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**Pathways to lexical ambiguity: fMRI evidence for bilateral fronto-parietal involvement in  
language processing**

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## **Abstract**

Numerous functional neuroimaging studies reported increased activity in the pars opercularis and the pars triangularis (Brodmann's areas 44 and 45) of the left hemisphere during the performance of linguistic tasks. The role of these areas in the right hemisphere in language processing is not understood and, although there is evidence from lesion studies that the right hemisphere is involved in the appreciation of semantic relations, no specific anatomical substrate has yet been identified. This event-related functional magnetic resonance imaging study compared brain activity during the performance of language processing trials in which either dominant or subordinate meaning activation of ambiguous words was required. The results show that the ventral part of the pars opercularis both in the left and the right hemisphere is centrally involved in language processing. In addition, they highlight the bilateral co-activation of this region with the supramarginal gyrus of the inferior parietal lobule during the processing of this type of linguistic material. This study, thus, provides the first evidence of co-activation of Broca's region and the inferior parietal lobule, succeeding in further specifying the relative contribution of these cortical areas to language processing.

**Keywords:** event-related fMRI; lexical ambiguity; homonymy; polysemy; metaphor; Broca's area 44; supramarginal gyrus; inferior parietal lobule

## **Highlights**

Event-related fMRI investigated the contribution of the right hemisphere in linguistic tasks.

Bilateral involvement of the pars opercularis (Brodmann's area 44).

Bilateral involvement of the supramarginal gyrus of the inferior parietal lobule.

Strong connections between areas 44 and 40 through SLF III.

Delineate anterior-posterior language processing system bilaterally.

Increased right hemisphere involvement during metaphorical interpretations.

## 1. INTRODUCTION

Lexical ambiguity, where a single word has more than one meaning, is common in natural language. With respect to lexical semantics in general, an increasing amount of evidence from lesion and divided visual field studies with young healthy individuals suggests that both the left hemisphere (LH) and the right hemisphere (RH) contribute to the comprehension of semantic relations. Although the left hemisphere is dominant for language processes, it is now acknowledged that the right hemisphere also contributes to certain aspects of linguistic processing (Tompkins, Klepousniotou & Scott, 2011). A review of the literature on language abilities after RH damage reveals abnormalities in the interpretation of lexical items (as well as larger linguistic units) that have multiple meanings (i.e., lexically ambiguous items), and an inability to revise an initial interpretation (Chiarello, 1991). However, the extent of the contribution of the right hemisphere to the understanding of ambiguous words is still under investigation.

The present study aims to investigate the processing of ambiguous words that have either two literal interpretations (as in homonymy: e.g., bank) or one literal and one metaphorical interpretation (as in metaphor: e.g., star) in order to examine the effects of lexical ambiguity resolution, and to identify the neural substrates that underlie these processes.

Lesion studies on lexical ambiguity have focused on whether and how focal brain damage disrupts lexical-semantic processing. Early off-line (i.e., pen and paper) studies (e.g., Brownell, 1988; Brownell, Potter, Michelow, & Gardner, 1984; Brownell, Simpson, Bihrlé, Potter, & Gardner, 1990; Schmitzer et al., 1997; Winner & Gardner, 1977) showed that patients with focal RH damage have problems with lexical ambiguity in general, and metaphor in particular. These researchers compared the performance of patients with right hemisphere damage (RHD), left hemisphere damage (LHD) and normal control individuals by using either sentence/context-picture matching

(e.g., Schmitzer et al., 1997; Winner & Gardner, 1977) or word triad relatedness judgment (e.g., Brownell, 1988; Brownell, Potter, Michelow, & Gardner, 1984; Brownell, Simpson, Bihrlé, Potter, & Gardner, 1990) paradigms. Overall, it was found that when individuals with LHD were presented with ambiguous adjectives (e.g., “warm” → to refer to “hot” or “loving”), they chose metaphoric interpretations (e.g., “loving”) more frequently and they were less likely to select literal foils (e.g., “blanket”) than were individuals with RHD. In contrast, individuals with RHD were as likely to choose metaphoric interpretations as literal ones. In addition, in comparisons of comprehension performance across neutral, connotation-biased and denotation-biased contexts, RHD patients exhibited decreased accuracy levels in the neutral and connotation-biased contexts. Thus, it was suggested that secondary or subordinate (i.e., non-literal, connotative) meanings are much less salient when the right hemisphere is dysfunctional (Brownell et al., 1990; Schmitzer et al., 1997). Subsequent online studies further revealed that RHD patients are impaired in their ability to effectively use context (e.g., Beeman, 1993; Grindrod & Baum, 2003; Klepousniotou & Baum, 2005; Schmitzer et al., 1997; Tompkins et al., 2000; but cf. Leonard & Baum, 1998; Leonard, Baum & Pell, 2001), and coupled with the lack of any time-course effects on their performance, RHD patients seem to be unable to effectively select only the contextually appropriate meaning and eventually suppress inappropriate ones.

