

The functional organisation of the fronto-temporal language system: Evidence from syntactic and semantic ambiguity

Jennifer M. Rodd^{a,*}, Olivia A. Longe^b, Billi Randall^b, Lorraine K. Tyler^b

^a Department of Cognitive, Perceptual and Brain Sciences, University College London, London, UK

^b Centre for Speech, Language and the Brain, Department of Experimental Psychology, University of Cambridge, Cambridge, UK

ARTICLE INFO

Article history:

Received 17 March 2009

Received in revised form

10 December 2009

Accepted 22 December 2009

Available online 28 December 2009

Keywords:

fMRI

Speech

Syntax

Semantics

Comprehension

ABSTRACT

Spoken language comprehension is known to involve a large left-dominant network of fronto-temporal brain regions, but there is still little consensus about how the syntactic and semantic aspects of language are processed within this network. In an fMRI study, volunteers heard spoken sentences that contained either syntactic or semantic ambiguities as well as carefully matched low-ambiguity sentences. Results showed ambiguity-related responses in the posterior left inferior frontal gyrus (pLIFG) and posterior left middle temporal regions. The pLIFG activations were present for both syntactic and semantic ambiguities suggesting that this region is not specialised for processing either semantic or syntactic information, but instead performs cognitive operations that are required to resolve different types of ambiguity irrespective of their linguistic nature, for example by selecting between possible interpretations or reinterpreting misparsed sentences. Syntactic ambiguities also produced activation in the posterior middle temporal gyrus. These data confirm the functional relationship between these two brain regions and their importance in constructing grammatical representations of spoken language.

© 2010 Elsevier Ltd. All rights reserved.

Successful spoken language comprehension involves processing a number of different types of linguistic information (e.g., phonetic, phonological, semantic, morphological and syntactic). How these different aspects of speech comprehension are functionally organised within the brain is a key, and contentious, issue in cognitive neuroscience.

Functional imaging studies have identified an extensive left-dominant network of brain regions as being important for speech comprehension. Studies that compare simple spoken sentences to unintelligible noise stimuli have found activation in the superior and middle temporal gyri (STG and MTG) both anterior and posterior to primary auditory cortex (Binder et al., 2000; Crinion, Lambon Ralph, Warburton, Howard, & Wise, 2003; Davis & Johnsrude, 2003; Narain et al., 2003; Scott, Blank, Rosen, & Wise, 2000), while studies that vary the linguistic properties of spoken utterances have observed activation in a number of additional brain regions including the left inferior frontal gyrus (LIFG) (Caplan, Alpert, & Waters, 1999; Friederici, Meyer, & von Cramon, 2000; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Ni et al., 2000; Rodd, Davis, & Johnsrude, 2005a; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Tyler et al., 2009), the MTG

(Stamatakis, Marslen-Wilson, Tyler, & Fletcher, 2005; Tyler et al., 2005), the posterior portion of the inferior temporal gyrus (ITG) and fusiform gyrus (Kuperberg et al., 2000; Rodd et al., 2005a), the inferior parietal cortex and supramarginal gyrus (Ni et al., 2000; Tyler & Marslen-Wilson, 2008), the insula (Kuperberg et al., 2000; Friederici et al., 2003) and the basal ganglia (Friederici et al., 2003). Although this network is primarily left lateralised, right hemisphere regions are also activated under some conditions, albeit to a lesser extent (Tyler & Marslen-Wilson, 2008). Despite the consistency with which this fronto-temporal network is activated, the precise functional role of its component parts remains controversial (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Hickok & Poeppel, 2004, 2007; Tyler & Marslen-Wilson, 2008).

A popular approach to this issue has been to assume that individual brain regions within the speech comprehension network are specialised for processing particular types of linguistic information. For example, Friederici and colleagues have proposed a model in which there are separate left hemisphere regions for the processing of syntactic and semantic information (Friederici, 2002, 2006; Friederici & Kotz, 2003; Friederici et al., 2003; Grodzinsky & Friederici, 2006). The initial stage of local syntactic structure building is supported by the left anterior portion of the STG as well as the left frontal operculum (the area medial to the most inferior portion of the LIFG). During a second phase of processing, information about the individual words (both semantic and syntactic) is used to determine the dependency relationships between the constituent words. Crucially, the semantic and syntactic processing domains

* Corresponding author at: Division of Psychology and Language Sciences, University College London, London, UK. Tel.: +44 020 7679 1096; fax: +44 020 7436 4276.

E-mail address: j.rodde@ucl.ac.uk (J.M. Rodd).

Table 1
Descriptive statistics (frequency: log-transformed Celex lemma frequency).

	N	Length (words)	Length (s)	Frequency Word 1	Frequency Word 2	Frequency Verb	Dominance (%)	Naturalness
Syntax								
High-ambiguity (e.g., He noticed that <u>landing planes frightens</u> some new pilots)	52	9.71	4.10	1.68	1.84	2.15	22	5.7
Low-ambiguity (e.g., She thought that <u>renting flats requires</u> a large deposit)	52	9.75	4.10	1.64	1.80	2.07	100	6.7
Semantic								
High-ambiguity (e.g., The reporter commented that modern compounds <u>react</u> unpredictably)	52	10.23	3.98	2.06	1.62	1.43	25	5.8
Low-ambiguity (e.g., The article commented that <u>fiction writers publish</u> infrequently)	52	10.21	3.88	1.92	1.60	1.72	100	6.7

are assumed to work in parallel (but independent of each other) and they are associated with distinct cortical regions: the morpho-syntactic process of thematic role assignment is associated with Broca's area itself (BA 44/45), while semantic processing is associated with the posterior portion of the STG and the MTG together with a more ventral portion of the IFG (BA 45/47).

In contrast to this view that distinct portions of the speech processing network are specialised for processing particular types of linguistic information, Kaan and Swaab (2002) propose a different view in which different brain regions are specialised for particular processing operations that can be applied to both syntactic and semantic information. They suggest that the middle and superior temporal lobes are involved in activating the syntactic, semantic and phonological information associated with the incoming words, the anterior temporal lobe is involved in combining the activated information or encoding it for later use and the LIFG is involved in storing non-integrated material when processing load increases. Yet a different view, proposed by some of us, stresses the inter-activity between these anatomically distinct regions rather than their functional specificity, and the ways in which linguistic functions are achieved by the co-modulation of activity between regions (Stamatakis et al., 2005; Tyler & Marslen-Wilson, 2008).

In this paper we investigate how semantic and syntactic information is processed within the speech processing network by using fMRI to measure the processing that is required to understand sentences that contain either semantic or syntactic ambiguities. By observing the increases in activation that occur when listeners hear different types of ambiguity we can determine the extent to which the semantic and syntactic aspects of speech are processed by distinct or overlapping brain regions. We chose ambiguity as the means for exploring syntactic and semantic aspects of spoken language processing because it is a ubiquitous and natural property of language. Many words are semantically and/or syntactically ambiguous, and can be interpreted differently according to their context. For example, in "*The shell was fired towards the tank*" the words "*shell*", "*fire*" and "*tank*" all have more than one meaning, but are disambiguated by the meanings of the other words in the sentence. Additionally, a word's syntactic role can be ambiguous. For example, in a sentence beginning "*Visiting relatives...*" the initial noun phrase is syntactically ambiguous, but is immediately disambiguated by the inflection of the subsequent verb (e.g., "... *is tedious*" / "... *are tedious*" (Tyler & Marslen-Wilson, 1977).

In this study we compare sentences that contain either syntactic or semantic ambiguities with closely matched low-ambiguity sentences. Although syntactic ambiguities have consequences for the semantics of a sentence, we assume that the increased activation produced by syntactic ambiguities will primarily reflect the processes of assigning the correct syntactic structure on the basis of syntactic cues, whereas the activation produced by the semantic ambiguities will primarily reflect the process of assigning the correct semantics to individual words on the basis of semantic cues. To the extent that there are differences between the pat-

terns of activity that are produced by the two types of ambiguity, this assumption is confirmed. Although semantic and syntactic ambiguity have previously been investigated separately using fMRI (Fiebach, Vos, & Friederici, 2004; Mason & Just, 2007; Mason, Just, Keller, & Carpenter, 2003; Rodd et al., 2005a; Rodd, Davis, & Johnsrude, 2005b; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007), this is the first study to directly compare these two types of ambiguity within the same group of individuals. This design varies the demands on syntactic and semantic processes during online sentence comprehension, while holding constant task-related processing demands that are not directly associated with sentence comprehension.

This approach has several clear advantages over previous studies that have directly compared syntactic and semantic processing. These earlier studies, which have failed to produce a consistent pattern of results, often use highly unnatural stimuli that contain either syntactic or semantic anomalies (Friederici et al., 2003; Kang, Constable, Gore, & Avrutin, 1999; Kuperberg et al., 2000; Kuperberg et al., 2003; Luke, Liu, Wai, Wan, & Tan, 2002; Newman, Just, Keller, Roth, & Carpenter, 2003; Ni et al., 2000) or meaningless nonwords (Friederici et al., 2000; Roder, Stock, Neville, Bien, & Rosler, 2002), or they encourage the use of meta-linguistic decision making processes (Dapretto & Bookheimer, 1999). In this study, listeners hear the high- and low-ambiguity sentences in random order and their attention is not explicitly drawn to the different types of ambiguity within the experiment. By directly comparing the activation produced by the two types of ambiguity, we can identify the brain regions that are associated with the syntactic and semantic aspects of online sentence comprehension for sentences that are both grammatically correct and meaningful.

