

Dissociating Linguistic and Task-related Activity in the Left Inferior Frontal Gyrus

Paul Wright¹, Billi Randall¹, William D. Marslen-Wilson²,
and Lorraine K. Tyler¹

Abstract

■ The left inferior frontal gyrus (LIFG) has long been claimed to play a key role in language function. However, there is considerable controversy as to whether regions within LIFG have specific linguistic or domain-general functions. Using fMRI, we contrasted linguistic and task-related effects by presenting simple and morphologically complex words while subjects performed a lexical decision (LD) task or passively listened (PL) without mak-

ing an overt response. LIFG Brodmann's area 47 showed greater activation in LD than PL, whereas LIFG Brodmann's area 44 showed greater activation to complex words compared with simple words in both tasks. These results dissociate task-driven and obligatory language processing in LIFG and suggest that PL is the paradigm of choice for probing the core aspects of the neural language system. ■

INTRODUCTION

The left inferior frontal gyrus (LIFG) has long been considered a key region in language processing. However, the exact role that it—or subregions within it—plays within the neural language system remains a topic of considerable controversy. The subregions of particular interest here are Brodmann's areas (BAs) 44, 45, and 47 in the left hemisphere (LH), but there is little consensus about the role of each of these regions in language function. With respect to spoken language comprehension—the focus of the research presented here—a variety of processes are involved in the mapping of auditory inputs onto lexical, syntactic, and semantic representations. At one time or another, each of these subregions of LIFG has been claimed to be involved in syntactic, semantic, phonological, and/or morphological processes across the published literature (Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Fiez, 1997). Adding to the uncertainty about the functional role of these regions in language comprehension is the possibility that some LIFG subregions may have domain-general cognitive functions and not be language specific at all. Several studies have implicated subregions of the LIFG in domain-general processes such as strategic retrieval, selection between competing alternatives, and attentional control (Hampshire & Owen, 2006; Dobbins & Wagner, 2005; Thompson-Schill, Bedny, & Goldberg, 2005).

The research reported here is based on the hypothesis that a key difficulty in pinning down the functional role of the LIFG in language is the variety of different tasks used in different studies, compounded by the fact that many of

them may not be orthogonal to the linguistic manipulations included in a study and may interact with them. The possibility that many results in the imaging literature may reflect task effects as well as—or instead of—linguistic processes is particularly challenging because it is likely that task effects may show up as increased activity in the LIFG. Although detailed analyses of the component processes involved in different tasks and their effects on different cognitive domains have been fruitfully studied in the context of issues of cognitive control mechanisms (for a recent review, see Badre & Wagner, 2007), similar detailed analyses of the relationship between tasks and linguistic processes are rare in the language domain (but see Gold et al., 2006).

The issue of how task-related effects contribute to patterns of activation in language functions has been raised sporadically in the imaging literature (Giesbrecht, Camblin, & Swaab, 2004). Most such investigations, however, have adopted the strategy of comparing activation across different tasks (Nagel, Schumacher, Goebel, & D'Esposito, 2008). This approach does not completely eliminate the problem because there may be task-related effects associated with each task. To the extent that different tasks share common properties, they will produce similar task-related activity, but this does not eliminate the possibility that these are still task-related effects. To avoid these potential problems, we have taken a different approach in which we compare patterns of activation in response to spoken words, both when subjects are performing an explicit task and when they have no overt task, and are simply listening to the words attentively. This latter situation is standardly called “passive listening”; however, as we argue below, we take simple listening to be intrinsically active. It is only “passive” in the sense that it does not involve an overt, task-defined response.

¹University of Cambridge, UK, ²MRC Cognition and Brain Sciences Unit, UK

Investigating the neural system involved in speech comprehension by having subjects passively listen to spoken language is founded on the assumption that comprehending spoken language is an automatized and obligatory process (Marslen-Wilson, 1975, 1987; Marslen-Wilson & Tyler, 1980). If a speaker hears speech in his or her native language, the mapping from sound to meaning is rapid (within the order of 150 msec), automatic, and obligatory. These automatic processes are revealed in neural responses to spoken words even when subjects are passively listening to speech. For example, when subjects hear spoken sentences, they activate bilateral superior/middle temporal gyri (STG/MTG) irrespective of whether they are merely passively listening or performing a task (Tyler et al., 2010; Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003). In the present study, we contrast passive listening (PL) with the lexical decision (LD) task, in which subjects make a timed word/nonword decision to a spoken input. This is one of the most commonly used tasks in psycholinguistic studies of spoken word recognition and has frequently been used in imaging studies of spoken word processing (Gold, Andersen, Jicha, & Smith, 2009; Heim, Eickhoff, Ischebeck, Supp, & Amunts, 2007; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006; Rissman, Eliassen, & Blumstein, 2003).