Based on these findings, two major theories have been proposed to account for the deficits observed after RH damage, namely the “suppression deficit” and the “coarse semantic coding” hypotheses. According to the “suppression deficit” hypothesis, RHD patients’ deviant performance with ambiguous words could be attributed to problems with suppressing interpretations that are initially activated, but eventually become irrelevant or incompatible with the context (Tompkins & Lehman, 1998). The suppression mechanism is compromised in individuals with RHD, and

suppression function after RHD is assumed to correlate with comprehension (Tompkins & Lehman, 1998).

The other major hypothesis concerning RH processing abilities, known as the “coarse semantic coding” hypothesis, has been proposed by Beeman (1998). According to this hypothesis, during word processing, the LH is most selective, strongly activating small semantic fields, while the RH diffusely activates large semantic fields (Beeman, 1998). In particular, the RH is assumed to coarsely code semantic input resulting in weak activation of large semantic fields, thus allowing for vague interpretations only. Although such semantic processing would make the RH less effective for selecting the appropriate meaning of single words, it would be more sensitive to distant semantic overlap and the maintenance of multiple word meanings. In contrast, the LH is assumed to finely code semantic input, so that a word strongly activates a limited subset of semantic features that are related to its primary meaning. As a result, fine semantic coding would make the LH very efficient at selecting the frequent or contextually appropriate meaning for further processing. In general, it has been shown that following biased priming sentences at longer intervals, only the contextually appropriate meaning is facilitated in the LH, whereas all related targets (i.e., both contextually appropriate and inappropriate) are facilitated in the RH. In other words, although irrelevant meanings are suppressed in the LH, no suppression or limited suppression effects are observed in the RH (Faust & Gernsbacher, 1996). These results indicate that the two hemispheres respond differently to lexical ambiguity. The RH maintains activation of all meanings for a longer time, whereas the LH focuses on the most dominant or contextually appropriate meaning of ambiguous words, dampening irrelevant interpretations more quickly.

Although lesion studies strongly suggest the involvement of the RH in the appreciation of alternative interpretations, the findings of neuroimaging studies have failed to provide



unequivocal evidence. Several neuroimaging experiments have investigated the neural systems underlying the processing of ambiguous words (Chan, Liu, Yip, Fox, Gao, & Tan, 2004; Copland, de Zubicaray, McMahon, & Eastburn, 2007; Mason & Just, 2007; Rodd, Davis, & Johnsrude, 2005; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007), and although some studies have shown increased activation in the RH during the processing of lexical ambiguity (e.g., Bilenko et al, 2008; Chan et al, 2004; Mason & Just, 2007; Rodd et al., 2005; Zempleni et al., 2007), others have not (e.g., Bedny et al., 2008; Chen et al., 2008; Grindrod et al, 2008; Hoenig & Scheef, 2009; Ihara et al., 2007; Rapp et al., 2004; Rapp et al., 2007; Lee & Dapretto, 2006), leading to unanswered questions regarding the role of the RH in the processing of lexical ambiguity.

Focusing on the neuroimaging studies that have shown some RH involvement during the processing of lexical ambiguity, it becomes clear that the areas reported can be quite diverse raising further questions about their specific contributions. For example, Stringaris et al. (2007) using visual sentence presentation with sensicality judgements found middle temporal gyrus activations for the contrast between metaphorical versus literal sentences. Chan et al. (2004), on the other hand, using a covert word generation task with visual single word presentation reported increased activation in the RH in the mid-superior frontal gyrus and the inferior parietal lobe for the contrast between ambiguous versus precise words. Finally, Zempleni et al. (2007) using auditory presentation of sentences congruent either with the dominant or subordinate interpretation of ambiguous words found increased RH activations in the inferior middle temporal gyrus. Given that no studies so far have made concrete predictions about specific RH areas that should show differential activations during the processing of lexical ambiguity, the possibility exists that any differences observed in RH activations so far could be due to

differences in the method of presentation (visual vs. auditory) or the experimental task demands rather than the processing of lexical ambiguity per se.

Nevertheless, one area that has been highlighted more consistently in relation to processing alternative interpretations is the inferior frontal gyrus (IFG). Several neuroimaging studies (Kan & Thompson-Schill, 2004; Petrides et al., 1995; Thompson-Schill et al., 2002; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) indicate that the left inferior frontal gyrus (LIFG) plays an important role in the selection among competing alternatives in semantic memory. In particular, Thompson-Schill and colleagues (Thompson-Schill et al., 1997) investigated the role of the left IFG in selecting among semantically competing alternatives in unambiguous words across three different tasks, namely generation, classification, and comparison. They found differentially increased left IFG activation for the comparison of high and low selection conditions in all three tasks, indicating that the left IFG is involved in selection among competing alternatives. These findings, thus, suggest that when processing lexical ambiguity, there should be increased activation at least in the LIFG as participants have to consider alternative meanings and eventually select one of them. What is less clear is which cytoarchitectonic area within the IFG (which consists of areas 44, 45 and 47, as well as the ventral opercular parts of this region) is primarily responsible for selection and whether the homologue of LIFG in the RH also plays a role when processing lexical items with multiple interpretations.