In addition to the direct comparisons between high- and low-ambiguity sentences, we look for effects of subjects' preference for the different interpretations of the ambiguities, which we refer to as "dominance". For example, in the sentence "*in some circumstances, unwanted moles...*" the ambiguous word *mole* has a dominance score of close to 50% because the two possible interpretations of the word *moles* (mammal that lives underground; growth on the skin) are equally preferred by listeners in this context. In contrast, an ambiguity such as "*the schoolgirl noticed that brown hares/hairs...*" has a dominance score of 0% because at the point of the ambiguity subjects show a strong preference for the "*hairs*" interpretation, which is inconsistent with the actual sentence completion "... *hop around the field*". The cognitive literature has shown that dominance is important in determining the ease with which ambiguities are resolved (e.g., Rayner & Duffy, 1986) and is therefore likely to influence the neural response to ambiguities. In particular, the way in which dominance affects the activation of a particular brain region will give us important clues about the role of that region in sentence comprehension. For example, if activation is only seen when the disambiguating information is inconsistent with the preferred reading of the ambiguity, then this would suggest that its function is to reanalyse sentences that have been misinterpreted. In contrast,

if activation is seen for all ambiguities regardless of dominance, then this would suggest that its function may be to hold different sentence interpretations in working memory or to select between these different interpretations.

In summary, the present study investigates how semantic and syntactic processing is organised within the speech comprehension network by identifying the brain regions that are recruited when listeners hear sentences that contain syntactic or semantic ambiguities. In addition, by varying the dominance ratings of each ambiguity we are also able to investigate claims about how these different kinds of ambiguities are processed.

1. Material and methods

1.1. Stimuli

We constructed 104 sentence-pairs (Table 1; see Appendix A for example stimuli). Half these pairs consist of a high-ambiguity sentence that contains a syntactic ambiguity and a matched low-ambiguity sentence.¹ The other half consists of a sentence that contains a semantic ambiguity and a matched low-ambiguity sentence.

Each of the 52 syntactic high-ambiguity sentences contained a two-word phrase that had two possible syntactic roles that was disambiguated by the inflection of the subsequent verb (e.g., “He noticed that landing planes frightens some new pilots” (Tyler & Marslen-Wilson, 1977). The ambiguity arises because it is initially unclear, as the listener hears the sentence, whether it is the “landing” or the “planes” that is the subject of the sentence. For example, in the case of the phrase “landing planes frightens some new pilots”, the participle “landing” is used as a noun (gerund) and is the subject of the sentence (i.e., it is the action of landing that is frightening the pilots). In contrast, in the phrase “landing planes frighten some new pilots”, the noun “planes” (which is modified by the participle *landing*) is the subject of the sentence (i.e., it is the planes themselves that are frightening the pilots). Each syntactic high-ambiguity sentence was initially ambiguous between these two syntactic structures, but was disambiguated by the subsequent verb inflection (“frightens” vs. “frighten” in the example above) such that half of the sentences used each of the two structures. Each ambiguous sentence was matched to a control low-ambiguity sentence where the critical phrase (e.g., “crying babies” or “describing paintings”) is only consistent with a single syntactic structure. We refer to this condition as “low-ambiguity” and not as “unambiguous” because the prevalence of words that are consistent with more than one syntactic class in English makes it impossible to construct stimuli that contain no transient syntactic ambiguities. For example, the phrase “Her mother told her that crying babies...” does contain syntactic ambiguity to the extent that “crying” is initially consistent with the gerund interpretation (e.g., “Her mother told her that crying is for babies”). Our aim instead is to use a set of high-ambiguity sentences that contain additional ambiguity over and above that which is seen in the low-ambiguity sentences such that the direct contrast between these conditions can be used to reveal the processes involved in syntactic ambiguity resolution.

The 52 semantic high-ambiguity sentences contained an ambiguous word (e.g., “bark”) whose meaning was disambiguated by the subsequent verb’s meaning. The ambiguous words were either homonyms, which have two meanings that have the same spelling and pronunciation ($N = 33$, e.g., “In Australia, strange *barks* grow on many trees”) or homophones, which have two meanings that have the same pronunciation but have different spelling ($N = 19$, e.g., “The housewife hoped that both *pears/pairs* taste sweet”).² The ambiguous words were disambiguated by the meaning of the subsequent verb. Each semantic high-ambiguity sentence was matched individually to a control low-ambiguity sentence. As with the syntactic case, it is impossible to construct control sentences that are entirely unambiguous but our aim was to ensure that the high-ambiguity sentences contained additional ambiguity over and above that seen in the low-ambiguity sentences. In both cases the ambiguity that we have manipulated is systematic—other extraneous ambiguities are randomly distributed across all conditions.

¹ Unlike most behavioural studies of ambiguity, the critical lexical items were not repeated across conditions. This between-item design allows all the items to be heard by all the participants and thereby increases the power of the design. This approach necessarily introduces differences between the experimental conditions in terms of the propositional content of the sentence, but the relatively large sets of stimuli used in this study make it unlikely that any of the observed differences are the result of differences in propositional content.

² Following Rodd et al. (2005a, 2005b), this study focuses on the ambiguity resolution processes that are shared by both types of ambiguous words. Although we assume that these spelling differences are likely to have minimal processing consequences due to the auditory presentation, future studies should explore whether this factor plays a role in auditory ambiguity resolution. The absence of explicit matching between the two types of ambiguous words makes it impossible to explore any effects of spelling consistency.

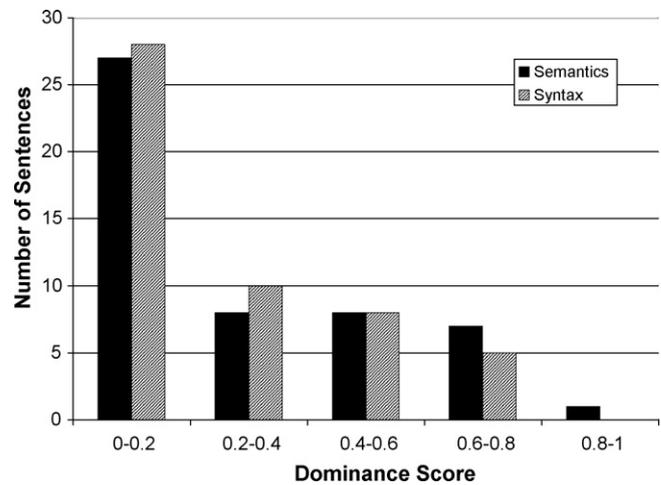


Fig. 1. Distribution of dominance scores for sentences containing semantic or syntactic ambiguities.

There were 52 sentences in each of the four sentence conditions. The two sets of high-ambiguity sentences were matched to their control low-ambiguity sentences for syntactic structure, number of words and syllables, and physical duration (seconds). They were also matched for the word frequencies of the two words in the ambiguous phrase and the disambiguating verb (lemma frequency taken from the Celex lexical database; Baayen, Piepenbrock, & Gulikers, 1995) (in all cases the total lemma frequency for the spoken word-form was used) (Table 1). In addition, although the high-ambiguity sentences were rated as being less natural than their low-ambiguity control sentences, there was no difference between the two sets of low-ambiguity sentences or the two sets of high-ambiguity sentences (both $p > .3$) (Table 1). Naturalness ratings were obtained from an auditory pre-test in which 16 subjects who did not take part in the fMRI study rated the sentences on a 9-point scale. The two types of high-ambiguity sentence were matched for the position of the ambiguity within the sentence.

Dominance ratings (a measure of listeners’ preferences for the different interpretations of the ambiguities) were obtained in an auditory sentence completion pre-test. Subjects who did not take part in the fMRI experiment listened to versions of the sentences in which the sentences were cut off after the ambiguous phrase (e.g., “In Australia, strange barks...”) and were asked to write down a plausible end to the sentence fragment. These completions were coded with regard to whether they were consistent with the interpretation that was used in the actual sentence continuation. We initially tested 22 participants on this pre-test. It was then necessary to test some additional participants on subsets of items for which some of the initial responses were ambiguous. For example, for the sentence fragment “The story in the newspaper warned that forgotten mines...” some participants gave the response “are dangerous”, which is consistent with both the “ore extraction” and “military weapon” interpretations. All such ambiguous responses that did not clearly indicate a preference for one interpretation were excluded, and additional data were collected until every sentence was associated with exactly 22 unambiguous responses. This ensured that the dominance scores were equally sensitive for all items. The dominance scores reflect the percentage of these unambiguous continuations that were consistent with the actual continuation used in the experiment and therefore reflect the likelihood that a listener who did not hear the disambiguating information would select the correct interpretation. The semantic and syntactic ambiguities were matched for the mean dominance of the sentences and have similar distributions (Fig. 1). Where possible, the sentences were constructed to use the less frequent interpretation of the ambiguity (in order to maximise the ambiguity effect). This resulted in a skewed distribution of dominance scores with the large proportion of sentences having low scores. To address this issue, additional analyses were conducted in which a square-root transformation was performed on these dominance scores. This transformation has the effect of making the distribution of dominance scores more symmetrical and ensures that any effects of dominance are not disproportionately influenced by the small number of items with relatively large dominance scores.

