Resolving Semantic Ambiguities in Sentences: Cognitive Processes and Brain Mechanisms

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Abstract

fMRI studies of how the brain processes sentences containing semantically ambiguous words have consistently implicated (i) the left inferior frontal gyrus (LIFG) and (ii) posterior regions of the left temporal lobe in processing high-ambiguity sentences. This article reviews recent findings on this topic and relates them to (i) psycholinguistic theories about the underlying cognitive processes and (ii) general neuro-cognitive accounts of the relevant brain regions. We suggest that the LIFG plays a general role in the cognitive control process that are necessary to select contextually relevant meanings and to reinterpret sentences that were initially misunderstood, but it is currently unclear whether these control processes should best be characterised in terms of specific processes such as conflict resolution and controlled retrieval that are required for high-ambiguity sentences, or whether its function is better characterised in terms of a more general set of 'unification' processes. In contrast to the relatively rapid progress that has been made in understanding the function of the LIFG, we suggest that the contribution of the posterior temporal lobe is less well understood and future work is needed to clarify its role in sentence comprehension.

Introduction

Most words are ambiguous and can refer to multiple different concepts. For example, the word “band” can refer either to a group of musicians or to a circular strip of material. This form of ambiguity is often referred to as ‘lexical ambiguity’. We prefer the term ‘semantic ambiguity’ as this makes it clear that it is the *meaning* of the word that is ambiguous and not its form or grammatical properties.

Whenever we hear (or read) a semantically ambiguous word it seems that we can rapidly retrieve one of its meanings and ignore the other meaning(s). For example, if you were asked to define the word “organ” you could rapidly generate an appropriate definition (e.g., “a part of the body”), without being overly distracted by its alternative meaning (e.g., “a musical instrument”). Similarly, if this word occurred in a context that supported just one of its meanings (e.g., “The doctors successfully transplanted the organ”) you could rapidly select the appropriate meaning without being overly confused by your knowledge of the alternative interpretation. The only situation in which we usually become explicitly aware of such ambiguity is the case of puns, which are carefully constructed so that both meanings relate to some part of the surrounding context. For example, in the joke “Why were the teacher’s eyes crossed? Because she couldn’t control her pupils” both meanings of the ambiguous word “pupil” (i.e. a student; a part of the eye) are partially consistent with the sentence context and both meanings must be accessed for the pun to be understood. But such puns are the exception – in natural listening environments listeners are usually able to rapidly select the appropriate meaning of a word without much apparent effort or awareness (Rodd, Davis, & Johnsrude, 2005).

There are different kinds of semantic ambiguities. Sometimes the alternative meanings are not related in meaning or etymology, i.e. they do not share a common origin within the history of the language. For example, it is a historical accident that the two meanings of “bark” (i.e. the sound made by a dog; the outer covering of a tree) share both their spelling and pronunciation. These unrelated meanings are usually given separate entries in dictionaries and are referred to as homonyms, but they can also be referred to as homographs (because they share their spelling) or homophones (because they share their pronunciation). True homonyms are relatively rare; for example, they constitute only about 7% of common English words, (Rodd, Gaskell, & Marslen-Wilson, 2002). English also contains homophones that share only their pronunciation (e.g., “meet/meat”, “buy/by”, “there/their/they’re”) as well as homographs that only share their spelling (e.g., “sow”, “lead”, and “close”) which make these words ambiguous only in spoken or written language respectively.

More common than these unrelated meanings is the ambiguity between semantically related word senses - usually referred to as polysemy. For example, the word “run” has a range of different dictionary definitions (e.g., “the sprinter runs in the race”, “the candidate runs in the election”, “the software runs on the computer”) which seem to overlap somewhat in their meanings. In fact the list of senses that are explicitly listed in a dictionary is probably only the tip of the iceberg in terms of the multitude of ways in which we use these words to express a range of subtly different concepts. Additionally, current words continue to acquire new meanings that are shared within a language community which will need to be dealt with by the comprehension system (Rodd, Berriman, et al., 2012). For example, “tweet”, “tablet”, “spam”, “window”, “blackberry” and many more words have recently acquired novel technological meanings.

These examples demonstrate that many words can only be fully understood by taking into account the context in which they occur. Studying the brain mechanisms that underlie these semantic disambiguation processes is important for several reasons. First, given the ubiquity of semantic ambiguity, these processes are fundamental to everyday communication and, thus are a necessary component of any complete account of language processing. Second, these words provide a window into important cognitive processes, such as selection, inhibition and contextual integration, and examining the brain’s responses to such ambiguities can likewise elucidate the brain mechanisms that underlie these critical cognitive operations.