More recently, Bilenko, Grindrod, Myers & Bumstein (2008) used ambiguous words with two or more literal unrelated meanings (i.e., homonymous words) and unambiguous words in an auditory lexical decision task to investigate the involvement of the LIFG when using a more implicit task of semantic processing. When comparing ambiguous with unambiguous word pairs,

they found differentially increased activation not only in the LIFG (including both areas 44 and 45) but also in the right inferior frontal gyrus (again both areas 44 and 45). These results indicate that increased processing resources recruit areas in the inferior frontal gyrus bilaterally under conditions of competition, even when the experimental task does not impose overt selection (see also Mason and Just, 2007 and Rodd et al., 2005 for similar findings in the presence of sentential context).

However, although it is now clear that the inferior frontal gyrus in the left hemisphere plays an important role in linguistic processing and selection among competing alternatives in language processing, studies typically do not distinguish between the different language areas that constitute the IFG, in particular the pars opercularis and the pars triangularis (i.e., Brodmann's areas 44 and 45, in addition to the pars orbitalis area 47) and their specific contributions; rather they seem to refer to the IFG as a single, uniform structure. Similarly, the contribution of the homologue of IFG and its constituent areas in the right hemisphere is less well understood. This lack of specificity of the particular contributions of the pars opercularis and pars triangularis in language processing impacts on our understanding of the contributions of more posterior brain areas that may be co-activated when processing linguistic material with multiple interpretations. Tractography studies in humans as well as anatomical tracer studies in non-human primates can provide important information about the connections of the pars opercularis and pars triangularis and thus guide predictions about areas that would potentially work together in processing linguistic material and in activating and selecting among competing alternatives.

In particular, Frey et al. (2008), using diffusion fiber tractography demonstrated that area 44 (pars opercularis) has distinct connections with rostral inferior parietal lobule, namely the

supramarginal gyrus, through the third branch of the superior longitudinal fasciculus (SLF III), while area 45 (pars triangularis) connects with the superior temporal gyrus via the extreme capsule fiber system (see also Dick & Tremblay, 2012; Kaplan et al., 2010). These results which replicated previous findings from experimental anatomical tracer studies in the macaque monkey (Petrides & Pandya, 1984, 2002, 2009) highlight the differences in connectivity between areas 44 and 45 both of which previously were thought to be connected with the posterior temporal region via the arcuate fasciculus. This differentiation is crucial as it allows us to make predictions about areas that may be co-modulated during the processing of linguistic material. In particular, given the evidence of the involvement of the IFG in lexical ambiguity processing, we can now be more specific in the prediction of the areas that will show differential activation during processing. In particular, we are predicting that if activation in the IFG is localised mainly in the pars opercularis, then we should expect co-modulations in activation in the rostral part of the inferior parietal lobule (supramarginal gyrus). Studies have shown that the inferior parietal lobule is responsible for processing more than spatial information, including information involved in both motor and nonmotor tasks (Rauschecker and Tian, 2000) including speech (Wise et al., 2001). On the other hand, if activations in the IFG are mainly localised in the pars triangularis (Brodmann's area 45), then differential co-activations may be expected in posterior temporal areas. The present study, thus, investigated the processing of lexical ambiguity as a means to dissociate the particular contributions of Brodmann's areas 44 and 45, and their connections with more posterior cortical areas, bilaterally in meaning computation and selection among competing alternatives.

## **2. EXPERIMENT**

On the basis of the above, we tested, in a functional magnetic resonance imaging (fMRI) study, the hypothesis that if activation in the IFG is localised mainly in the pars opercularis (Brodmann's area 44), then we should expect co-modulations in activation in the inferior parietal lobule (Brodmann's area 40), while if activation in the IFG is mainly localised in the pars triangularis (Brodmann's area 45), then differential co-activations may be expected in the lateral temporal region. In addition, activations are expected in both the left and right hemispheres, with right hemisphere loci being especially involved when processing becomes more taxing (i.e., in metaphor and subordinate interpretations). To test this hypothesis, we designed an event-related fMRI study to compare brain activity changes due to the processing of ambiguous words with literal or metaphorical alternative interpretations.

### **2.1 EXPERIMENTAL METHODS**

**2.1.1 Participants.** Fifteen right-handed normal human subjects (7 females and 8 males, mean age: 26.2 years, StDev = 3.5 years; mean education: 19 years, StDev = 2.04 years) participated in the present fMRI study after informed, written consent according to the guidelines established by the Ethics Committee of the Montreal Neurological Hospital and Institute.

**2.1.2. Materials.** Prime-target pairs representing two distinct types of lexical ambiguity were constructed in the following way. Thirty of each of two types of ambiguous words were selected as primes: 1) unbalanced homonymous words (i.e., one meaning is more frequent/dominant than the other/subordinate meaning – for example, “bank”) and 2) metaphorical words (i.e., the

first/dominant meaning is literal while the other/subordinate meaning is figurative – for example, “mouth”).