To investigate the relative involvement of the LIFG (and its subregions) in the obligatory and automatic neurolinguistic processes involved in mapping from sound to meaning as opposed to activations driven primarily or partially by task demands, we carried out a study in which we asked subjects to listen to spoken words, some of which were morphologically complex (regularly inflected past tense forms, such as *opened*) and some of which were morphologically simple (e.g., *cream*). Previous research has shown that processing spoken inflected words involves the LIFG, specifically, the left BA 44/45, compared with morphologically simple words (Tyler et al., 2005). This left frontal activation seems, furthermore, to specifically reflect the operations of neural subsystems for morphosyntactic analysis, activated by linguistically complex inputs (Marslen-Wilson & Tyler, 2007). We compared activation to these words when subjects were either carrying out an LD task or when they simply listened attentively to the words. Because previous studies have shown that BA 47 is activated in the LD task (Ruff, Blumstein, Myers, & Hutchison, 2008), the two manipulations of task and morphological complexity enable us to test the extent to which subregions of the LIFG are differentially responsive to a linguistic manipulation (simple vs. complex words) compared with a task manipulation (LD vs. PL).

METHODS

Subjects

We recruited 14 healthy adults aged 19–34 years ($M = 23.9$ years, $SD = 4.1$ years), each of whom gave informed

consent. The study was approved by the Suffolk Research Ethics Committee. Major exclusion criteria included bilingualism, left-handedness, MR contraindications, neurological or hormonal disorders, recent treatment (within 1 year) for psychiatric disorders, major head trauma, stroke, or dyslexia. All volunteers were screened to exclude neurological or psychiatric illness and had not been taking psychoactive medication for at least 5 months before scanning.

Design and Materials

The stimuli in the LD experiment included 80 real words, 40 of which were morphologically complex, regularly inflected past tense forms (e.g., *carved*, *played*). The other 40 were morphologically simple (e.g., *cream*). To minimize the potential processing complexity of these simple words, none of them contained an embedded word; that is, none of them were words like *claim*, which contains within it the word *clay*. The past tense and the simple conditions were matched on word form frequency, lemma frequency, familiarity, and imageability (see Table 1). Simple and complex words were matched on constant-vowel (CV) structure and were all monosyllables. Complex words were slightly longer than simple words, $t(78) = 2.7$, $p < .01$. The 60 nonwords were matched to the structure of the real words.

As a baseline condition, we used acoustic stimuli, which were constructed to share the complex auditory properties of speech without triggering phonetic interpretation. This was envelope-shaped “musical rain” (MuR; Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006) in which the long-term spectro-temporal distribution of energy is matched to that of the corresponding speech stimuli. This provided a baseline to control for nonspeech auditory processing for both LD and PL. Contrasting speech with MuR reveals the language network with nonspeech auditory processing removed. Half the MuR items were low-pass filtered and half were not. In this way, we created a set of low-frequency and high-frequency items for subjects to make a high/low-frequency judgment to each MuR stimulus during LD. Subtracting MuR from speech in LD enables us to control for general components of a decision task (e.g., left motor cortex activation related to a button press). We also included 40 trials of silence, and the presentation of all items was pseudorandomized so that there was a maximum of three consecutive trials of any one condition.