The aims of this article are to (i) summarise what is known about the *cognitive* processes involved in semantic ambiguity resolution, (ii) review the key findings concerning the brain regions that support these cognitive processes, and (iii) explore how these findings relate to general neuro-cognitive accounts of the relevant brain regions.

Cognitive Processes underlying Semantic Ambiguity Resolution

The neuroimaging literature looking at the brain mechanisms that support semantic ambiguity resolution is necessarily grounded in the psycholinguistic literature concerning the relevant *cognitive* processes. This literature has converged on the view that when a listener (or reader) encounters an ambiguous word they rapidly and automatically retrieve multiple meanings in parallel, and then rapidly select the one that is most likely to be correct (Duffy, Morris, & Rayner, 1988; Rodd, Johnsrude, & Davis, 2010; Simpson, 1994; Twilley & Dixon, 2000). This view is somewhat counterintuitive and does not fit with most people's intuitions of what happens: when we hear a phrase like "the tree's bark" we do not usually have any conscious experience of retrieving and then having to reject inappropriate meanings.

According to the early versions of these "exhaustive access" models (so called because we 'exhaustively' retrieve all possible meanings), all meanings are automatically accessed regardless of contextual information or the relative frequencies of the words' meanings (also known as meaning dominance) (Onifer & Swinney, 1981). This assumption was primarily supported by cross-modal semantic priming studies in which participants made responses to visual probe words that followed the ambiguous word (e.g., Seidenberg, Tanenhaus, Leiman, & Bienkowski, 1982; Swinney, 1979), which found that immediately after the ambiguous word, responses were faster for probes that were semantically related to either meaning (compared to unrelated probes) indicating that both meanings had been automatically activated. However, subsequent studies found that if the context contained a very strong semantic constraint that indicated that the dominant (more frequent) meaning was correct (e.g., "the violent hurricane did not damage the ships which were in the PORT), then only the contextually appropriate meaning was primed (e.g., Tabossi, 1988; Tabossi & Zardon, 1993). Taken together with convergent evidence from eye-movement research (Duffy, Kambe, & Rayner, 2001), the field has converged on the view, exemplified in the reordered access model (Duffy et al., 2001; Duffy et al., 1988), that multiple meanings are usually activated in parallel but this activation is modulated by a combination of the sentence context and meaning frequency (e.g., Duffy et al., 2001; MacDonald, Pearlmutter, &

Seidenberg, 1994; Simpson, 1994; Twilley & Dixon, 2000). In particular, meanings that are highly frequent or very strongly associated with the preceding context are more readily available. More recent studies have additionally highlighted the contribution of recent experience, demonstrating that we are also biased to select recently-encountered meanings (Rodd, Lopez Cutrin, Kirsch, Millar, & Davis, 2013).

As well as providing evidence that multiple meanings are usually accessed in parallel, the early priming studies found that listeners do not maintain multiple meanings for long but instead make a rapid selection within a few hundred milliseconds of encountering an ambiguous word even when both meanings are consistent with the sentence context (e.g., Seidenberg et al., 1982; Swinney, 1979). Seidenberg et al. (1982) proposed that such selection may occur because of limits on processing capacity that make it difficult to maintain multiple interpretations in parallel (although see Mason & Just, 2007; Miyake, Just, & Carpenter, 1994). One unfortunate consequence of 'early selection' is that sometimes listeners (and readers) will initially select the inappropriate meaning. For example, in the sentence "usually the bank is not the place to start if you want to catch a *fish in this stream"* most readers/listeners will initially select the wrong, financial, meaning of "bank". Numerous studies have shown that additional processing is required to recover from such misinterpretations (e.g., Duffy et al., 1988; Kambe, Rayner, & Duffy, 2001; Rodd, Johnsrude, et al., 2010).

In summary, current research suggests that whenever an ambiguous word is encountered multiple meanings are initially activated, but that a single meaning is then rapidly selected on the basis of the immediate sentence context, the frequency (dominance) of the different meanings, and recent experience with the word. The exact fate of the non-selected meaning, however, is uncertain. For example, non-selected meanings may be completely suppressed (Gernsbacher & St John, 2001; MacDonald et al., 1994) or retain a low level of activation (McRae, Spivey-Knowlton, & Tanenhaus, 1998). This psycholinguistic research provides a well-informed cognitive foundation to examine the neural basis underlying the different processes that are required to understand a sentence that contains an ambiguous word.