Unbalanced homonymous words were chosen from standardized lists of ambiguous words (e.g., Gilhooly & Logie, 1980; Nelson, McEvoy, Walling, & Wheeler, 1980; Twilley, Dixon, Taylor, & Clark, 1994; Yates, 1978). The frequency of occurrence of the dominant meaning was never less than 63%, and the frequency of occurrence of the subordinate meaning was never greater than 32%. Overall, the dominant meaning had a mean frequency of occurrence of 80% (range: 63% - 95%) and the subordinate meaning had a mean frequency of 14% (range: 1% - 32%). The average frequency of occurrence of the unbalanced homonymous words was 34 (range: 1-120) (Francis & Kucera, 1982).

As there are no standardized lists of metaphorical words, these were chosen to exhibit specific relations between their two senses as documented in the theoretical linguistics literature (e.g., Nunberg, 1979; Pustejovsky, 1995). In order to investigate the effects of a broader range of words with metaphorical meaning extensions, as well as to control for repetition effects and semantic facilitation effects from one experimental stimulus to another, multiple types of and metaphorical words were included. In particular, metaphorical words exhibited three types of metaphorical relations, namely 10 body part/object words (e.g., “mouth”), 10 animal/human characteristic words (e.g., “fox”), and 10 object/human characteristic words (e.g., “star”). The average frequency of occurrence of the metaphorical words was 33 (range: 1-103) (Francis & Kucera, 1982).

The classification of all stimuli as homonymous or metaphorical was also verified by consulting standard dictionaries (see also Rodd, Gaskell, & Marslen-Wilson, 2002). All such dictionaries respect the distinction between homonymy and polysemy by listing the different

meanings of homonymous words as separate entries, whereas the different senses of metaphorical words are listed within a single entry. In addition, all standard dictionaries respect sense dominance by listing the central or dominant sense of metaphorical words first and then providing the extended or subordinate senses. Finally, all ambiguous words were matched for frequency of occurrence [ $F(1, 58) = 0.01, p > 1$ ] (Francis & Kucera, 1982), syllable and letter length [ $F(1, 58) = 0.4, p > 1$ ] with mean letter length of 4.4 letters (range: 3-8), and grammatical category (i.e., all words and meanings were predominantly nouns).

Three types of targets were used: 1) words related to the dominant meaning of the ambiguous word primes; 2) words related to the subordinate meaning of the ambiguous word primes; and 3) control words unrelated to the ambiguous word primes. Word associates were obtained from standardized lists of word association norms (e.g., Gilhooly & Logie, 1980; Nelson, McEvoy, & Schreiber, 1998; Nelson, McEvoy, Walling, & Wheeler, 1980; Twilley, Dixon, Taylor, & Clark, 1994; Yates, 1978). Target words were matched for frequency of occurrence [ $F(5, 174) = 0.02, p > 1$ ] (Francis & Kucera, 1982), syllable and letter length [ $F(5, 174) = 0.9, p > 1$ ]. In particular, word associates to the dominant meaning had a mean frequency of 30.5 (range: 1-115), word associates to the subordinate meaning had a mean frequency of 30 (range: 1-141), and unrelated control words had a mean frequency of 29.5 (range: 1-112).

In the experiment, each word prime was followed either by a target word related to its dominant meaning, a target word related to its subordinate meaning, or an unrelated control target word. Each testing session consisted of six runs. Each run contained 10 ambiguous word primes (5 homonymous and 5 metaphorical words) followed by dominant meaning related word targets, 10 ambiguous word primes followed by subordinate meaning related word targets, 10 ambiguous word primes followed by unrelated control word targets and another 10 ambiguous word primes followed

by unrelated word targets so that there was balance between related and unrelated responses (for a total of 40 trials per run and a total of 240 trials per scanning session). Thus, within each session the primes were repeated three times but the targets were only presented once. However, targets were never repeated within the same run. In addition, there were two baseline control conditions. In the first baseline condition, crosses “+” were presented instead of words in the centre of the projection screen. In the other baseline condition, a series of non-letter symbols was presented instead of the words. This baseline condition was designed to ensure that observed effects to the word stimuli were due to linguistic analysis and not due to pattern effects irrespective of linguistic value. The order of presentation of the runs was counterbalanced and trials within a run were presented in fixed random order.

**2.1.3. Testing Procedure during Scanning.** All participants were tested in a single session that lasted approximately one and a half hours. Each trial began with the visual presentation of a fixation point (+) that was presented on the screen for 400 ms indicating to the participants that a stimulus was about to be presented. After 100 ms, the prime was presented for 200 ms and 50 ms later the target was presented for 500 ms. Following a variable delay of 2.5-9 sec, a question mark (?) appeared on the screen for 1250 ms indicating to the participants that they have to make a semantic judgment about the prime and target (i.e., whether the two words are related in meaning or not). Participants were instructed to respond as accurately as possible using the mouse keys by pressing the YES key if they thought the words were related, and the NO key if they thought they were unrelated. Following the participant’s response, there was another variable delay (2.5-9 sec) before the next trial was presented. Reaction times (in ms) and accuracy rate were recorded by the



computer. Reaction times were recorded from the onset of the question mark (?) cue until the participant responded.