The stimuli for the PL study consisted of 40 monosyllabic real words not heard during LD, which matched the LD items in their structure, with 20 regular past tense items and 20 simple words. The simple and complex words were matched on word form frequency, lemma frequency, imageability, and familiarity, and they matched the items in the LD task on these factors (Table 1). As with the LD items, the past tense items were slightly longer than the simple words, $t(38) = 2.50$, $p < .05$. There were also 20 MuR stimuli and 20 null events, and items in the conditions were pseudorandomized. Stimuli were recorded onto a flash

Table 1. Descriptive Statistics of the Stimuli in LD and PL

<i>(A) Stimulus Statistics and Comparisons between Tasks</i>						
	<i>LD</i>		<i>PL</i>		<i>LD vs. PL</i>	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>T(58)</i>	<i>p</i>
<i>Complex</i>						
Duration (msec)	621	64	618	58	0.19	<.05
WFF	24	31	31	39	-0.76	<.05
LF	65	95	80	117	-0.52	<.05
Fam	499	83	505	99	-0.26	<.05
Image	441	127	440	76	0.03	<.05
<i>Simple</i>						
Duration (msec)	581	69	563	79	0.88	<.05
WFF	25	31	32	66	-0.63	<.05
LF	36	56	40	71	-0.19	<.05
Fam	491	95	476	88	0.57	<.05
Image	452	145	437	135	0.39	<.05
<i>(B) Comparisons between Complex (Past Tense) and Simple Words for Each Task</i>						
<i>Complex-Simple</i>	<i>LD</i>		<i>PL</i>			
	<i>T(78)</i>	<i>p</i>	<i>T(38)</i>	<i>p</i>		
Duration	2.7	<.001	2.5	<.05		
WFF	-0.1	>.05	-0.1	>.05		
LF	1.6	>.05	1.3	>.05		
Fam	0.4	>.05	1.0	>.05		
Image	-0.4	>.05	0.1	>.05		

LD = lexical decision task; PL = passive listening; WFF = word form frequency; LF = lemma frequency; Fam = familiarity; Image = imageability.

disk at 44,100 Hz and transferred to computer and down sampled to 22,050 Hz using CoolEdit software (Syntrillium Software Corp., Phoenix, AZ). Each item was stored in a single file in .wav format.

Procedure

Participants listened to the stimuli through Etymotic tube headphones worn underneath ear-protecting headphones. In the LD task, they were asked to make a yes/no LD to each word or nonword and to make a high-frequency/low-frequency yes/no decision to each MuR stimulus. They made their decisions via an MRI-compatible button box. They did not respond to the null events. Trials were presented in a fixed, pseudorandom order with the silent null events interspersed between the other trials to jitter the SOA and

to improve the detectability of the hemodynamic response (Burock, Buckner, Woldorff, Rosen, & Dale, 1998). In PL, participants were asked to listen carefully to the items. LD and PL were presented during separate scans on the same day, with structural scans acquired between the two functional scans.

Image Acquisition and Preprocessing

We used a sparse imaging method to avoid scanner noise while participants were listening to the spoken items (Hall et al., 1999). Auditory stimuli were presented in a 1.4-sec silent period that occurred between each 2-sec scan such that scanning started 1020–1300 msec after stimulus onset. Participants were scanned at the MRC Cognition and Brain Sciences Unit, Cambridge, with a Siemens 3-T Tim Trio MRI scanner (Siemens Medical Solutions, Camberley, UK). Each functional volume consisted of 32 oblique axial slices, 3 mm thick with interslice gap of 0.75 mm, and in-plane resolution of 3 mm. Slices were angled such that those covering MTG passed superior to the eyes to prevent eye motion from obscuring activation in language areas; field of view = 192 × 192 mm, repetition time = 3.4 sec, acquisition time = 2 sec, TE = 30 msec, flip angle 78°.

The fMRI data were preprocessed and analyzed using SPM5 software (SPM5, Wellcome Institute of Cognitive Neurology, London, UK). Preprocessing comprised within-subject realignment, spatial normalization of images to a template in standard space, and spatial smoothing using an 8-mm Gaussian kernel. Unified normalization was used, which improves upon standard normalization by correcting for magnetic field inhomogeneity and by fitting the image to the template using only brain tissue (Ashburner & Friston, 2005).

Imaging Analysis

Following preprocessing, task-related responses were localized for each subject using a voxel-wise general linear model. The model comprised predicted response time series for each stimulus type, generated by convolving stimulus onset times with a canonical hemodynamic response. In addition, the six movement parameters calculated during realignment were included to reduce the probability of obtaining false positives that could be attributed to residual movement-related artifacts. We removed low-frequency noise by applying a high-pass filter with a period of 128 sec. The relative contributions of each stimulus were used to calculate contrasts of interest, and the resulting contrast images were entered into group random effects analyses.