The Neural Network underlying Semantic Ambiguity Resolution

The first fMRI study to investigate semantic ambiguity resolution within sentence contexts was conducted by Rodd et al. (2005). Participants listened to spoken sentences that each contained several ambiguous words (e.g., “There were <u>dates</u> and <u>pears</u> on the kitchen table”). Activation was greater for ambiguous than well-matched unambiguous sentences in the left inferior frontal gyrus (LIFG) and a region of the left posterior temporal cortex that included the inferior temporal gyrus (LITG), fusiform and middle temporal gyrus (LMTG), and (to a lesser extent) the right inferior frontal gyrus (RIFG).

The specific regions highlighted by this early study were surprising for several reasons. First, the LIFG activation resided in its middle and posterior sub-divisions (pars triangularis and pars opercularis), which were traditionally attributed to either speech production (e.g., Broca, 1861; Geschwind, 1970; Indefrey & Levelt, 2004; Penfield & Roberts, 1959) or to non-semantic linguistic aspects of comprehension, including syntactic computations (e.g., Caplan, Alpert, & Waters, 1998; Caramazza & Zurif, 1976; Dapretto & Bookheimer, 1999; Grodzinsky, 1986). Second, when prior research had attributed the LIFG to semantic processing, it was often highlighted as being important for explicit semantic decisions that required the strategic retrieval, maintenance or selection of semantic information rather than for natural speech comprehension (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Gabrieli, Poldrack, & Desmond, 1998; Novick, Trueswell, & Thompson-Schill, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). However, in Rodd et al.'s (2005) study, LIFG activation was higher for ambiguous sentences despite the fact that participants were not usually aware of the ambiguity and did not rate them as sounding less natural. Such activation in the absence of explicit awareness makes it unlikely that they were due to strategic processes, and suggested a more routine involvement of this region in the semantic aspects of natural sentence comprehension. Furthermore, the posterior temporal activation was intriguing because it contrasted with accounts that highlighted anterior temporal structures as being important for semantic processing (Chan et al., 2001; Mummery et al., 2000; Nobre, Allison, & McCarthy, 1994).

This simple contrast between high- and low-ambiguity sentences provided a useful way of identifying the overall network of brain regions that are recruited by high-ambiguity sentences. Experiments using these stimuli have subsequently shown that these aspects of speech comprehension are (i) substantially disrupted when participants are even lightly sedated using an anaesthetic drug (Davis et al.; 2007), and (ii) seen in a small number of patients who were clinically diagnosed as being in a vegetative state or minimally conscious (Coleman et al., 2009; Coleman et al., 2007). However, the stimuli in these studies were heterogeneous in terms of their properties and were likely loading on a range of different cognitive processes associated with disambiguation, which means they cannot reveal the specific cognitive roles of the individual regions within this network.

Subsequent fMRI studies have used a range of more specific types of high-ambiguity sentences to provide further clues about the precise functional roles of these key brain regions (Bekinschtein, Davis, Rodd, & Owen, 2011; Davis et al., 2007; Mason & Just, 2007; Rodd et al., 2005; Rodd, Johnsrude, & Davis, 2012; Rodd, Longe, Randall, & Tyler, 2010; Vitello, Warren, Devlin & Rodd, 2014; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007; see Johnsrude & Rodd, in press, for review; see Figure 1).

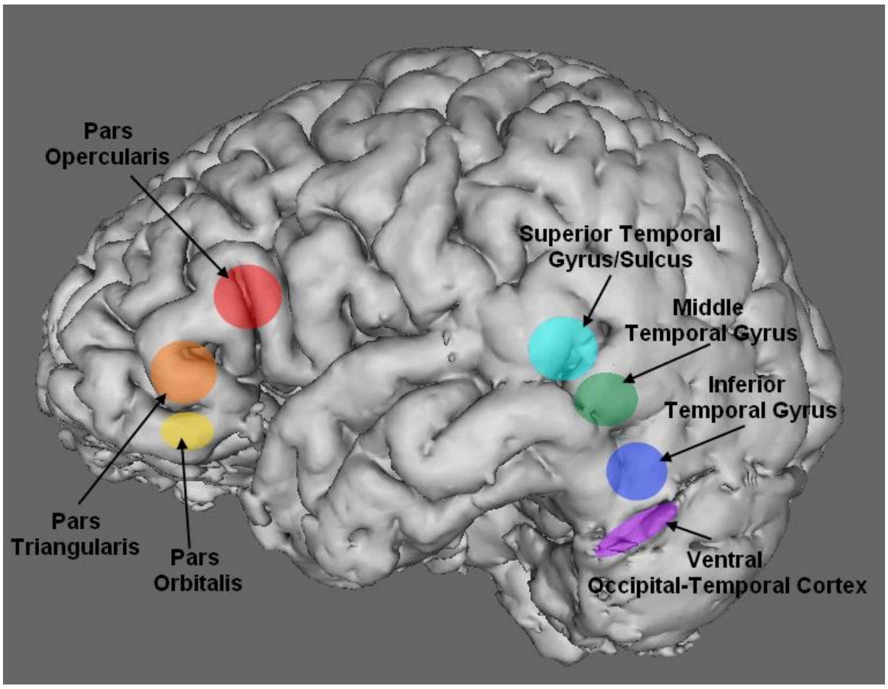

Figure 1: Left hemisphere regions that have been shown to have greater BOLD signal for semantically ambiguous than unambiguous sentences. (Structural scan from single participant rendered using FSL (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012).