The sentences were spoken by a female native speaker of British English. The speaker was aware of the different experimental conditions: this was necessary to ensure that the syntactic ambiguities were not disambiguated by intonational cues. 52 baseline items were created by taking a randomly selected subset of the sentences and converting them to signal correlated noise (SCN; Schroeder, 1968) using Praat software (<http://www.praat.org>). After processing, the sentences retain the same spectral profile and amplitude envelope as the original speech, but since all spectral detail is replaced with noise they are entirely unintelligible. In addition, there were 52 “rest” trials on which no sound was presented. These two sets of baseline items are important for monitoring data quality and for the interpretation of any differences between the experimental conditions.

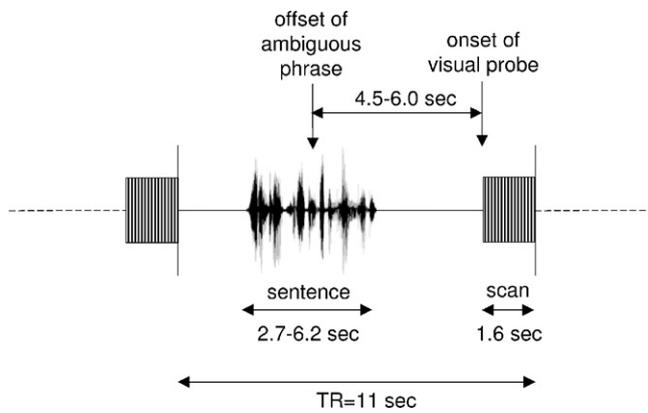


Fig. 2. Details of the sparse-imaging procedure (see Section 1) in which a single stimulus item was presented in the silent period between scans. The offset of the ambiguous phrase was timed such that the predicted BOLD response to the ambiguity in each sentence (based on the canonical haemodynamic response function in the SPM software) would be approximately at the time of the scan. Visual probes occurred at the onset of the scan, minimising sensitivity to the BOLD effect of these events.

1.2. Subjects

14 subjects (right-handed, healthy, native English speakers, aged 19–37) took part in the fMRI experiment. All gave informed consent. The study was approved by Addenbrooke's NHS Trust Ethical Committee.

1.3. Task

A previous study (Rodd et al., 2005a) showed that, compared with passive listening conditions, the variability in fMRI data can be reduced by requiring listeners to perform a simple task while listening to the sentences. For this reason, on 50% of sentences (randomly assigned) listeners were required to press a button to indicate whether a word, which was visually presented after the sentence end, was related or unrelated to the sentence's meaning. The sole purpose of the task was to ensure that subjects' attention was directed to the sentences and it was designed to be easy in all four sentence conditions. Importantly, the timings of the sentences, visual probes and scans were carefully controlled (following Rodd et al., 2005a) to ensure that each single 1.6-s scan (single brain volume) was insensitive to task-related activity (see Section 1.4), and no differences between conditions were predicted. The probe words were presented for 1 s at the onset of the scan.

The probe words were selected to be clearly related or unrelated to the meaning of the preceding sentence, and were never related to the inappropriate interpretation of the semantic ambiguities. The visual probes were matched for word length across the four speech conditions. For the baseline noise stimuli, on 50% of trials the words "left" or "right" appeared on the screen and participants pressed the corresponding button. This task was introduced in order to elicit the same motor activations as in the sentence relatedness decision task.

1.4. Imaging methods

A sparse-imaging method was used such that stimuli were presented in a 9.4 s silent period that occurred between each 1.6 s scan (see Fig. 2) (Hall et al., 1999). The timings of events were based on estimates of the time course of the haemodynamic response to auditory stimuli (Hall et al., 2000) and a similar study by Rodd et al. (2005a). These timings were chosen to ensure that the scans were maximally sensitive to the online processing of the ambiguity and subsequent disambiguation, but insensitive to effects of scanner noise and the visual probes, which were presented during the scan. To allow data to be collected over a larger time window than the 1.6 s TR (and thus to avoid missing the peak of the haemodynamic response) the position of the sentences within the silent period was jittered such that scanning started either 4.5, 5.0, 5.5 or 6.0 s after the end of the ambiguous phrase. Four versions of the experiment were created such that each sentence was heard in each of the four jitter positions by approximately a quarter of the subjects. Each subject heard a quarter of the sentences in each of these jitter positions.

Stimulus items were pseudo-randomly ordered such that the four sentence conditions, the noise trials and rest scans were evenly distributed across four sessions, and items from each condition occurred equally often after each of the six conditions (four speech conditions and two baseline conditions). Stimuli were presented to both ears using a high-fidelity auditory stimulus-delivery system incorporating flat-response electrostatic headphones inserted into sound-attenuating ear defenders (Palmer, Bullock, & Chambers, 1998). To further attenuate scanner noise, participants wore insert earplugs. DMDX software running on a Windows 98 PC (Forster

& Forster, 2003) was used to present the stimulus items and record button-press responses.

The imaging data were acquired at the Wolfson Brain Imaging Unit, Cambridge, using a Bruker Medspec (Ettlingen, Germany) 3-T MR system with a head gradient set. Each volume consisted of 21 mm × 4 mm thick slices with interslice gap of 1 mm; FOV: 25 cm × 25 cm; matrix size, 96 × 96 in plane resolution = 2 mm × 2 mm; TE = 27 ms; TA = 1.6 s; TR = 11 s. Acquisition was transverse-oblique, angled away from the eyes.

The fMRI data were pre-processed and analysed using SPM2 (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk). Pre-processing included within-subject realignment, spatial normalisation of functional and structural images to a standard structural template, and spatial smoothing (8 mm Gaussian kernel). Parameter estimates for individual subjects were derived from a General Linear Model in which each scan was coded according to the experimental condition of the preceding sentence. In addition to these categorical effects of stimulus condition, to assess which brain regions show a significant correlation between their activation level and the degree to which participants prefer an interpretation other than that which is used in the high-ambiguity sentence, dominance scores were included in the model as parametric modulators for the semantic and syntactic high-ambiguity sentences. These parametric modulators were zero-mean corrected within the design matrix and so cannot alter the effect size of other main effects. In addition, although parametric modulators can soak up additional between-scan variance (and hence increase the significance of other main effects in first level analysis), they do not alter the effect size nor therefore the significance of random effects analyses in which only between-subject variance is relevant (Büchel, Holmes, Rees, & Friston, 1998). Each of the four scanning runs was modelled separately within the design matrix. Additional columns encoded subject movement (as calculated from the realignment stage of pre-processing) as well as a constant term for each of the four scanning runs. These estimates were entered into second-level group analyses with inter-subject variation treated as a random effect (Friston, Holmes, & Worsley, 1999). In order to assess the robustness of any dominance effects, a supplementary analysis was conducted in which the dominance scores were subjected to a square-root transformation.

2. Results

Subjects' responses to the visual probes were not analysed in detail because no differences were predicted and due to the timings of the events, the fMRI data were insensitive to whether the task was present or absent on any given trial (see subsequent fMRI analyses). The mean response time for correct responses to the visual probes was 791 ms for the baseline items and 799 ms for the speech items. The error rates were 1.4% and 2.5%, respectively.

In the imaging analyses, we consider activations to be significant if they reach a threshold of $p < .05$ corrected for multiple comparisons at the cluster level (using a voxel-level threshold of $p < .001$ uncorrected).

2.1. Speech-noise

Relative to unintelligible noise (SCN), speech produced large bilateral clusters of activation centred on the superior temporal sulcus (STS) (See Fig. 3 and Table 2). In the left hemisphere, this cluster extended from the mid STS to anterior STS and included extensive portions of the MTG. In the right hemisphere, the cluster was reduced in extent (Fig. 3). In addition there were smaller bilateral clusters of activation in the hippocampi. Activation in the LIFG did not reach corrected significance, although at a lower threshold (voxel-level threshold $p < .001$ uncorrected) there was a significant peak in BA 44/45 (−50, 22, 6).

