Brain & Language 131 (2014) 56–64

Contents lists available at SciVerse ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

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

Ekaterini Klepousniotou [a,b,*,1], Vincent L. Gracco [b,c], G. Bruce Pike [a,b]

[a] McConnell Brain Imaging Centre, Montreal Neurological Institute, McGill University, 3801 University Street, Montreal, QC H3A 2B4, Canada
[b] Centre for Research on Language, Mind, and Brain, McGill University, 3640 de la Montagne, Montreal, QC H3G 2A8, Canada
[c] School of Communication Sciences and Disorders, McGill University, 1266 Pine Avenue West, Montreal, QC H3G 1A8, Canada

ARTICLE INFO

Article history:
Available online 1 November 2013

Keywords:
Event-related fMRI
Lexical ambiguity
Homonymy
Polysemy
Metaphor
BROCA'S area 44
Supramarginal gyrus
Inferior parietal lobule

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.

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, Bihrle, Potter, & Gardner, 1990; Schmitzer, Strauss, & DeMarco, 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 et al., 1984; Brownell et al., 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

* Corresponding author. Address: McConnell Brain Imaging Centre, Room WB325, Montreal Neurological Institute, McGill University, 3801 University Street, Montreal, QC H3A 2B4, Canada. Fax: +1 (514) 398 2975.

E-mail addresses: ekaterini.klepousniotou@mail.mcgill.ca, e.klepousniotou@leeds.ac.uk (E. Klepousniotou).

[1] Present address: Institute of Psychological Sciences, University of Leeds, Leeds LS2 9JT, UK. Fax: +44 113 3435749.

0093-934X/$ - see front matter © 2014 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.bandl.2013.06.002

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, Baumgaertner, Lehman, & Fassbinder, 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, Grindrod, Myers, & Blumstein, 2008; Chan et al., 2004; Mason & Just, 2007; Rodd et al., 2005; Zempleni et al., 2007), others have not (e.g., Bedny, McGill, & Thompson-Schill, 2008; Chen, Page, & Chatterjee, 2008; Grindrod, Bilenko, Myers, & Blumstein, 2008; Hoenig & Scheef, 2009; Ihara, Hayakawa, Wei, Munetsuna, & Fujimaki, 2007; Lee & Dapretto, 2006; Rapp, Leube, Erb, Grodd, & Kircher, 2004; Rapp, Leube, Erb, Grodd, & Kircher, 2007), 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, Medford, Giampietro, Brammer, and David (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, Alivisatos, & Evans, 1995; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 2002) 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, D'Esposito, Aguirre, & Farah, 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