Functional Contribution of the LIFG

The LIFG is the most consistent brain region that shows increased BOLD signal for high-ambiguity sentences, being reported in all published studies of ambiguity resolution that use sentence materials (Bekinschtein et al., 2011; Davis et al., 2007; Mason & Just, 2007; Rodd et al., 2005; Rodd, Johnsrude, et al., 2012; Rodd, Longe, et al., 2010; Rodd, Vitello, Woollams & Adank, 2015; Tahmasebi et al., 2012; Zempleni et al., 2007). Additionally, a recent study (Vitello, Warren, Devlin, & Rodd, 2014) has confirmed the reliability of this effect across individuals: 80% of participants showed an ambiguity-related response within a single subdivision of the LIFG: pars triangularis. Importantly, the LIFG responds to different types of ambiguous sentences that load differently on the different cognitive components of disambiguation, suggesting that this region supports multiple aspects of disambiguation, including (i) the initial selection between alternative interpretations and (ii) the subsequent reinterpretation of any sentences that have been initially misunderstood.

The most direct evidence for its role in selecting between multiple possible meanings comes from a second study using spoken materials (Rodd et al., 2012) which found activation within an LIFG region of interest that extended across both pars triangularis and pars opercularis for spoken sentences in which disambiguating information preceded the ambiguous word (e.g., “the *hunter* thought that the <u>hare/hair</u> in the field was actually a rabbit”). According to psycholinguistic theories, sentences of this type should *only* load on the processes of selecting the correct meaning and inhibiting the inappropriate meaning. This study also provided evidence for a role of this region in sentence reinterpretation by observing the time-course of responses to high-ambiguity sentences in which the ambiguous words were preceded by a neutral context that was consistent with both meanings. Specifically, spoken sentences in which disambiguating information was presented only a few words after the ambiguous word (e.g., “the scientist thought that the film on the *water* was from the pollution”) produced greater responses in early processing time-windows than sentences in which context was delayed until several words later (“e.g., the ecologist thought that the plant by the river should be *closed down*”). In contrast the latter sentences produced more activation in later time-windows. This difference in the time-course between these conditions indicates that the activation could *not* solely reflect responses to the ambiguous word itself, which occurred at the same time for the two types of sentences, and must therefore have been driven by the disambiguating information, and so is likely to reflect the reinterpretation process triggered by this information. This activation profile was seen in a large cluster of activation within the LIFG that has its peak in the posterior portion of pars triangularis, but extended posteriorly into the pars opercularis and precentral gyrus, and anteriorly into pars orbitalis.

This view that the LIFG is important for sentence reinterpretation is further supported by three studies, using both visually and auditorily presented materials, which have used sentences where the disambiguation comes towards the end of the sentence (e.g., “the woman had to make the toast with a very old *microphone* "), and which specifically manipulated the dominance (i.e. relative frequency) of the meaning of the ambiguous word that was used in the sentence. The reinterpretation account predicts that activation should be greatest for these sentences when the non-preferred (subordinate) meaning of an ambiguous word is used as these are most likely to require reinterpretation. Mason and Just (2007) report increased activation in a large region of the LIFG for visually presented sentences of this type (compared with low-ambiguity control sentences), but also show that a small anterior/ventral subregion of the LIFG near the border of pars triangularis and pars orbitalis (as well as the insula) was most active for subordinate ambiguities compared with ambiguities with two more balanced meanings. Zempleni et al., (2007) again used visually presented sentences and found an ambiguity effect in a more posterior region of the LIFG (pars opercularis/triangularis), that was sensitive to sentence dominance, such that there was more activation when the non-preferred meaning was used. Finally, Vitello et al., (2014) confirmed the presence of a similar dominance effect for spoken sentences: activation in a large region within the LIFG, that had its peak in pars triangularis, was modulated by the dominance of the ambiguous word's meaning such that activation was greater for sentences which disambiguated towards the subordinate meaning compared with more balanced ambiguities. These three experiments are all consistent with the view that the LIFG is recruited more by a condition in which reinterpretation is most likely, although the reason for the apparent variation in the precise sub-region of the LIFG that is activated is as yet unclear. These studies also suggest that recruitment of the LIFG for ambiguity-related processing occurs regardless of input modality, although it is as yet unknown whether the different processing loads associated with spoken and visual language (e.g., transient versus long-lasting signal) might modulate the involvement of these regions. Direct comparisons of these two modalities and ambiguity resolution have not yet been conducted.