2.2. Effects of ambiguity and dominance: all sentences

The effects of ambiguity were assessed in two different ways. First, high-ambiguity sentences were compared to their matched low-ambiguity sentences. Second, we identified the brain areas that were correlated with the dominance scores, which were included as parametric modulators. Both positive and negative correlations were assessed although it is predicted that most effects should emerge as negative correlations as this corresponds to an increase in activation for items where the non-preferred

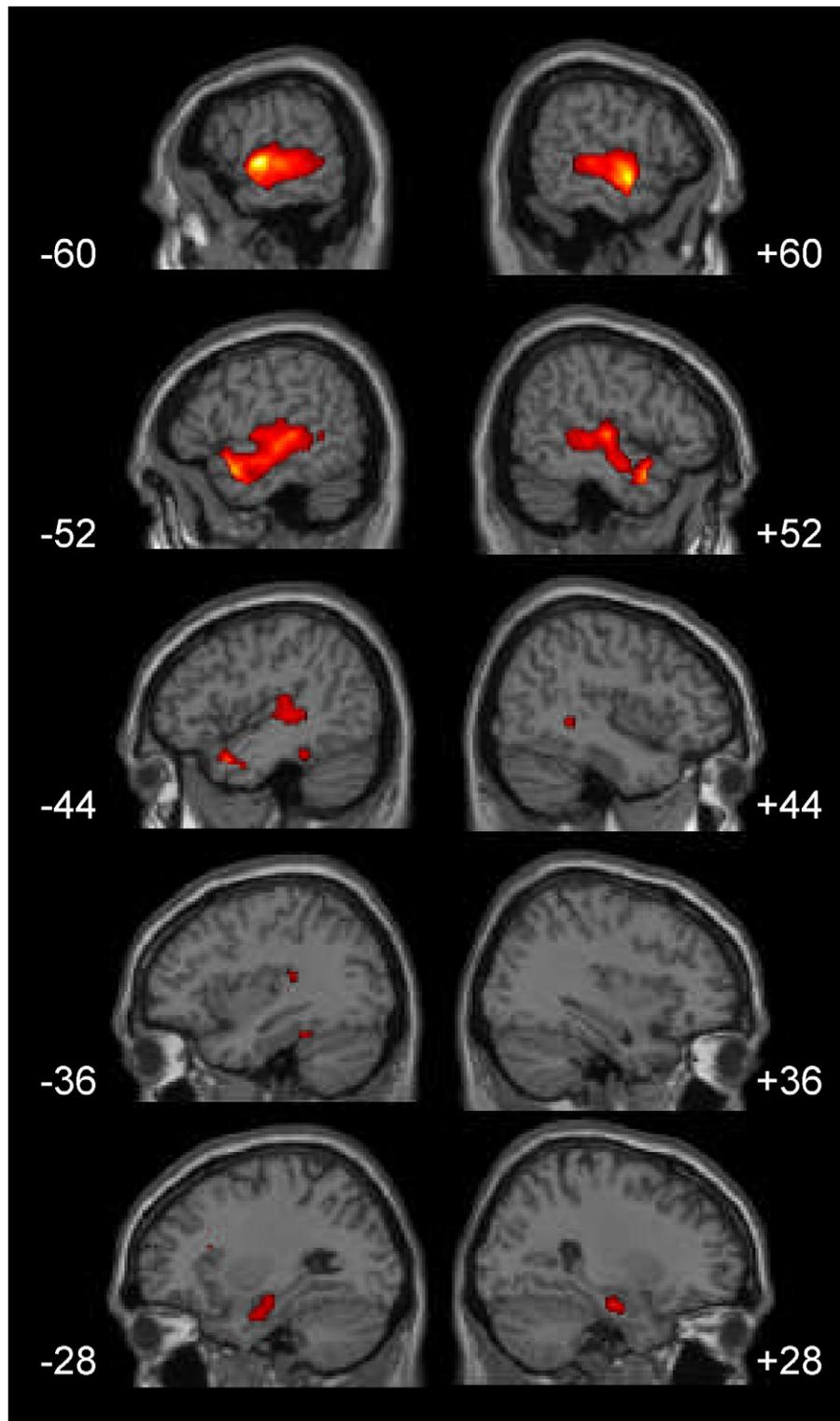


Fig. 3. Speech–noise: significant activations shown at $p < .001$ uncorrected for clusters that reach $p < .05$ corrected (Z co-ordinate shown at the bottom of each slice, L=L, superimposed on the normalised high-resolution T1-weighted scan of a single individual made available with SPM2).

(subordinate) meaning is used. The results of these different analyses are summarised in Table 3 for the syntactic and semantic ambiguities combined, as well as for each type of ambiguity individually.

To look for a main effect of ambiguity (irrespective of its linguistic properties) we combined the sets of syntactic and semantic high-ambiguity sentences and compared them to the set of low-ambiguity sentences. For this overall ambiguity contrast there were

no clusters that reached corrected significance, although there was a marginally significant cluster in the posterior, inferior portion of the pars opercularis (Table 3: 1a). The reverse contrast showed that no brain regions were significantly more active for the low-ambiguity sentences compared with the high-ambiguity sentences (Table 3: 1b).

A significant negative correlation with dominance (more activation for sentences that used the non-preferred meaning, combined

Table 2
Significant clusters of activation for speech–noise.

	Brodman area	<i>p</i> (corrected) at cluster level	Cluster size	<i>p</i> (corrected) at voxel level	Z-score	X	Y	Z
Left STG	22	.001	2592	.001	6.35	−60	−10	0
L Anterior STS	21/38			.001	5.63	−48	10	−22
L Anterior STS	38			.002	5.59	−52	8	−20
L Anterior STG	38			.006	5.37	−50	12	−16
L STS	21/22			.009	5.31	−64	−22	0
L STS	22/21			.032	5.07	−54	−6	−14
L STS	21/22			.049	4.99	−52	−30	2
Right STG	22	.001		1644	.001	5.99	60	−4
R Anterior STS	21		.004		5.45	52	6	−22
R STG	22		.019		5.17	66	−18	−2
R STG	22		.019		5.17	52	−18	2
L Hippocampus		.005	137	.805	4.13	−24	−12	−20
R Hippocampus		.03	97	.835	4.09	30	−14	−20

Clusters selected using cluster-level threshold of *p* < .05 corrected with voxel-level threshold of *p* < .001 uncorrected. Within each cluster the most significant peak is reported together with any other peaks more than 4 mm apart that reach corrected significance at the voxel level (*p* < .05). STS: superior temporal sulcus, STG: superior temporal gyrus. Co-ordinates given in MNI space.

across ambiguity types) was seen in posterior LIFG (Table 3: 1c). No regions showed a significant positive correlation with dominance (Table 3: 1d).

2.3. *Effects of ambiguity and dominance: syntactic ambiguities*

In addition to these analyses which include both syntactic and semantic ambiguity, we also conducted separate analyses of these two types of ambiguity to determine whether any additional brain regions were recruited by either type of ambiguity that did not emerge in the combined analysis.

The contrast between the syntactic high and low-ambiguity sentences showed no significant activations (Table 3: 2a). Similarly, the reverse contrast between low- and high-ambiguity

sentences showed no significant activations (Table 3: 2b). In contrast, three clusters showed a significant negative correlation with syntactic dominance such that they were more active when the non-preferred meaning was used (Table 3: 2c; Fig. 4). The cluster within the LIFG had its peak in pars opercularis (BA 44) and extended anteriorly into both pars triangularis (BA 45) and pars orbitalis (BA 47) (Table 3, Fig. 4). Additional clusters were located in the mid and posterior LMTG. At a slightly lower threshold this activation extended from the middle to posterior extent of the LMTG and included posterior STG and inferior parietal cortex (including both the angular and supramarginal gyri; see Fig. 4). There was also a small cluster of activation in the right STS. No brain regions showed a significant positive correlation with syntactic dominance (Table 3: 2d).

Table 3
Peak voxels from significant clusters of activation for ambiguity effects.

	Location	Brodman area	<i>p</i> Value	Cluster size	Z-score	X	Y	Z
1. All sentences (syntax and semantics combined)								
(a) High–low ambiguity	LIFG	44	.051	80	4.29	−50	8	12
(b) Low–high ambiguity	–	–	>.9	–	–	–	–	–
(c) –Dominance	LIFG	44	.01	117	4.27	−44	14	20
(d) +Dominance	–	–	>.9	–	–	–	–	–
2. Syntactic ambiguities								
(a) High–low ambiguity	–	–	>.4	–	–	–	–	–
(b) Low–high ambiguity	–	–	>.2	–	–	–	–	–
(c) –Dominance	LIFG	44	.03	88	3.79	−52	16	16
	LMTG	21	.005	124	3.94	−58	−34	−2
	pLMTG	37	.001	242	4.22	−48	−64	12
	R STS	21/22	.001	187	4.36	56	−22	−4
(d) +Dominance	–	–	>.6	–	–	–	–	–
3. Semantic ambiguities								
(a) High–low ambiguity	LIFG	44	.001	164	4.26	−52	10	12
(b) Low–high ambiguity	R Occipital	39	.02	91	4.13	40	−72	26
(c) –Dominance	–	–	>.9	–	–	–	–	–
(d) +Dominance	LSTG	22	.001	233	3.82	−48	−14	−4
	RSTS	21/22	.02	98	3.92	44	−30	2
4. Syntactic vs. semantic ambiguities								
(a) Ambiguity: syntax > semantics	–	–	>.5	–	–	–	–	–
(b) Ambiguity: semantics > syntax	LIFG	45	.09	61	3.94	−52	22	4
(c) –Dominance: syntax > semantics	LMTG	21	.001	315	4.77	−58	−30	−4
	RSTS	22	.001	667	4.45	50	−34	6
(d) –Dominance: semantics > syntax	–	–	>.9	–	–	–	–	–

Clusters selected using cluster-level threshold of *p* < .05 corrected with voxel-level threshold of *p* < .001 uncorrected. pLIFG: posterior left inferior frontal gyrus, MTG: middle temporal gyrus, pLMTG: left posterior MTG, STS: superior temporal sulcus, STG: superior temporal gyrus. Reported statistics refer to corrected cluster-level statistics.