At the group level, effects across tasks and word types were tested by within-subjects ANOVA on task (LD vs. PL) and complexity (past tense vs. simple words). The ANOVA was implemented as a flexible factorial analysis in SPM5

with subject as an explicit variable, and the four cells of the 2×2 design were filled using contrast images for each condition versus MuR. The nonindependence between factor levels was accounted for using nonsphericity correction. The main effects of task and complexity and their interaction were assessed using F tests.

Results were subject to voxel-level thresholds of $p < .001$ uncorrected, and within this we report clusters that yielded corrected cluster-level significance of $p < .05$. Where noted, we report marginal effects in regions of a priori theoretical interest. Cluster-level statistics were calculated for simple t tests using random field theory in SPM5 and for F tests in the ANOVA using the nonstationarity toolbox (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004). The Montreal Neurological Institute (MNI) coordinates are reported. To identify anatomical regions within clusters and cluster maxima, the MNI coordinates were converted to Talairach equivalent coordinates (Brett, 2001). Anatomic labels and BAs were identified using the Talairach atlas (Talairach & Tournoux, 1988) and confirmed using the template developed by the van Essen lab as implemented in MRICron (<http://www.MRIcron.com>/MRICron).

RESULTS

The analysis of the LD data showed the typical main effect of lexical status with nonwords (mean RT = 979 msec) being responded to more slowly than real words (915 msec), $F(1, 135) = 18.91, p < .001$, with stimulus duration included as a covariate. RTs to simple words (mean = 960 msec) were only marginally slower than those to complex words (mean = 933 msec), $F(1, 135) = 3.26, p < .08$, and there was no interaction between lexical status and complexity ($F < 1$). Subjects made very few errors ($< 10\%$), and there were no differences in error rates between any of the conditions (all F s < 1).

In the analysis of the fMRI data, a conjunction analysis combining the real-word data from both LD and PL tasks showed that words compared with MuR activated bilateral STG/MTG (Figure 1 and Table 2). The LH cluster was larger (572 voxels) than that in the RH (340 voxels) with a left superior temporal gyrus (LSTG)/MTG peak in $-60 -3 -6$ and a right superior temporal gyrus (RSTG)/MTG peak in $63 -18 -3$. This is the neural network typically activated when hearing spoken words (Tyler & Marslen-Wilson,

Figure 1. Brain regions showing greater activation to speech over musical rain baseline (MuR) during both tasks (A), lexical decision (LD) task only (B), and passive listening (PL) only (C). Voxel-level $p < .001$, cluster-level $p < .05$ corrected. Activation shown in inferior frontal and peri-sylvian temporal regions.