One final piece of experimental evidence concerning the role of the LIFG in ambiguity resolution comes from another study using spoken materials from Rodd, Longe et al. (2010) who found that (within the same group of participants) the same posterior LIFG region (peak in pars opercularis) was activated for both semantic ambiguities and *syntactically* ambiguous sentences (e.g., “visiting relatives is/are…”). This indicates that this region is not specialized for processing semantic information, but instead provides a more general resource that can be utilised for a range of different types of ambiguity.

This finding that recruitment of this region is not specific to *semantic* ambiguities is consistent with studies that report activation in this region for a wide range of different types of sentences, which do not contain semantic ambiguities, but instead require additional sentence-level contextual processing due to the presence of a linguistic violations, such as semantically or syntactically anomalous words (Baumgaertner, Weiller, & Büchel, 2002; Hagoort et al., 2004; Kuperberg, Sitnikova, & Lakshmanan, 2008; Zhu et al., 2012, see also Lau, Phillips & Poeppel, 2006 for a review of relevant ERP studies) or syntactically complex structure (Bornkessel-Schlesewsky, Schlesewsky, and von Cramon, 2009; Just, Carpenter, Keller, Eddy,& Thulborn, 1996; see Rodd et al., 2015 for detailed review and formal meta-analysis). This region is also activated by a wide range of semantic tasks that use non-sentential stimuli, such as studies in which participants make explicit semantic judgements to word pairs/triples that contain ambiguous words (e.g., SUMMER-FAN vs. CEILING-FAN; Bedny, McGill, & Thompson-Schill, 2008; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011) and high-competition verb generation or picture naming tasks (e.g., Kan & Thompson-Schill, 2004; Persson et al., 2004; Thompson-Schill et al., 1997). This view that semantic ambiguity resolution relies on relatively general *neural* mechanisms is also consistent with evidence from dual-task methodologies that indicate the involvement of relatively general *cognitive* mechanisms (Rodd, Johnsrude & Davis, 2010). It is therefore important to view its role in the context of other more general neuro-cognitive accounts of LIFG function (see Novick et al., 2005; Rogalsky & Hickok, 2011).

One important theory of LIFG function is the conflict resolution account (Novick, Kan, Trueswell, & Thompson-Schill, 2009; Novick et al., 2005; Thompson-Schill et al., 1997), which suggests that the role of the *posterior* LIFG (pars opercularis and pars triangularis) is to resolve competition between activated representations. This theory follows the bias competition framework whereby the prefrontal cortex provides top-down bias signals to information processing in other brain regions to support context-appropriate behaviour (Desimone & Duncan, 1995; Miller & Cohen, 2001). Specifically, Novick et al. (2009) suggested that the LIFG supports conflict resolution either when there is a prepotent but irrelevant response, or when multiple representations are available but no dominant response exists. The former situation occurs for ambiguous words with one strongly dominant (i.e. prepotent) but contextually inappropriate meaning (e.g., "the sheep was in the <u>pen</u>"); the latter occurs for words with two equally likely meanings in a neutral context (e.g.., "he mentioned the organ"). Strong support for the LIFG's role in both types of conflict resolution comes from a diverse range of neuroimaging studies outside the field of sentence comprehension. These studies employed tasks including verb generation or picture naming, where stimuli are associated with several possible responses (Kan & Thompson-Schill, 2004; Persson et al., 2004; Thompson-Schill et al., 1997), semantic decision tasks in which the stimuli evoke strongly associated, but task-irrelevant, responses (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Thompson-Schill et al., 1997) and representational interference paradigms, such as Stroop tasks (January, Trueswell, & Thompson-Schill, 2009; Milham, Banich, & Barad, 2003).

In contrast to this proposed role for the *posterior* LIFG in conflict resolution, Badre and colleagues specifically attribute the *anterior* LIFG (pars orbitalis) to controlled retrieval of semantic information from long-term memory (Badre et al., 2005; Badre & Wagner, 2007). This process is required when stimulus-driven cues are insufficient to activate information relevant to one's goal or task. Various neuroimaging studies that manipulated semantic context between pairs of words and sentences show support for this theory by, for example, finding increased activity for semantically unrelated conditions than baseline (see Lau, Philips & Poeppel, 2006 for a review). In addition, a recent TMS study provides support for a causal role of this region in controlled semantic retrieval by showing that stimulating the LIFG impaired performance on semantic decision tasks for conditions with weak, but not strong, semantic associates (Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). This retrieval process may be critical for ambiguous sentences that refer to the subordinate meaning of an ambiguous word, as these meanings are more weakly associated to the ambiguous words than their dominant meaning.