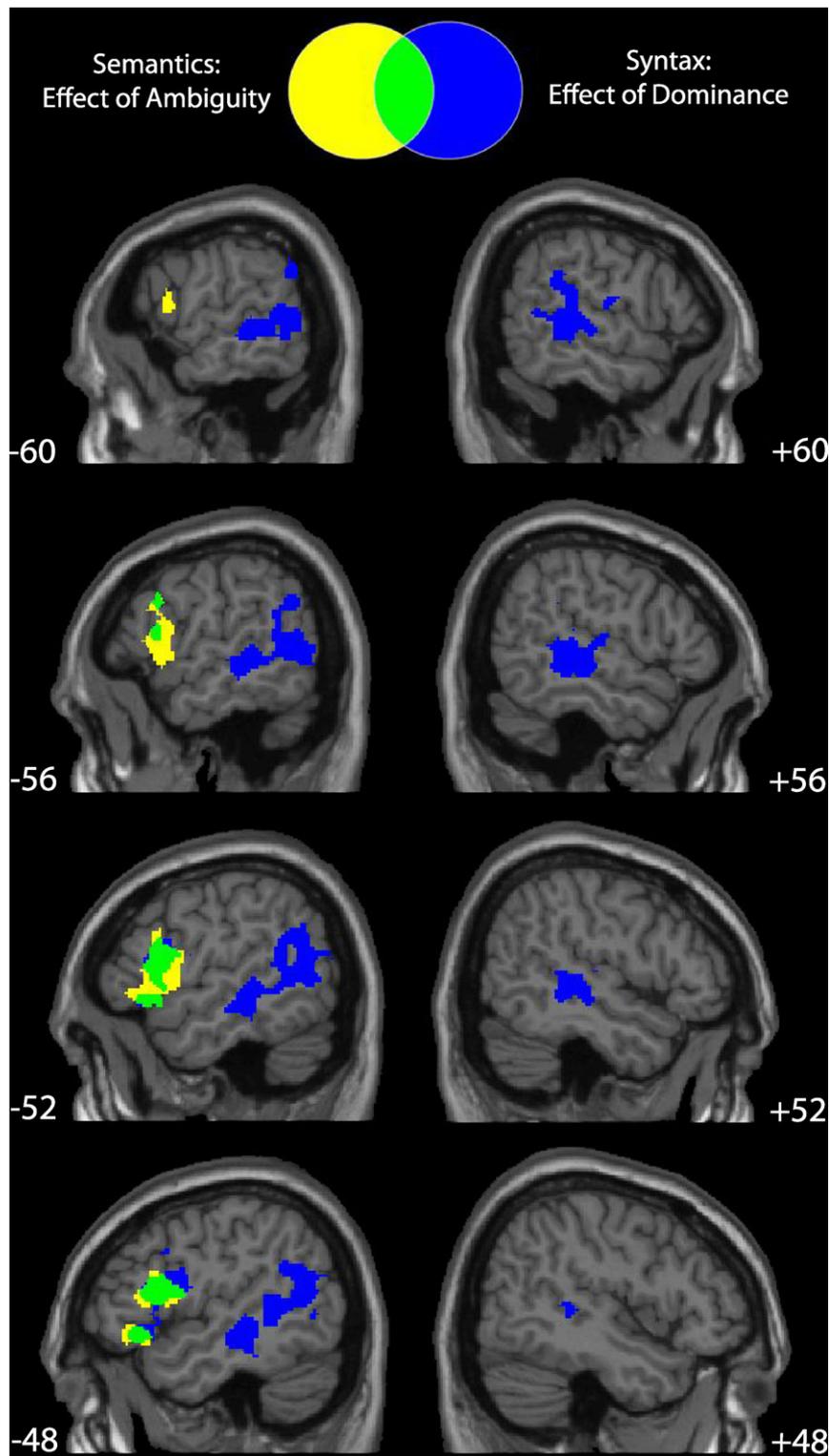


Fig. 4. Effects of semantic ambiguity and syntactic dominance: significant activations shown at $p < .01$ uncorrected for clusters that reach $p < .05$ corrected (Z co-ordinate shown at the bottom of each slice, L=L, superimposed on the normalised high-resolution T1-weighted scan of a single individual made available with SPM2).

2.4. Effects of ambiguity and dominance: semantic ambiguities

The contrast between the semantic high- and low-ambiguity sentences produced a single cluster of activation in LIFG (Table 3: 3a; Fig. 4). This voxel lies within the pars opercularis and is 3 mm from the peak of the marginally significant effect in which seman-

tic and syntactic ambiguities were combined (Table 3: 1a). As with the syntactic dominance effect, the peak of this cluster is in pars opercularis (BA 44) although it extends anteriorly into both pars triangularis (BA 45) and pars orbitalis (BA 47). At a lower threshold, there was an additional small region of activation in LMTG ($-52 -44 -4$; $p < .001$ uncorrected) which was a subset of the

LMTG activation found in the syntactic dominance correlation. No brain regions showed a significant activation for the reverse contrast between low- and high-ambiguity sentences. No brain regions were significantly negatively correlated with semantic dominance such that they were more active for those sentences in which the non-preferred interpretation was used (Table 3: 3c), but there were two clusters of cortical activation that showed a positive correlation with dominance, such that they were less active for the sentences in which the non-preferred interpretation was used (Table 3: 3d).

2.5. Effects of ambiguity and dominance: syntactic vs. semantic ambiguities

We then assessed whether the main effect of ambiguity was greater for either syntactic or semantic ambiguities by computing the interaction between degree of ambiguity (high- vs. low-) and type of ambiguity (syntactic vs. semantic). No brain regions showed a significantly larger ambiguity effect for syntax than for semantics. For the reverse contrast, a marginally significant cluster was seen within the LIFG (pars triangularis, BA 45) that showed more activation for semantic than syntactic ambiguity.

To assess whether any main effects of dominance were significantly modulated by ambiguity type we computed the direct contrast between the syntactic and semantic dominance effects. When using a whole-brain correction, the negative correlation with dominance was significantly larger for the syntactic ambiguities than the semantic ambiguities in the LMTG and the RSTS (Table 3: 4c). No brain regions showed a significantly larger negative dominance effect for semantics than syntax. We then used a voxel of interest approach to assess whether there was a significant difference between the effects of syntactic and semantic dominance within the posterior LIFG peak that showed a significant correlation with dominance (Table 3: 1a). Although the parameter estimates at this voxel of interest were greater for syntactic dominance compared with semantic dominance, there was no significant difference between the magnitude of the two types of dominance ($p > .1$ uncorrected).

Finally, an additional model was set up in which each scan was coded according to whether or not subjects performed a task on that trial. The contrast between task and no-task trials produced no significant activation differences ($p > .4$ at corrected significance for both cluster and voxel statistics). Together with the results of the speech–noise contrasts, this result confirms that the scans were sensitive to sentence comprehension processes, but were insensitive to the processes related to performing the semantic judgement task.³

3. Discussion

The aim of this study was to use semantic and syntactic ambiguity to identify the neural regions that are involved in processing the semantic and syntactic aspects of spoken utterances. These two types of ambiguity are common and natural in language and the brain systems that support them form a critical part of the speech comprehension network. Unlike many other studies which have

attempted to dissociate semantic and syntactic aspects of sentence comprehension (Friederici et al., 2000; Kang et al., 1999; Kuperberg et al., 2000; Kuperberg et al., 2003; Luke et al., 2002; Newman et al., 2003; Ni et al., 2000), all the stimuli consisted of grammatically well-formed, semantically plausible sentences. This ensured that the observed activations reflected cognitive processes that are engaged during natural sentence comprehension. In addition, the use of a sparse-imaging protocol with carefully controlled event timings ensured that we were maximally sensitive to the initial, online processing of the sentences, and that the differences between the conditions were not due to meta-linguistic task differences.

Relative to unintelligible noise, speech produced large bilateral clusters of activation centred on the STS (Fig. 3) that are consistent with previous studies that compare spoken language to signal correlated noise (Davis & Johnsrude, 2003; Rodd et al., 2005a; Tyler et al., 2005). As with previous studies of syntactic and semantic ambiguity, the results highlight the role of the LIFG in ambiguity resolution. This region showed an effect of syntactic dominance as well as an effect of semantic ambiguity. In addition syntactic dominance produced significant activation in the posterior portion of the LMTG.

We focus first on the activations observed within the LIFG. In the case of syntactic ambiguities, LIFG activation emerged as a significant negative correlation with dominance: more activation was seen for those ambiguities where the non-preferred meaning was used. This cluster of activation has its peak in the anterior portion of the pars opercularis (BA 44) and extends anteriorly into both pars triangularis (BA 45) and pars orbitalis (BA 47) (Table 3: 2c; Fig. 4). This is broadly consistent with previous fMRI studies of syntactic ambiguity. Mason et al. (2003) found an ambiguity-related increase in activation within a large LIFG region of interest (ROI) which included pars opercularis, pars triangularis and pars orbitalis (BA 44, 45, 47). They also found a dominance effect in this ROI such that more activation was seen for ambiguous sentences which used the non-preferred syntactic structure. In a second study of syntactic ambiguity, Fiebach et al. (2004) varied the delay between the ambiguity and the disambiguation as well as the syntactic complexity of the sentences. Ambiguity-related activation was seen in the superior portion of BA 44, which showed a complex interaction such that activation only increased for syntactically complex sentences and when disambiguation was delayed. This was only seen for readers who were classified as having a low memory span. The peak of this reported cluster lies in white matter directly medial to the activation reported here. Taken together, these studies confirm the importance of the LIFG in resolving syntactic ambiguities.