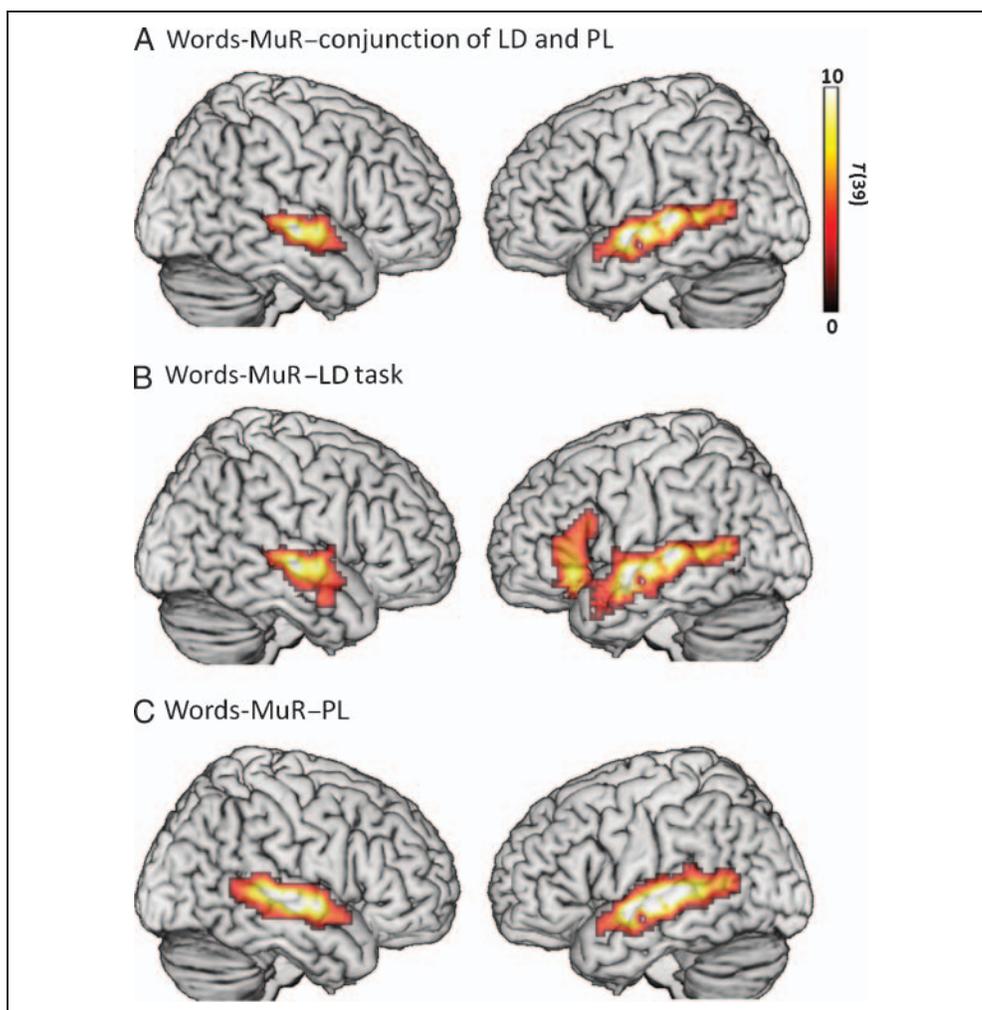


Table 2. Brain Regions Showing Greater Activation for Speech over MuR Baseline

Cluster Location	Cluster		Voxel		MNI			BA
	<i>p</i> _{corr}	Size	<i>p</i> _{uncorr}	Z	x	y	z	
<i>Words-MuR (Conjunction of LDT and Passive)</i>								
L MTG	<.001	572	<.001	>8.00	-60	-3	-6	21
			<.001	>8.00	-60	-30	3	21
			<.001	7.35	-63	-18	-3	22
R STG	<.001	340	<.001	7.36	63	-18	-3	22
			<.001	6.85	60	-6	-3	22
			<.001	6.22	54	-27	3	22

*p*_{corr} cluster-level statistic corrected using Random Field Theory; size is measured in 27 mm³ voxels. Whole cluster and peak voxel statistics are presented in boldface; secondary peaks >8 mm apart are presented in plain text. MuR = musical rain; MNI = Montreal Neurological Institute coordinates; BA = Brodmann's area; MTG = middle temporal gyrus; STG = superior temporal gyrus.

2008; Crinion et al., 2003). When each task was analyzed separately, the LD task generated activity in BA 47 in the LH whereas PL did not (see Figure 1).

In an ANOVA, comparing task (LD, PL) and complexity (simple words, morphologically complex words) showed a main effect of task in the left inferior parietal lobule, right inferior parietal lobule, left posterior inferior temporal gyrus (LpITG), left BA 47, and right posterior STG/MTG (see Table 3 and Figure 2). Plots of the effects of each condition compared with MuR showed that the task-related activity in the IPL bilaterally was generated by greater activation for the hi/lo decision task in the MuR baseline compared with the yes/no decision task in LD (Figure 2A). Plots of the task effects in the left pars orbitalis (BA 47) and left inferior temporal cortex (Figure 2C) showed a different pattern of enhanced activation during the LD task over MuR and no effect during PL. Finally, there was greater activation in the right posterior STG/MTG in PL compared with the LD task, in contrast to the LSTG/MTG that was equally activated by both tasks (as shown by the conjunction analysis). These plots suggest that different regions are involved in different components of the LD task, differentiating between components involved in explicit decisions and those involved in linguistic analyses.