## **2.2. FMRI Scanning and Data Analysis**

The data were acquired on a 1.5 T Siemens Sonata MR scanner (Siemens AG, Erlangen, Germany) at the Montreal Neurological Institute. Thirty-eight axial slices (whole brain coverage) oriented parallel to the AC-PC line (thickness=3.4mm, no gap, FOV=256×256mm<sup>2</sup>, matrix=64×64) were acquired in 2.98s using a multislice EPI sequence (TE=45ms, TR=3.5s). The slices had a spatial resolution of 3.4×3.4×3.4mm. Six experimental runs (12.5 min each) resulted in the acquisition of 220 T2\*-weighted BOLD images acquired in descending order.

High-resolution T1-weighted volumes were acquired for anatomical localization (matrix 256×256mm, 160 slices, 1×1×1mm, no gap, TE=9.2ms, TR=22ms). Subject's head was immobilized by means of a vacuum-bag filled with polystyrene balls and a forehead-restraining device (HybexInnovations, St-Leonard, Qc, CAN). Visual stimuli were presented through an LCD projector with a mirror system and the responses of the subjects were recorded with an MR compatible optical computer mouse.

The onset of the first trial in each run was synchronized with the scanner acquisition via a trigger signal generated by the scanner. Behavioural and imaging data were acquired in all trials. Stimulus presentation and the recording of motor responses were computer controlled and were programmed with E-prime 1.1 (Psychology Software Tools Inc.).

The functional images were realigned across runs by performing a rigid-body transform with the fourth frame of the fourth functional run as a target image (AFNI, Cox and Jesmanowicz, 1999). The six movement parameters (x, y, z and roll, pitch and yaw) were

inspected for each volume. Volumes in which the movement correction algorithm was unable to compensate for the motion were discarded from the analysis. Data were low-pass filtered using a 6mm FWHM Gaussian kernel. Statistical analysis of fMRI data was performed using a linear model with correlated errors (FMRISTAT, Worsley et al., 2002). The fMRI data were first converted to percentage of whole volume. The design matrix of the linear model was convolved with a hemodynamic response function modeled as a difference of two gamma functions timed to coincide with the acquisition of each slice. Temporal drift was removed by adding a cubic spline in the frametimes to the design matrix (one covariate per 2 min of scan time), and spatial drift was then removed by adding a covariate in the whole volume average. The correlation structure was modeled as an autoregressive process of degree 1. At each voxel, the autocorrelation parameter was estimated from the least squares residuals using the Yule-Walker equations, after a bias correction for correlations induced by the linear model. The autocorrelation parameter was regularized by spatial smoothing, then used to ‘whiten’ the data and the design matrix. The linear model was then re-estimated using least squares on the whitened data to produce estimates of effects and their standard errors. In order to compute group data, subject data were transformed into stereotaxic space (Collins et al., 1994), and combined using a mixed effects linear model for the effects (as data) with fixed effects standard deviations taken from the previous analysis. This was fitted using restricted maximum likelihood (REML) implemented by the Expectation/Maximization (EM) algorithm. A random effects analysis was performed by first estimating the ratio of the random effects variance to the fixed effects variance, then regularizing this ratio by spatial smoothing with a Gaussian filter. The variance of the effect was then estimated as the smoothed ratio multiplied by the fixed effect variance. The amount of smoothing

was chosen to achieve 100 effective degrees of freedom. More information on the fMRI analysis is available at <http://www.math.mcgill.ca/keith/fmristat>.

The resulting T statistic images were thresholded using the minimum given by a Bonferroni correction and random field theory, taking into account the non-isotropic spatial correlation of the errors. For a single voxel in a directed search within predicted brain regions, the threshold for significance ( $p < 0.05$ ) was set at  $t = 4.06$ . For a single voxel in an exploratory search involving all peaks within an estimated grey matter of  $600\text{cm}^3$  covered by the slices, the threshold for reporting a peak as significant ( $p < 0.05$ ) was  $t = 4.56$ . Finally, a predicted cluster of voxels with a volume extent  $> 110\text{ mm}^3$  with a  $t$ -value  $> 3$  was significant ( $p < 0.05$ ) corrected for multiple comparisons using the method of Friston et al. (1995; 1997).

### **3. RESULTS**

In order to assess which cortical areas were specifically involved in the processing of lexically ambiguous material, we compared the blood oxygenation level dependent (BOLD) signal obtained during the presentation of the ambiguous word pairs (Homonymy-Dominant, HD; Homonymy-Subordinate, HS; Metaphor-Dominant, MD; Metaphor-Subordinate, MS) with the corresponding signal during the presentation of the baseline control condition (Baseline Cross, CR). These comparisons consistently demonstrated four peaks of increased activity during the processing of the lexically ambiguous stimuli, bilaterally in the inferior frontal gyrus (IFG) area 44 and the inferior parietal lobule (IPL) area 40. The coordinates of the activity peaks are provided in the Montreal Neurological Institute (MNI) standard stereotaxic space.