In the current study, LIFG activation was also seen for semantic ambiguities: the activation emerged as a main effect of ambiguity with more activation for the semantic high-ambiguity sentences compared with the low-ambiguity control sentences. As with the syntactic dominance effect, the peak of this LIFG cluster is in pars opercularis (BA 44) although it extends anteriorly into both pars triangularis (BA 45) and pars orbitalis (BA 47) (Table 3: 3a; Fig. 4). Again this is broadly consistent with previous findings. Rodd et al. (2005a) compared high-ambiguity sentences, which contained at least two ambiguous words, with well-matched low-ambiguity sentences and reported a large cluster of activation that was centred on the dorsal part of the LIFG and extended up into the inferior frontal sulcus (IFS). The peak of this cluster was within the pars opercularis, dorsal to the cluster reported here. In addition both Mason and Just (2007) and Zemleni et al. (2007) found increased LIFG activation in response to semantic ambiguities in visually presented sentences. In the case of Mason and Just (2007) the LIFG activation cluster lies within pars triangularis (BA 45) and extends inferiorly into the insula, although there is clear overlap between the anatomical locations of these clusters of activation and those

³ The results from a supplementary model in which the dominance scores were subjected to a square-root transformation showed a highly similar pattern of results. The significant clusters in the speech–noise contrast and main effects of ambiguity had the same peak voxels and there were only minor variations in the cluster sizes and z-scores. For the effects of dominance, two minor differences emerged. First, for syntactic dominance, the LMTG and LpMTG clusters merged to form a single larger cluster. Second, the RSTS cluster that showed a significant positive effect of semantic dominance was no longer significant ($p = .14$ corrected). There was also some variation in the location of the peak voxels, but all the voxels reported in Table 3 fell within significant clusters in this supplementary analysis.

reported in the current study. Zempleni et al. (2007) report an ambiguity-related peak within BA 44 which lies within the cluster reported in the current study, as well as a more dorsal peak within BA 45. There are several important methodological differences between these different studies of semantic ambiguity (e.g., modality, timing of disambiguation relative to ambiguity, nature of controls) and future work is clearly needed to determine whether the precise location of these activations within the LIFG reflects underlying specialisation within the LIFG for different aspects of ambiguity resolution. Interestingly, two of these studies (Mason & Just, 2007; Zempleni et al., 2007) have shown that the ambiguity-related LIFG activation was modulated by dominance such that more activation was seen when the non-preferred meaning was used. This is in contrast with the current study where a main effect of ambiguity was seen in the absence of a dominance effect. This difference is likely to reflect important differences in the structure of the sentences used in these different studies. We will return to this issue later.

Two important issues need to be considered with respect to the LIFG activations reported here. First, is there a reliable difference in the location of the effects for the two types of ambiguity, and second, is there a reliable difference between the types of ambiguity with respect to whether they produce a main effect of ambiguity or a correlation with dominance?

This study provides no evidence that the region of the pLIFG that is engaged in response to these two types of ambiguity depends on the linguistic nature of the ambiguity. There is almost complete overlap in the location of the semantic ambiguity cluster and the syntactic dominance cluster (see Fig. 4). In both cases, the cluster includes most of the pars opercularis (BA 44), as well as the inferior portion of the pars triangularis (BA 45) and the most posterior portion of the pars orbitalis (BA 47). The peak LIFG voxels in these two clusters are both within the pars opercularis and are 7.5 mm apart. Although it is not possible to conduct a direct statistical comparison between these two activation maps to determine whether there is a condition by location interaction (since the semantic effect is a main effect of ambiguity while the syntactic effect is a correlational effect of dominance), all of the pLIFG peak voxels identified in the above analyses show a highly similar pattern of response: the effect of semantic ambiguity is (non-significantly) greater than the effect of syntactic ambiguity, while the effect of syntactic dominance is (non-significantly) greater than the effect of semantic dominance. This finding that syntactic and semantic ambiguities recruit a similar region of the posterior LIFG is inconsistent with the view that there are separate regions within the LIFG for processing syntactic and semantic information (Dapretto & Bookheimer, 1999), but instead supports the view that the pLIFG performs processing operations that can be carried out over different kinds of inputs, in this case syntactic and semantic information. While there is some suggestion that a more anterior region of the LIFG may show more activation for semantic than syntactic ambiguities, this effect did not reach corrected significance and further studies are needed to determine whether this is a meaningful result.

However the conclusion that syntactic and semantic aspects of speech comprehension are recruiting the same region of the LIFG relies on the assumption that our design has successfully isolated these two aspects of linguistic analysis. It is therefore important to acknowledge the possibility that the syntactic ambiguities may have consequences for semantic processing. For example, in the phrase “landing planes frighten . . .” the listener is likely to use the syntactic properties of the verb “frighten” as the primary source of disambiguating information, but it is impossible to rule out the possibility that the semantics of the verb is also involved in this process. We may get similarities in areas of activation because it is almost impossible to stop syntactic manipulations from having semantic implications. Despite this, we would argue that the increased acti-

vation produced by syntactic ambiguities will primarily reflect the processes of assigning the correct syntactic structure on the basis of syntactic cues, whereas the activation produced by the semantic ambiguities will primarily reflect the process of assigning the correct semantics to individual words on the basis of semantic cues. Future studies are needed to confirm that this pattern of results can be replicated with a range of other forms of syntactic ambiguity.

The second issue that arises with respect to the observed LIFG activations is whether there is an important difference between the nature of the effects: while the semantic ambiguity effect emerged as a main effect of ambiguity (in the absence of a significant dominance effect), for the syntactic ambiguities a significant dominance effect was seen (in the absence of a main effect of ambiguity). To understand the potential implications of this pattern of results we will consider the nature of the sentence materials and the predictions made by current psycholinguistic models of ambiguity resolution. For all the sentences in this study the ambiguous phrase was preceded by contexts that were designed to contain no strong biases towards either meaning and to ensure that both interpretations were plausible. However, the results of the dominance pre-test showed that even in these relatively neutral contexts listeners often have strong preferences for one or other interpretation. For example, the syntactically ambiguous phrase “boring colleagues” is more likely to be interpreted with “colleagues” as the subject of the sentence (as in “boring colleagues are . . .”) whereas the phrase “hanging pictures” is more likely to be interpreted with “hanging” as the subject of the sentence (as in “hanging pictures is . . .”). Similarly, a semantically ambiguous phrase such as “brown hairs/hares” is much more likely to be understood as referring to the more frequent “hairs”. In contrast, other ambiguous phrases (e.g., “amusing youngsters”, “unwanted moles”) have two equally preferred interpretations. These biases are largely driven by the relative frequency of the two interpretations over the experience of the listeners, but they may also be biased to some extent by the meanings of the preceding words.⁴

For the syntactic ambiguities, these preferences have a critical effect on the degree of processing difficulty (as indexed by an increased haemodynamic response), such that activation in both the LIFG and pLMTG is negatively correlated with the sentence’s dominance score, i.e., there is most activation when the non-preferred (subordinate) interpretation is used. This finding is consistent with interactive or constraint-based models of syntactic processing (MacDonald, Pearlmutter, & Seidenberg, 1994; Tyler & Marslen-Wilson, 1977) in which the processor immediately draws on all possible sources of information (including semantics, discourse context and information about the frequencies of syntactic structures) and activates all the possible interpretations in parallel (exhaustive access). McRae et al. (1998) provide a computationally implemented model of this type, which is known as the “the competition integration model”. This model, which was analysed in detail by Green and Mitchell (2006), makes clear predictions for how these sentences are processed and demonstrates that the degree of competition (and therefore processing difficulty) in the model is maximised when information is received that is incompatible with its currently preferred interpretation. For our sentences this occurs for those sentences with low dominance scores, where the subsequent context is in conflict with the listeners’ initial prefer-

⁴ The dominance scores used in this study combine two aspects that make a particular meaning accessible to the listener: (i) the relative frequency of the two interpretations over the experience of the listener and (ii) the suitability of the meanings in the context in which it occurs. This approach is consistent with the models discussed above which assume that these two properties act jointly to affect meaning accessibility, but future studies are needed to determine whether there are important differences in how these two factors operate.

ence. Therefore this model is consistent with the observed negative correlation with dominance, and suggests that the observed activation reflects the additional processing that is required to overturn a currently preferred interpretation. The finding of a syntactic dominance effect is also consistent with an earlier study of syntactic ambiguity which reported similar effects of dominance (Mason et al., 2003).

These constraint-based interactive models of syntactic ambiguity resolution have much in common with current models of semantic ambiguity resolution, such as the Reordered Access Model (Duffy, Morris, & Rayner, 1988). According to this highly influential model, the different meanings of ambiguous words are initially retrieved in parallel and the relative frequencies (dominance) of these meanings as well as other contextual biases influence the speed with which the individual meanings are retrieved. In the case where one meaning is highly favoured on the basis of its dominance or context it will be rapidly integrated into the ongoing representation of the text without being hindered by the other meaning. If this meaning then turns out to be incorrect, the reader must reinterpret the inconsistent portion of the sentence. According to this model the sentences with low dominance scores should be associated with increased difficulty and it is therefore surprising that although a significant main effect of semantic ambiguity was observed, we did not observe a similar dominance effect for the semantic ambiguities to that seen for the syntactic ambiguities.