In summary, the data from studies looking at semantic ambiguities in sentences are fully consistent with the view that the function of the LIFG should be characterised in terms of conflict resolution (posterior LIFG) and controlled retrieval (anterior LIFG). However it is important to note that the evidence for this dissociation between the functions of posterior and anterior subregions comes largely from studies using single words – there is currently no evidence from within the semantic ambiguity literature to support this dissociation (see Rodd et al., 2012).

An alternative, and more general, explanation for why the LIFG is recruited by semantically ambiguous sentences comes from Hagoort and colleagues (Hagoort, 2005, 2013). According to this theory, the LIFG constitutes a unification space that combines basic units of information to form larger complex representations of a sentence or discourse. In contrast to the conflict resolution account, which ascribes very specific functions to the LIFG, this unification account argues that it is the combinatorial demands, i.e. the need to combine together the representations of individual words, that drives LIFG activation. The need to resolve conflicts between competing representations and select contextually relevant semantic information are just one specific function of a more general sentence processing resource.

The substantial overlap between this unification account and the view that the LIFG is more specifically associated with conflict resolution and controlled retrieval has made it difficult to determine which account provides a better characterization of the function of the LIFG. Some authors have suggested that the key to discriminating between these accounts is to consider the extent to which the LIFG is activated by low-ambiguity sentences (see Vitello et al., 2014). While the conflict resolution/controlled retrieval accounts clearly predicts that low-ambiguity sentences should place minimal load on the LIFG, the unification view seems to suggest that although ambiguity places an increased demand on this region, the LIFG should be routinely activated by *all* sentences, even those with relatively low levels of ambiguity as, even for low-ambiguity sentences, the listener/reader must combine together the meanings of the individual words.

In general, the available data supports the former view - that the LIFG is not necessary for language comprehension for low-ambiguity sentences. For example, patients with “Broca’s Aphasia” or damage to the LIFG itself have relatively preserved comprehension of single words and simple sentences (Caplan, Hildebrandt, & Makris, 1996; Caramazza & Zurif, 1976; Schwartz, Saffran, & Marin, 1980; Yee, Blumstein, & Sedivy, 2008) and can produce and comprehend sentences that have low conflict demands, such as those with dominant interpretations (Novick et al., 2009; Robinson, Shallice, & Cipolotti, 2005). In addition, neuroimaging studies do not always report significantly greater activation in the LIFG for simple or unambiguous sentences over baseline (e.g., Crinion et al., 2003; Rodd, Johnsrude, et al., 2012; Scott, Blank, Rosen, & Wise, 2000; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006). In particular, a recent study found that the region of the LIFG that showed an ambiguity response showed *no* significant response to sentences without an ambiguous word, compared with an unintelligible baseline condition (Vitello, et al., 2014). This finding suggests this region may not be routinely involved during speech comprehension of low-ambiguity speech and that they may therefore perform functions that are more pertinent to ambiguity resolution than sentence processing in general. (Although see Hagoort, Hald, Bastiaansen, & Petersson, 2004; Rodd et al., 2005; Willems, Özyürek, & Hagoort, 2007 for contrasting findings).

However the absence of frontal activation for low-ambiguity sentences cannot allow us to completely rule out the unification account. First, this account can be reconciled with these findings by assuming that the LIFG is also being recruited by the baseline unintelligible sentences, for example by any stimulus-independent thought processes that participants may engage in when not being required to process speech (Binder et al., 1999). If this is the case then the LIFG may indeed be being activated for the low-ambiguity sentences, but this activation is not observed using standard analysis approaches because it is ‘subtracted out’ when contrasted with the baseline conditions (see Vitello, 2014 for further discussion). Alternatively, it is possible that low-ambiguity sentences do not in fact always recruit unification processes. For example, according to the ‘good enough’ approach to language comprehension (Ferreira, Bailey, & Ferraro, 2002; Ferreira, & Patson, 2007) listeners/readers may often process language in a relatively shallow manner that focuses on the local properties of individual words and may not engage in higher level integration processes unless the demands of their current situation requires them to do so.