In particular, for the comparison HD minus CR, there were bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -33, 15, 14,  $t$ -value=3.29] and in the

right IFG area 44 [MNI coordinates (x, y, z) 55, 8, 9, t-value=3.25]. Furthermore, there were peaks only in the left IPL area 40 [MNI coordinates (x, y, z) -62, -43, 36, t-value=5.35] (Fig. 1a).

For the comparison HS minus CR, there were bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -34, 16, 8, t-value=3.81] and the right IFG area 44 [MNI coordinates (x, y, z) 58, 10, 14, t-value=3.34]. Furthermore, there were bilateral peaks in the left IPL area 40 [MNI coordinates (x, y, z) -60, -44, 36, t-value=4.38] as well as in the right IPL area 40 [MNI coordinates (x, y, z) 48, -46, 42, t-value=4.13] (Fig. 1b).

For the comparison MD minus CR, there were also bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -34, 16, 8, t-value=3.28] and in the right IFG area 44 [MNI coordinates (x, y, z) 43, 7, 12, t-value=4.01]. Furthermore, there were bilateral peaks in the left IPL area 40 [MNI coordinates (x, y, z) -60, -44, 36, t-value=3.69] as well as in the right IPL area 40 [MNI coordinates (x, y, z) 52, -38, 44, t-value=3.25] (Fig. 2a).

For the comparison MS minus CR, there were bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -31, 14, 8, t-value=3.09] and in the right IFG area 44 [MNI coordinates (x, y, z) 38, 18, 10, t-value=3.22]. Furthermore, there were bilateral peaks in the left IPL area 40 [MNI coordinates (x, y, z) -62, -44, 34, t-value=4.07] as well as in the right IPL area 40 [MNI coordinates (x, y, z) 52, -36, 42, t-value=4.68] (Fig. 2b).

We also compared the blood oxygenation level dependent (BOLD) signal obtained during the presentation of the ambiguous word pairs combined across ambiguity type (i.e., Homonymy&Metaphor-Dominant, HMD; Homonymy&Metaphor-Subordinate, HMS) with the corresponding signal during the presentation of the baseline condition (Baseline Cross, CR). As expected, for the comparison HMD minus CR, there were bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -58, 8, 16, t-value=3.26] and the right IFG area 44

[MNI coordinates (x, y, z) 58, 8, 10, t-value=3.58]. Furthermore, there were bilateral peaks in the left IPL area 40 [MNI coordinates (x, y, z) -60, -44, 36, t-value=5.15] as well as in the right IPL area 40 [MNI coordinates (x, y, z) 47, -44, 42, t-value=3.55] (Fig. 3a).

For the comparison HMS minus CR, there were bilateral peaks of increased activity in the left IFG area 44 [MNI coordinates (x, y, z) -34, 16, 8, t-value=3.93] and in the right IFG area 44 [MNI coordinates (x, y, z) 58, 10, 24, t-value=3.49]. Furthermore, there were bilateral peaks in the left IPL area 40 [MNI coordinates (x, y, z) -60, -42, 36, t-value=4.66] as well as in the right IPL area 40 [MNI coordinates (x, y, z) 52, -36, 44, t-value=4.62] (Fig. 3b).

Finally, we compared the blood oxygenation level dependent (BOLD) signal obtained during the presentation of the subordinate ambiguous word pairs with the corresponding signal during the presentation of the dominant ambiguous word pairs (Fig. 4). These direct contrasts revealed that, for both comparisons, there were unilateral peaks of increased activity in the right IPL area 40 [HS minus HD: MNI coordinates (x, y, z) 53, -47, 45, t-value=3.33; MS minus MD: MNI coordinates (x, y, z) 50, -30, 46, t-value=3.31], indicating a specialised role for the right IPL in the computation of subordinate/alternative meanings.

Overall, the comparisons employed in the present study yielded very similar patterns of cerebral activity. In all comparisons against the baseline, increased activity was found in the frontal operculum in IFG area 44 bilaterally as well as in the IPL area 40 bilaterally (except for the contrast HD minus CR for which the IPL activation was observed only in the left hemisphere) consistent with studies that have shown strong connections between these two areas (Frey et al., 2005; Frey et al., 2008; Kaplan et al., 2010). Furthermore, direct contrasts between the subordinate and dominant meanings revealed increased activity only in the right IPL (area 40)

implicating that area especially in the computation of alternative interpretations (see Table 1 for the complete list of peaks of increased activity).

#### **4. DISCUSSION**

The present findings demonstrate that activity increases related to the interpretation of lexical items with multiple meanings occur bilaterally within a specific part of the human IFG: the ventral part of the pars opercularis. Furthermore, there was co-activation with the posterior supramarginal region of the IPL that has been shown to be anatomically connected and functionally related to this IFG region.