This finding that dominance does not appear to be the primary factor driving all ambiguity-related activity may be more compatible with the view that for these very transient semantic ambiguities listeners do not make an immediate commitment to one of the word's meanings, but instead are able to maintain all meanings of the words in mind for the brief amount of time until the disambiguating verb is encountered. According to this account, for the semantic ambiguities, LIFG activity does not reflect a reinterpretation process, but instead reflects a competitive selection process that is engaged for all ambiguous words at the point in time when the disambiguating context is encountered. However there are several reasons to be cautious when interpreting the apparent null effect for semantic dominance. First, when the significance threshold was reduced an effect of semantic dominance was observed in the pLIFG ($-42\ 18\ 22$; voxel $p < .001$ uncorrected, cluster $p = .12$ corrected). In addition, although the magnitude of the effect sizes was greater for syntactic dominance compared with semantic dominance, the direct contrast between syntactic and semantic dominance did not reveal a significant difference between the magnitudes of these effects, suggesting that there may not be a reliable difference between the ways in which the two types of ambiguity are being processed. It is also interesting to note that previous studies of semantic ambiguity, which have used visual presentation, have found a significant dominance effect (Mason & Just, 2007; Zemleni et al., 2007), although it may be important that in these studies the disambiguation was delayed until towards the end of the sentence and the interval between the ambiguity and the disambiguation was considerably longer. This pattern of results is consistent with the view that multiple activation only occurs for a relatively short time window and that in the absence of clear disambiguation readers select their preferred meaning on the basis of the relative frequencies of the meanings. Clearly, further studies are needed to clarify whether the different pattern of results seen here for the two types of ambiguity is reliable and to assess whether the relative position of the ambiguity and disambiguation does indeed play a critical role in determining how ambiguous words are processed.

In addition to this LIFG activation, there was a significant correlation between syntactic dominance and activation in a large swathe of the LMTG (including pLMTG) that extended into the

angular and supramarginal gyri, together with a smaller right hemisphere STS/MTG cluster (Fig. 4). Although the semantic ambiguities also produced some activation in LMTG, this did not reach corrected significance and was confined to the middle of the MTG and did not extend into the LpMTG. In addition the direct contrast between the dominance effects for syntactic and semantic ambiguities showed that the dominance effect was significantly stronger in this region for syntactic ambiguities. This finding is consistent with the syntactic ambiguity study by Mason et al. (2003) who found an ambiguity-related increase in activation within a large left temporal lobe ROI which included both STG and MTG.

The coactivation of the LIFG and LpMTG is a frequent finding in neuroimaging studies of both spoken (Binder et al., 2000; Dapretto & Bookheimer, 1999; Davis & Johnsrude, 2003; Ni et al., 2000; Rodd et al., 2005a; Roder et al., 2002; Stamatakis et al., 2005; Tyler et al., 2005, 2009) and written language (Cooke et al., 2002; Fiebach, Schleewsky, Lohmann, von Cramon, & Friederici, 2005; Fiebach et al., 2004; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Kuperberg et al., 2003; Luke et al., 2002). The results of this study emphasize the close functional relationship between the LIFG and the posterior portion of the temporal lobe during language comprehension and raise the question of why this LMTG activation was more extensive for syntactic ambiguities. As previously discussed it is likely that in the case of these ambiguities listeners make an early commitment to a single interpretation and therefore frequently need to reinterpret the sentence when this initial parse turns out to be incorrect. We therefore speculate that the LpMTG is additionally engaged when the listener needs to reinterpret parts a sentence that were initially misinterpreted.

Finally, we should note that although the sparse-imaging paradigm used in this experiment has several advantages in terms of allowing us to focus on online sentence processing under conditions in which sentences are both well-formed and easy to perceive, we cannot rule out the possibility that some aspects of ambiguity resolution are not being detected either because they are too transient to detect using a haemodynamic measure, or because their timing is such that they are missed by the "snap-shot" scans used in sparse-imaging designs. The results also need to be replicated with other types of syntactic ambiguity to ensure that the results do not reflect some idiosyncratic property of the construction that was used and the nature of our low-ambiguity controls.

In summary, these results confirm that meaningful speech activates a large left-dominant network of fronto-temporal brain regions. Within this network, activation in left inferior frontal and posterior temporal regions is modulated by the presence of temporary ambiguities. We suggest that activity in the LIFG reflects multiple processes that are required to resolve ambiguity. We have argued that the high degree of overlap in the regions activated by the two types of ambiguity make it unlikely that these regions are selective for processing either semantic or syntactic information (Dapretto & Bookheimer, 1999; Friederici & Kotz, 2003; Hagoort, 2005; Ullman, 2001). In addition, the presence of a main effect of semantic ambiguity makes it unlikely that this region is specialised for reanalysing sentences that have been misinterpreted (Novick, Trueswell, & Thompson-Schill, 2005). Instead we suggest that current evidence is consistent with the view that this portion of the LIFG can be engaged to perform a number of complex cognitive operations for both semantic and syntactic information. According to this view the role of the LIFG is not restricted to ambiguity resolution but forms a core part of the language comprehension system. In addition, these data add to the growing evidence of the close functional relationship between this region of the LIFG and the posterior portion of the temporal lobe in constructing meaningful, grammatical representations of spoken language (Caplan, Hildebrandt, & Makris, 1996; Tyler & Marslen-Wilson, 2008).

Acknowledgements

This research was supported by an MRC programme grant and Newton Trust grant to LKT and fellowships from Peterhouse, Cambridge and the Leverhulme Trust to JMR. We thank the radiographers at the Wolfson Brain Imaging Unit for their help with the study.

Appendix A. Example stimuli (randomly selected subset): ambiguity underlined, disambiguating information in italics

High ambiguity	Low ambiguity
Semantics	
The housewife hoped that <u>both pears</u> <i>taste sweet</i>	The doctor suggested that painful ankles heal slowly
The old man showed them how <u>old pipes</u> <i>smoke</i> better than modern varieties	The young man informed them that traditional ciders taste better than commercial brands
In some circumstances <u>unwanted moles</u> <i>tunnel</i> through people's lawns	In some regions calm rivers meander through green valleys
Most people think that <u>new decks</u> <i>shuffle</i> more easily than older cards	Some people believe that sudden fame arrives more easily for younger performers
The mayor thought that <u>long chords</u> <i>attach</i> the new flag to the flagpole	The journal stated that prolonged illnesses weaken the immune system of the children
She quickly learnt that <u>injured calves</u> <i>moo</i> loudly	He quickly learned that green fruits ripen slowly
The expert explained that <u>other organs</u> <i>bleed</i> much more than the kidneys	The doctor suggested that young babies cry more frequently than older ones
The reporter commented that <u>modern compounds</u> <i>react</i> unpredictably	The article commented that fiction writers publish infrequently
Their father explained that <u>all spades</u> <i>trump</i> any other cards	Their mother noticed that permanent stains spoiled all the furniture
Usually <u>inexpensive chips</u> <i>shortcircuit</i> after a few years	Occasionally political poets publish in the mainstream press
She noticed that <u>colourful suites</u> <i>furnish</i> most show homes	She believed that foolish bets waste his spare cash
The plan was that <u>large polls</u> <i>survey</i> the public's opinion	The thief saw that valuable gems adorn the passengers hands
In some countries <u>hidden shells</u> <i>explode</i> in fields	In poor countries American dollars rise in value
He was informed that <u>incredible mussels</u> <i>taste</i> best in garlic sauce	She was warned that painful knees ache most in cold weather
It is important that <u>prominent boards</u> <i>advertise</i> the new supermarket	It was expected that unmistakable flags identify the new ships
Syntax	
On narrow roads reversing lorries <u>requires</u> quite a bit of experience	In many countries denouncing traitors shows quite a lot of courage
Experience had taught him that <u>boring colleagues</u> <i>damages</i> work relations	Experience had taught him that <u>neglecting risks</u> <i>irritates</i> safety experts
In warfare <u>advancing armies</u> <i>takes</i> a long time	At work <u>impressing employers</u> <i>improves</i> your job prospects
She had heard that <u>breeding pigeons</u> <i>make</i> a lot of noise	He was annoyed that <u>persisting problems</u> <i>waste</i> a lot of time
Her brother told her that <u>drowning kittens</u> <i>need</i> rescuing quickly	Her mother told her that <u>crying babies</u> <i>need</i> feeding soon
He will never learn that <u>roasting potatoes</u> <i>taste</i> best with olive oil	She did not realise that <u>despairing friends</u> <i>need</i> help with their problems
Early in the morning <u>clinking bottles</u> <i>annoys</i> all the neighbours	All through the year <u>preventing weeds</u> <i>infuriates</i> nearly all gardeners

Appendix A (Continued)

High ambiguity	Low ambiguity
In the long run <u>cheating partners</u> <i>causes</i> a lack of trust	In the short term <u>bandaging wounds</u> <i>prevents</i> a loss of blood
The tourist was surprised that <u>overtaking buses</u> <i>beep</i> their horns loudly	The umpire was disappointed that <u>competing teams</u> <i>break</i> the rules regularly
She told him that <u>shrugging shoulders</u> <i>express</i> boredom	He told her that <u>differing ideas</u> <i>stimulate</i> debate
Not every teenager thinks that <u>worrying parents</u> <i>is</i> really acceptable	Not every student thinks that <u>acquiring debts</u> <i>is</i> completely inevitable
The young woman found that <u>amusing youngsters</u> <i>entertain</i> the audience	The young employees believe that <u>interfering bosses</u> <i>hinder</i> their work
When on holiday <u>visiting relatives</u> <i>drink</i> lots of tea	When at school <u>sneering boys</u> <i>irritate</i> all the teachers
Her daughter was impressed that <u>playing cards</u> <i>look</i> shiny when they are new	The woman was aware that <u>glittering jewels</u> <i>appear</i> expensive when they are clean
The manager told them that <u>developing ideas</u> <i>attracts</i> new business from overseas	The headmaster told her that <u>marking essays</u> <i>demand</i> much time from teachers