There was also a marginally significant (at cluster corrected *p* = .06) main effect of complexity in one of our left inferior frontal ROIs, the left pars operculum (left BA 44), consistent with results from a previous study on past tense processing (Tyler et al., 2005). This increased activation in BA 44 reflects greater activation for complex than simple words (Table 3 and Figure 3A) for both LD and PL. Although there was no significant interaction between task and complexity in left BA 44, the complexity effect was numerically larger for PL than for LD (contrast estimates: LD

complex = .25, LD simple = .02, PL complex = .81, and PL simple = -.32). We also found a significant interaction between task and complexity in LSTG/MTG and RSTG (Table 3 and Figure 3B). Both regions showed greater activity for complex compared with simple words in PL. In LD, RSTG showed the opposite effect (simple > complex), and LSTG/MTG showed no difference in activation for simple and complex words (Figure 3B).

DISCUSSION

The aim of the current experiment was to determine how far the distribution of activity across different subregions of LIFG, typically elicited in language processing studies, in fact reflects qualitatively distinct types of process, with some regions being involved in language-specific processes and others being more responsive to the cognitive demands imposed by a task. We asked this question in the context of the persistent uncertainties about the role of different subregions of the LIFG in language function and the increasing evidence that LIFG is involved in a variety of tasks across cognitive domains, suggesting that it or subregions within it have domain-general cognitive functions (Goghari & MacDonald, 2009; Snyder, Feigenson, & Thompson-Schill, 2007; Dobbins & Wagner, 2005). We independently manipulated task requirements and the morphological structure of spoken words and found distinct neural regions showing main effects of task and of morphological complexity, together with a task by complexity interaction. The LIFG showed main effects of both task and complexity, but these were associated with different subregions: the pars orbitalis (BA 47) and the pars opercularis (BA 44), respectively. This is consistent with previous research implicating BA 44 in morphosyntactic processing (Tyler et al., 2005) and suggests that activity in left BA 47 needs to be interpreted in light of the demands of the tasks involved in fMRI studies of language function and not just in terms of the linguistic properties of the stimuli.

Turning first to the main effect of morphological complexity, we manipulated morphosyntactic processing by presenting morphologically complex, regularly inflected, past-tense-inflected words and simple monomorphemic words that contained no grammatical affixes. Comparing these conditions across both LD and PL revealed activation for complex words in LIFG BA 44 that was anatomically distinct from the main effect of task in BA 47 (BA 44: Figure 3A; BA 47: Figure 2B). This finding is consistent with previous research associating BA 44 with morphosyntactic processing (Tyler et al., 2005). We interpret this finding as implicating BA 44 in the automatic segmentation of spoken words with specific morphophonological properties (which we have termed the inflectional rhyme pattern; Marslen-Wilson & Tyler, 2007; Tyler et al., 2005) into their stem and potential affix and subsequent integration of the syntactic information carried by stems and affixes.

We also found a main effect of task that revealed differences in the responsiveness to PL and LD in a set of parietal,

Table 3. Brain Regions Modulated by Task and Complexity

Cluster Location	Cluster		Voxel		MNI			BA
	p_{corr}	Size	p_{uncorr}	Z	x	y	z	
<i>(A) Main Effect of Task</i>								
L inferior parietal lobule	.010	160	<.001	5.28	-36	-51	48	40
			<.001	5.01	-45	-51	48	40
L inferior temporal gyrus	.001	137	<.001	4.98	-42	-57	-3	37
			<.001	4.30	-48	-57	-12	37
			<.001	3.49	-39	-45	-15	37
L inferior frontal gyrus (pars triangularis)	.006	80	<.001	4.63	-36	33	-12	47
			<.001	4.23	-48	27	-6	47
R inferior parietal lobule	.005	186	<.001	4.50	39	-54	48	40
			<.001	4.35	45	-45	54	40
			<.001	4.27	51	-39	51	40
R STG and MTG	.013	95	<.001	4.39	66	-36	6	22
			<.001	4.26	69	-30	-9	21
			<.001	3.69	54	-42	15	42
<i>(B) Main Effect of Complexity</i>								
L inferior frontal gyrus pars opercularis	.069	28	<.001	4.00	-54	12	9	44
<i>(C) Interaction: Task × Complexity</i>								
R Heschl's and STG	.001	166	<.001	4.35	51	-27	9	22
			<.001	3.86	60	-18	12	22
			<.001	3.74	42	-15	6	41
L Heschl's and STG	.036	43	<.001	3.91	-48	-36	18	42
			<.001	3.42	-54	-33	-9	21
			<.001	3.20	-51	-33	9	22