The present study investigated the activation patterns during the processing of linguistic material with alternative interpretations by examining words with two literal meanings (i.e., homonyms) and words with one literal and one metaphorical meaning (i.e., metaphors). The results demonstrated that the ventral opercular part of the left IFG area 44 and the left IPL area 40 as well as the ventral opercular part of the right IFG area 44 are involved in the processing of both dominant and subordinate meanings. In addition, the right supramarginal region of the IPL shows increased activity only when processing subordinate meanings of words with two literal interpretations (i.e., homonyms) or when processing words that have metaphorical interpretations (i.e., metaphors). These findings are consistent with the hypothesis that the right hemisphere homologues to the ‘language areas’ are primarily involved when linguistic processing is more taxing and alternative interpretations (literal or figurative) need to be computed, and they are compatible with the hypothesized stronger involvement of the right hemisphere in the representation and processing of the subordinate meanings in metaphor (Beeman, 1998). Furthermore, the present results corroborate the neurolinguistic findings from lesion studies

(Klepousniotou & Baum, 2005; Tompkins, 1990; see also Tompkins, Klepousniotou & Scott, 2011 for a recent review on language deficits following right hemisphere damage) as well as the findings of a recent EEG study (Klepousniotou, Pike, Steinhauer & Gracco, 2012) regarding the involvement of the left and right cerebral hemispheres in the appreciation and resolution of lexical ambiguity.

Crucially, the present findings succeed in delineating the cortical sites that are differentially involved in the processing of lexical ambiguity, providing specific information about the particular role they play in processing and the interaction of the anterior language areas with more posterior language areas. The role of the IFG, especially in the left hemisphere, in verbal processing has been demonstrated in numerous previous functional imaging studies (Kan & Thompson-Schill, 2004; Petrides et al., 1995; Thompson-Schill et al., 2002; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997); overall these studies implicate the LIFG in the selection among competing alternatives in semantic memory. More recently, Bilenko et al. (2008), showed that increased processing resources recruit areas in the inferior frontal gyrus bilaterally under conditions of competition, even when the experimental task does not impose overt selection (see also Mason and Just, 2007 and Rodd et al., 2005). The present study not only provides further support to these findings, but succeeds in further delineating the specific area within the IFG that is involved in such processing. Furthermore, it was demonstrated that activity in the opercular region of the IFG was stronger in the right hemisphere for the metaphorical subordinate condition, consistent with lesion studies that indicate a special role for the RH in metaphorical language processing (Klepousniotou and Baum, 2005; Tompkins, 2000). We posit that this region of the IFG bilaterally is involved when alternative interpretations are available even in the absence of overt competition. It is the

activation and manipulation of such information in semantic memory that gives rise to bilateral differential activations in a part of ‘Broca’s area’ and its homologue in the right hemisphere. In accordance with Binder et al. (2009), Bokde (2001) and Price (2010), we suggest that the pars opercularis is involved in top-down predictions of a plausible sequence of events rather than selection per se, which we suggest is localised in the ventral IFG area 47.

The present study aimed to clarify further the contributions of more posterior brain areas that may be co-activated when processing linguistic material with multiple interpretations. Based on evidence from diffusion tractography studies (Frey et al., 2008) and resting state connectivity studies (Kelly et al., 2010) that suggested that the region of the pars opercularis has distinct connections with the supramarginal region of the IPL (area 40; area PF/PFG) through the third branch of the superior longitudinal fasciculus, while area 45 (pars triangularis) connects with the superior temporal gyrus and sulcus via the extreme capsule fiber system (see also Dick & Tremblay, 2012; Kaplan et al., 2010), it was hypothesised that if the IFG activations were localised in area 44, then co-modulations should be observed in IPL area 40. Indeed, the results of the present study revealed that the IPL area 40 bilaterally was involved in the computation of meaning of linguistic items with multiple interpretations. In particular, the strong cortico-cortical connections described in tracing studies (e.g., Frey et al., 2008; Petrides & Pandya, 2009) between area 44 and the inferior parietal lobule (area 40) were highlighted by showing that bilateral co-activations in IPL area 40 occur for all contrasts except for the contrast HD minus CR. This finding is not surprising as the dominant meaning of homonyms is very literal and dominant, thus exerting minimal demands on the RH network. In contrast, activations were stronger in the right hemisphere for the metaphorical subordinate condition as this is the most taxing condition. Finally, when looking at the direct contrasts between subordinate and dominant



meanings, the locus of activity was found in the right IPL area 40 pointing again to the involvement of that area when processing demands increase.

Several functional imaging studies have reported increased activity in the IPL area 40 in lexico-semantic processing (Demonet et al, 1992; Kawabata Duncan et al, 2013; Price, 2010). For example, Demonet et al. (1992) in an early study using PET compared activations during a phonological and a lexico-semantic task and found differential activations in area 40 in the left hemisphere only during the lexico-semantic task. They argued that in the lexico-semantic task, participants needed to access lexical and semantic information that is stored in the long-term memory and also possibly mental images to make semantic judgments, implicating, thus, area 40 in such processes. Similarly, Price (2010) in a review of 100 language fMRI studies points towards a role of parietal areas in semantic retrieval especially when comprehension is more taxing at the perceptual or semantic level. Finally, more recently, Kawabata Duncan et al. (2013) found increased connectivity between Broca's area and the supramarginal gyrus (area 40) in the left hemisphere when processing syllabographic Hiragana scripts, pointing again to the connections between these two language areas.