References

- Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). *The CELEX Lexical Database (CD-ROM). Linguistic data consortium*. Philadelphia, PA: University of Pennsylvania. [Ref type: Generic]
- Binder, J. R., Frost, J. A., Hammel, T. A., Bellgowan, P. S., Springer, J. A., Kaufman, J. N., et al. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, *10*, 512–528.
- Buchel, C., Holmes, A. P., Rees, G., & Friston, K. J. (1998). Characterizing stimulus-response functions using nonlinear regressors in parametric fMRI experiments. *NeuroImage*, *8*, 140–148.
- Caplan, D., Alpert, N., & Waters, G. (1999). PET studies of syntactic processing with auditory sentence presentation. *NeuroImage*, *9*, 343–351.
- Caplan, D., Hildebrandt, N., & Makris, N. (1996). Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension. *Brain*, *119*(Pt 3), 933–949.
- Cooke, A., Zurif, E. B., DeVita, C., Alsop, D., Koenig, P., Detre, J., et al. (2002). Neural basis for sentence comprehension: Grammatical and short-term memory components. *Human Brain Mapping*, *15*, 80–94.
- Crinion, J. T., Lambon Ralph, M. A., Warburton, E. A., Howard, D., & Wise, R. J. S. (2003). Temporal lobe regions engaged during normal speech comprehension. *Brain*, *126*, 1193–1201.
- Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, *24*, 427–432.
- Davis, M. H., & Johnsrude, I. S. (2003). Hierarchical processing in spoken language comprehension. *Journal of Neuroscience*, *23*, 3423–3431.
- Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, *92*, 145–177.
- Duffy, S. A., Morris, R. K., & Rayner, K. (1988). Lexical ambiguity and fixation times in reading. *Journal of Memory and Language*, *27*, 429–446.
- Fiebach, C. J., Schlesewsky, M., Lohmann, G., von Cramon, D. Y., & Friederici, A. D. (2005). Revisiting the role of Broca's area in sentence processing: Syntactic integration versus syntactic working memory. *Human Brain Mapping*, *24*, 79–91.
- Fiebach, C. J., Vos, S. H., & Friederici, A. D. (2004). Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers. *Journal of Cognitive Neuroscience*, *16*, 1562–1575.
- Forster, K. I., & Forster, J. C. (2003). A Windows display program with millisecond accuracy. *Behavior Research Methods Instruments & Computers*, *35*, 116–124.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*, 78–84.
- Friederici, A. D. (2006). The neural basis of sentence processing: Inferior frontal and temporal contributions. In Y. Grodzinsky, & K. Amunts (Eds.), *Broca's region* (pp. 196–217). Oxford: Oxford University Press.
- Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: Functional imaging and lesion studies. *NeuroImage*, *20*(Suppl. 1), S8–S17.
- Friederici, A. D., Meyer, M., & von Cramon, D. Y. (2000). Auditory language comprehension: An event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language*, *74*, 289–300.
- Friederici, A. D., Ruschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, *13*, 170–177.
- Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). How many subjects constitute a study? *NeuroImage*, *10*, 1–5.
- Green, M. J., & Mitchell, D. C. (2006). Absence of real evidence against competition during syntactic ambiguity resolution. *Journal of Memory and Language*, *55*, 1–17.

- Grodzinsky, Y., & Friederici, A. D. (2006). Neuroimaging of syntax and syntactic processing. *Current Opinion in Neurobiology*, 16, 240–246.
- Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, 9, 416–423.
- Hall, D. A., Haggard, M. P., Akeroyd, M. A., Palmer, A. R., Summerfield, A. Q., Elliott, M. R., et al. (1999). "Sparse" temporal sampling in auditory fMRI. *Human Brain Mapping*, 7, 213–223.
- Hall, D. A., Summerfield, A. Q., Goncalves, M. S., Foster, J. R., Palmer, A. R., & Bowtell, R. W. (2000). Time-course of the auditory BOLD response to scanner noise. *Magnetic Resonance in Medicine*, 43, 601–606.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92, 67–99.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8, 393–402.
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114–116.
- Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences*, 6, 350–356.
- Kang, A. M., Constable, R. T., Gore, J. C., & Avrutin, S. (1999). An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *NeuroImage*, 10, 555–561.
- Kuperberg, G. R., Holcomb, P. J., Sitnikova, T., Greve, D., Dale, A. M., & Caplan, D. (2003). Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. *Journal of Cognitive Neuroscience*, 15, 272–293.
- Kuperberg, G. R., McGuire, P. K., Bullmore, E. T., Brammer, M. J., Rabe-Hesketh, S., Wright, I. C., et al. (2000). Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: An fMRI study. *Journal of Cognitive Neuroscience*, 12, 321–341.
- Luke, K.-K., Liu, H.-L., Wai, Y.-Y., Wan, Y.-L., & Tan, L. H. (2002). Functional anatomy of syntactic and semantic processing in language comprehension. *Human Brain Mapping*, 16, 133–145.
- McRae, K., Spivey-Knowlton, M. J., & Tanenhaus, M. K. (1998). Modeling the influence of thematic fit (and other constraints) in on-line sentence comprehension. *Journal of Memory and Language*, 38, 283–312.
- MacDonald, M. C., Pearlmuter, N. J., & Seidenberg, M. S. (1994). The lexical nature of syntactic ambiguity resolution. *Psychological Review*, 101, 676–703.
- Mason, R. A., & Just, M. A. (2007). Lexical ambiguity in sentence comprehension. *Brain Research*, 1146, 115–127.
- Mason, R. A., Just, M. A., Keller, T. A., & Carpenter, P. A. (2003). Ambiguity in the brain: What brain imaging reveals about the processing of syntactically ambiguous sentences 3. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 1319–1338.
- Narain, C., Scott, S. K., Wise, R. J., Rosen, S., Leff, A., Iversen, S. D., et al. (2003). Defining a left-lateralized response specific to intelligible speech using fMRI. *Cerebral Cortex*, 13, 1362–1368.
- Newman, S. D., Just, M. A., Keller, T. A., Roth, J., & Carpenter, P. A. (2003). Differential effects of syntactic and semantic processing on the subregions of Broca's area. *Cognitive Brain Research*, 16, 297–307.
- Ni, W., Constable, R. T., Mencl, W. E., Pugh, K. R., Fulbright, R. K., Shaywitz, S. E., et al. (2000). An event-related neuroimaging study distinguishing form and content in sentence processing. *Journal of Cognitive Neuroscience*, 12, 120–133.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive Affective & Behavioral Neuroscience*, 5, 263–281.
- Palmer, A. R., Bullock, D. C., & Chambers, J. D. (1998). A highoutput, high-quality sound system for use in auditory fMRI. *NeuroImage*, 7, S359 [Ref type: Generic].
- Rayner, K., & Duffy, S. A. (1986). Lexical complexity and fixation times in reading — effects of word-frequency, verb complexity, and lexical ambiguity. *Memory and Cognition*, 14, 191–220.
- Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005a). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex*, 15, 1261–1269.
- Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005b). The timecourse of neural responses to ambiguous words: An fMRI study. *Journal of Cognitive Neuroscience*, 17, B245.
- Roder, B., Stock, O., Neville, H., Bien, S., & Rosler, F. (2002). Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: A functional magnetic resonance imaging study. *NeuroImage*, 15, 1003–1014.
- Schroeder, M. R. (1968). Reference signal for signal quality studies. *Journal of the Acoustical Society of America*, 44, 1735–1736.
- Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain*, 123, 2400–2406.
- Stamatakis, E. A., Marslen-Wilson, W. D., Tyler, L. K., & Fletcher, P. C. (2005). Cingulate control of fronto-temporal integration reflects linguistic demands: A three-way interaction in functional connectivity. *NeuroImage*, 28, 115–121.
- Tyler, L. K., & Marslen-Wilson, W. D. (1977). The on-line effects of semantic context on syntactic processing. *Journal of Verbal Learning and Verbal Behavior*, 16, 683–692.
- Tyler, L. K., & Marslen-Wilson, W. (2008). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 363, 1037–1054.
- Tyler, L. K., Shafto, M. A., Randall, B., Wright, P., Marslen-Wilson, W. D., & Stamatakis, E. A. (2009). Preserving syntactic processing across the adult life span: The modulation of the frontotemporal language system in the context of age-related atrophy. *Cerebral Cortex*.
- Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. (2005). Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing. *Neuropsychologia*, 43, 1963–1974.
- Ullman, M. T. (2001). A neurocognitive perspective on language: The declarative/procedural model. *Nature Reviews Neuroscience*, 2, 717–726.
- Zempleni, M. Z., Renken, R., Hoeks, J. C., Hoogduin, J. M., & Stowe, L. A. (2007). Semantic ambiguity processing in sentence context: Evidence from event-related fMRI. *NeuroImage*, 34, 1270–1279.