A second aspect in which the unification account differs from other accounts of LIFG function is that it explicitly proposes functional specialisation across the LIFG in terms of type of linguistic information. Based on a literature review by Bookheimer (2002), Hagoort (2005) argued that different types of information are processed between large overlapping regions. Specifically, semantic information is preferentially processed by pars orbitalis and pars triangularis, syntactic information by pars triangularis and par opercularis and phonological processes by pars opercularis and premotor cortex. Such a division has recently been supported by a resting state study showing different patterns of functional connectivity between the three sub-regions, suggesting that they form parts of different information processing streams (Xiang, Fonteijn, Norris, & Hagoort, 2010). This view of functional segregation of the LIFG on the basis of the linguistic nature of the ambiguity is compatible with a recent meta-analysis of sentence comprehension (Hagoort & Indefrey, 2014), but is inconsistent with a second formal meta-analyses that found that both semantic and syntactic aspects of sentence comprehension are both primarily associated with the *posterior* LIFG (Rodd et al., 2014) as well the finding from Rodd, Longe, et al. (2010) that semantic and syntactic ambiguities recruit similar regions of the posterior LIFG. Thus, while there is some evidence to support the view that anatomical subdivisions of the LIFG are associated with different types of linguistic information, it remains unclear, why semantic ambiguities are primarily associated with *posterior* and not *anterior* LIFG, as might have been expected.

One possible way in which this inconsistency might be resolved is to note that a variety of phonological processes have been associated with the posterior LIFG (pars opercularis). Aside from phonological unification (Hagoort, 2005, 2013) this region has been specifically associated with maintaining phonological representations (Nixon, Lazarova, Hodinott-Hill, Gough, & Passingham, 2004), articulatory operations (Hickok & Poeppel, 2007) and phonological sub-vocal rehearsal (Rogalsky, Matchin, & Hickok, 2008). These theories have received support from a variety of neuroimaging, TMS and lesion studies, employing paradigms such as letter/word rhyming judgements (Baldo & Dronkers, 2006; Gough, Nobre, & Devlin, 2005), delayed phonological matching of words/pseudowords (Nixon et al., 2004; Strand, Forssberg, Klingberg, & Norrelgen, 2008) and concurrent comprehension and articulation tasks (Rogalsky et al., 2008) . While most cognitive theories of semantic ambiguity resolution do not highlight phonological-based mechanisms, it is possible that the phonological working memory aspects of semantic reinterpretation may place a load on such operations, making these accounts broadly consistent with the finding of ambiguity-related activation in this region.

In summary, several very different theories of LIFG function, which were *not* developed primarily to explain semantic ambiguity effects, can explain the involvement of this region in ambiguity resolution, but several unresolved questions remain. In particular further work is needed to determine precisely which subregion(s) of the LIFG contributes to ambiguity resolution in light of converging research outside the field of ambiguity that suggests there is functional specialisations across the LIFG either in terms of linguistic content (anterior/semantic – posterior/phonological) or processing (anterior/controlled semantic retrieval – posterior/semantic selection). It is currently unclear whether and how these different subregions might make different specific contributions to ambiguity resolution. For example, Rodd et al. (2012) report a very large cluster of ambiguity-related activation that extends across all three anatomical sub-divisions of the LIFG (pars opercularis; pars triangularis; pars orbitalis), but, despite including a range of different types of sentences which were designed to load differently on the different cognitive components (i.e. selection between meanings; semantic reinterpretation), they found no evidence for functional specialization across these subdivisions.

Finally it is important to note that although this review has focused on the *left* IFG there is some evidence for activation in the homologous right hemisphere region, although in most studies this is either weaker than that found in the left hemisphere (Mason & Just, 2007; Rodd et al., 2005; Zempleni et al., 2007) or does not reach the required significance levels (Bekinschtein et al., 2011; Rodd, Johnsrude, et al., 2012; Rodd, Longe, et al., 2010; Vitello et al., 2014). The involvement of right hemisphere regions is of particular interest given claims that it plays a specific role in maintaining non-selected meanings in case subsequent reinterpretation is needed (e.g., Faust & Chiarello, 1998; Faust & Gernsbacher, 1996). Future work is needed to determine what (if any) functional contribution is made by the right IFG to semantic disambiguation (see Rodd et al., 2005).

Functional Contribution of left Posterior Temporal Cortex

The left posterior inferior temporal cortex is the second region that is often activated alongside the LIFG in response to semantically ambiguous sentences (Davis et al., 2007; Rodd et al., 2005; Rodd, Johnsrude, et al., 2012; Tahmasebi et al., 2012; Zempleni et al., 2007). In contrast to frontal regions, temporal lobe activation has only been found for those ambiguous sentences where reinterpretation is likely to be required (Rodd, Johnsrude, et al., 2012; Rodd, Longe, et al., 2010; Zempleni et al., 2007; Vitello et al., 2014).