Increased activity in the region of the IPL has been frequently observed in functional imaging studies during mental arithmetic (i.e., mental manipulation of information). For example, Cochon et al. (1999) found that quantity processing involved both the left and right IPL (with activations being centered on the intraparietal sulcus but also covering the inferior parietal lobules). We suggest that, although the cognitive domain of mental arithmetic is totally different from the computation of multiple meanings that was studied here, these two processes may both be conceived, fundamentally, as the manipulation (i.e. the re-arrangement) of stimulus information and this may be a basic contribution of the IPL. Thus, we suggest that the role of IPL

in language processing is the computation and manipulation of meaning. In typical language processing, we would expect the left IPL to be involved in the mental manipulation and computation of meaning. However, in cases of increased demands, such as the manipulation of multiple alternative interpretations, the right IPL seems to be involved in order to ensure successful meaning computation.

## **5. CONCLUSION**

The present study succeeds in delineating the specific contribution of a particular part of Broca's region in the processing of lexical ambiguity and mapping out the cortico-cortical connections between the ventral operculum area 44 (i.e., anterior language area) with more posterior language areas localised in the supramarginal gyrus of the inferior parietal lobule area 40. Furthermore, it is the first study that consistently demonstrates predicted bilateral involvement of these two cortical areas when processing lexical ambiguity consistent with lesion studies that show specific impairments in lexical ambiguity processing following RH lesions but not LH lesions (Klepousniotou & Baum, 2005; Tompkins, 1990). In particular, the present study demonstrates that this part of the IFG is primarily involved in the activation and manipulation of linguistic information in semantic memory. This processing gives rise to bilateral differential activation in a part of 'Broca's region' and its homologue in the right hemisphere, which we suggest is involved in top-down predictions of plausible sequence of events rather than selection per se. In addition, the present study captures significant co-activations in the anatomically and functionally connected IPL area 40 bilaterally. We suggest that area 40 is involved in the mental manipulation and computation of meaning, and when demands increase, such as when manipulating multiple alternative interpretations, the right IPL area 40 is differentially involved

in order to ensure successful meaning computation. The present study clarified understanding of the neuronal bases of higher-order cognitive functions by demonstrating the relative contribution of the IFG area 44 and the IPL area 40 to language processing.

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## Figure Legends

### **Figure 1. Activity during the presentation of the stimuli in the Homonymy condition.**

**a. Localization of the average activity increases from all 15 subjects in the comparison “Homonymy-Dominant minus Baseline” (HD minus CR).** The t statistical map of activity has been superimposed on the average T1 anatomical acquisition of the 15 subjects transformed into standard stereotaxic space. The areas surrounded by a yellow and red circle represent, respectively, the location of the activity increase within the ventral part of the pars opercularis and the supramarginal gyrus resulting from the comparison “HD minus CR”. The Y value corresponds to the antero-posterior level of the stereotaxic coordinates expressed in mm within the MNI stereotaxic proportional system. The colour scale indicates the t-value range.

**b. Localization of the average activity increases from all 15 subjects in the comparison “Homonymy-Subordinate minus Baseline” (HS minus CR).** Same as above but for the comparison “HS minus CR”.

### **Figure 2. Activity during the presentation of the stimuli in the Metaphor condition.**

**a. Localization of the average activity increases from all 15 subjects in the comparison “Metaphor-Dominant minus Baseline” (MD minus CR).** Same as in Figure 1 but for the comparison “MD minus CR”.

**b. Localization of the average activity increases from all 15 subjects in the comparison “Metaphor-Subordinate minus Baseline” (MS minus CR).** Same as in Figure 1 but for the comparison “MS minus CR”.

**Figure 3. Activity during the presentation of the stimuli in the combined Homonymy & Metaphor condition.**

**a. Localization of the average activity increases from all 15 subjects in the comparison “Homonymy&Metaphor-Dominant minus Baseline” (HMD minus CR).** Same as in Figure 1 but for the comparison “HMD minus CR”.

**b. Localization of the average activity increases from all 15 subjects in the comparison “Homonymy&Metaphor-Subordinate minus Baseline” (HMS minus CR).** Same as in Figure 1 but for the comparison “HMS minus CR”.

**Figure 4. Activity during the presentation of the stimuli in the direct contrasts between Subordinate and Dominant meaning.**

**a. Localization of the average activity increases from all 15 subjects in the comparison “Homonymy-Subordnate minus Homonymy-Dominant” (HS minus HD).** Same as in Figure 1 but for the comparison “HS minus HD”.

**b. Localization of the average activity increases from all 15 subjects in the comparison “Metaphor-Subordinate minus Metaphor-Dominant” (MS minus MD).** Same as in Figure 1 but for the comparison “MS minus MD”.