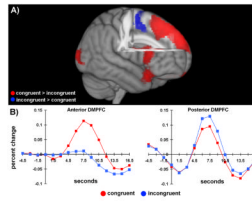
Figure 3.
Activation in left dorsal medial prefrontal cortex. A. Regions of dorsal medial prefrontal cortex (DMPFC) where congruent sentences elicited significantly greater activation than incongruent sentences (red) and regions in which incongruent sentences elicited significantly greater activation than congruent sentences (blue). All displayed activations are thresholded, p<.01, GRF cluster corrected. An anterior to posterior gradient in sensitivity to discourse congruence was observed in DMPFC. Regions that were more responsive to congruent sentences can also be seen in right inferior frontal gyrus and right temporal pole. B. Hemodynamic responses to congruent sentences (red) and incongruent sentences (blue) in anterior DMPFC (left) and posterior DMPFC (right).

Table 1

Examples of Experimental Stimuli

Condition	Example Sentences
Congruent Literal	The curious kids searched for wildlife. The pond creature was a water bug.
Incongruent Literal	He is biting into a piece of fruit. Frank's car is a dune buggy.
Congruent Metaphor	They casually traveled across the Mediterranean. A sailboat is a floating leaf.
Incongruent Metaphor	The name of the band is not creative. The policeman's hands are a traffic light.

Table 2

Regions of activation for effects of figurativeness and discourse congruence

Region	Hemisphere	BA	Max Z	X	Y	Z	# Voxels
Metaphor > Literal							
Inferior Frontal Gyrus	Left	47	3.69	−34	16	−18	1108
Dorsal Medial PFC	Left	9	3.95	−8	56	32	1070
Anterior MTG	Left	21, 38	4.39	−58	−18	−14	2342
Posterior MTG	Left	21, 22	3.79	−58	−42	4	1353
Cingulate Gyrus	Left	24	3.17	−8	−12	42	88
Occipital Gyri	Left, Right	17, 18, 19	3.70	30	−98	12	4474
Congruent > Incongruent							
Inferior Frontal Gyrus	Left	8, 9, 45, 47,	5.40	−46	34	−8	9163
	Right	45, 47	3.98	52	26	10	1744
Middle Frontal Gyrus	Right	6	3.09	36	2	46	45
Dorsal Medial PFC	Left	6, 8, 9, 32	5.19	−6	34	46	3627
Orbital Frontal Cortex	Left, Right	11	3.71	6	52	−24	340
Temporal Pole	Right	38	3.98	44	22	−22	344
Middle Temporal Gyrus	Left	20, 21, 37	5.75	−60	−40	−8	3286
Angular Gyrus	Left	19, 22, 39, 40	4.35	−40	−52	28	1136
Occipital Gyri	Left, Right 17,	18, 19	3.61	30	−92	8	4040
Brain Stem	Left, Right		4.77	0	−28	−10	10131
Incongruent > Congruent							
Superior Temporal Gyrus	Left	21, 22	4.14	−60	−4	−4	88
	Left	13, 42	3.92	−46	−22	24	510
Postcentral Gyrus	Left	3, 4, 6	4.18	−38	−26	68	3424

PFC - Prefrontal Cortex MTG - Middle Temporal Gyrus

*
There were no regions in which literal sentences elicited greater activation than metaphoric sentences.