There are two different interpretations of this finding. One possibility is that, unlike frontal regions, the posterior temporal lobe may make a relatively pure contribution to the reinterpretation aspect of semantic disambiguation (Rodd, Johnsrude, et al., 2012). An alternative explanation is that because reinterpretation is the most cognitive demanding aspect of semantic disambiguation (Johnsrude & Rodd, in press), it is the only aspect of disambiguation that produces a neural signal that is sufficiently strong to be observed using current methods, given the very considerable variability in the reported anatomical locations for these temporal lobe ambiguity-related activations, which have been seen in several functionally-distinct regions. While the most commonly activated regions are the posterior *inferior* temporal gyrus (Bekinschtein et al., 2011; Davis et al., 2007; Rodd et al., 2005; Rodd, Johnsrude, et al., 2012; Zempleni et al., 2007) and the posterior *middle* temporal gyrus (Rodd et al., 2005; Rodd, Johnsrude, et al., 2012; Zempleni et al., 2007), activation has also been seen more ventrally within the fusiform gyrus (Bekinschtein et al., 2011; Rodd et al., 2005; Rodd, Johnsrude, et al., 2012) and more superiorly in the posterior STS (Rodd et al., 2005) (Price & Devlin, 2011). It is currently unclear whether these discrepancies reflect inter-subject functional variability and/or relate, instead, to systematic differences in the ambiguous stimuli or experimental protocols used between studies. Some evidence for inter-subject variability comes from Vitello et al. (2014), who found that, while almost all subjects showed peaks in inferior temporal regions (ITG, occipitotemporal sulcus, fusiform gyrus), no single subregion showed consistent activation across the majority of participants.

This relatively restricted set of data about *when* ambiguity related activation is seen in posterior temporal cortex (i.e. just for when reinterpretation is required), together with the uncertainty about exactly *where* the activation is observed, makes it challenging, and perhaps premature, to relate these findings to current neurobiological accounts of this brain region. While explanations of the ambiguity-related activation in LIFG have broadly converged on the idea that this region supports cognitive control operations needed to resolve semantic ambiguities, there has been no equivalent convergence of the field with respect to the role of posterior temporal cortex. Different authors have linked their observed ambiguity effects to a heterogeneous set of cognitive processes.

One possibility is that this region plays a key role in the representation of the lexical-semantic information, either specifically in terms of the sound to meaning mapping that is required for *spoken* words (Hickok & Poeppel, 2004, 2007), or perhaps for more abstract representations of words and their meanings (Snijders et al., 2009). This view is consistent with several findings from the field of *syntactic* ambiguity research. First, Snijders et al., (2009) found that the posterior middle temporal gyrus responds to the presence of syntactically ambiguous words themselves irrespective of whether they occur within a sentential context, leading them to conclude that this region subserves “the retrieval of lexical-syntactic information from memory”. Second, a magnetoencephalography (MEG) study of syntactic ambiguity that tracked the spatial distribution of neural responses over time (Tyler et al., 2013) indicated that the posterior temporal response *preceded* the subsequent LIFG response, leading them to conclude that the posterior temporal lobe “represents and transmits lexical information to the LIFG”. Under this view this region is activated for high-ambiguity sentences because of the increased amount of lexical-semantic information that must be retrieved for such sentences.

However, other possible interpretations of these posterior temporal activations for high-ambiguity sentences remain. A second possibility is that, like the LIFG, the posterior temporal cortex plays a key role in cognitive control. Support for this view comes from a range of recent studies with both patients and healthy controls that associate this region with the semantic control processes that modulate access to stored semantic representations (Whitney et al., 2011; Jefferies, 2013). A third, distinct possibility is that the ambiguity related activations reflects processing of *visual* based semantic/orthographic information that could potentially aid in the resolution of ambiguities (Cohen, Jobert, Le Bihan, & Dehaene, 2004; Martin, 2007; Price & Devlin, 2003, 2011).

Summary

In summary, fMRI studies of semantic ambiguity resolution in speech have been remarkably consistent in finding significant activation in the posterior (and to a lesser extent) anterior LIFG. This is highly consistent with current neurobiological accounts of this region which focus on its role in either controlling the selection/retrieval of semantic information (Novick et al., 2009; Novick et al., 2005; Thompson-Schill et al., 1997), or in combining together the representations of individual words to form coherent representations of sentences or longer pieces of discourse (Hagoort, 2005, 2013). In contrast the activations seen in the posterior temporal lobe remain somewhat of a mystery – while the presence of such activations is highly replicable, their precise location is highly variable making it challenging to link these observed activations with current neurobiological accounts of the contribution of these regions to other aspects of cognition. We anticipate that this issue will only be adequately resolved when additional, anatomically precise, data is available about the responses of the different anatomical subregions in response to a range of different forms of linguistic ambiguity.

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