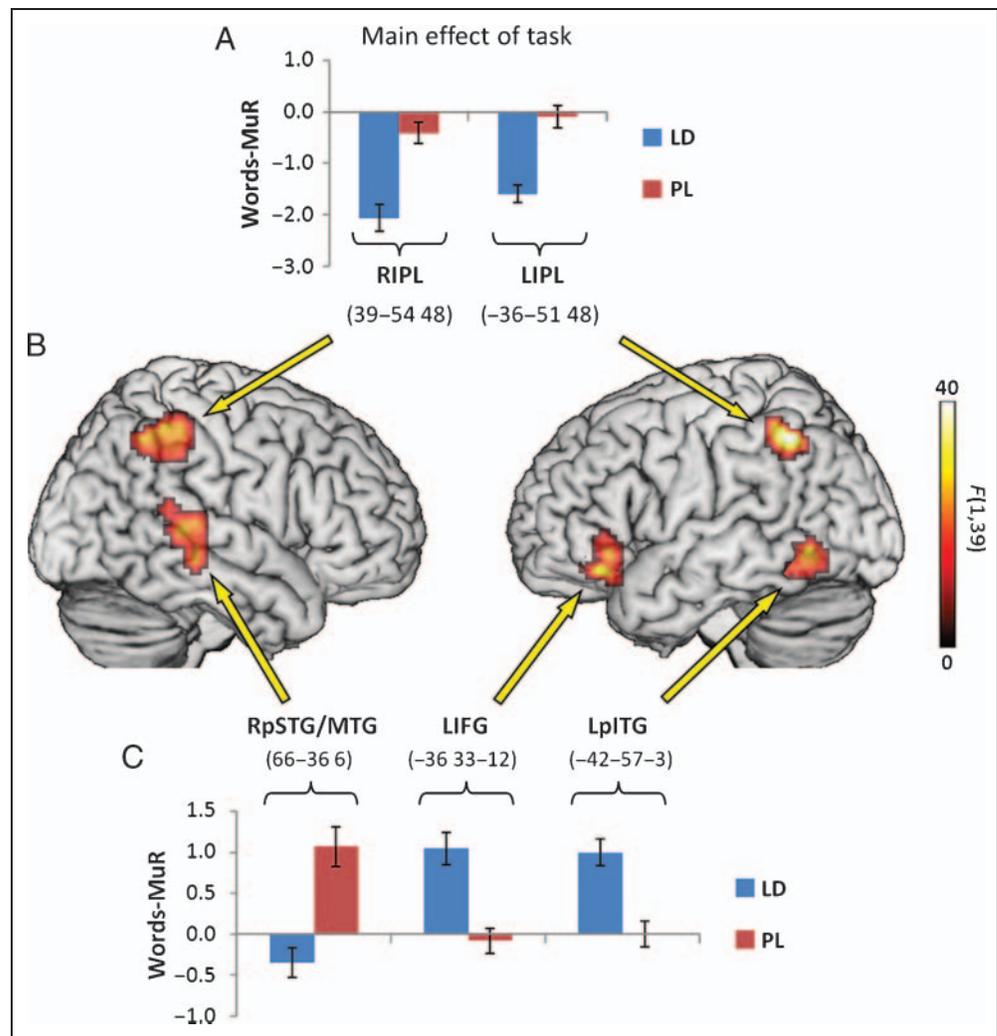
Note that F contrasts testing main effects and interactions are one sided and do not indicate direction. For details, see Results section and post hoc plots showing separate effects in Figures 2 and 3. p_{corr} cluster-level statistic corrected using random field theory. Whole cluster and peak voxel statistics are presented in boldface; secondary peaks >8 mm apart are presented in plain text. MNI = Montreal Neurological Institute coordinates; BA = Brodmann's area; MTG = middle temporal gyrus; STG = superior temporal gyrus.

frontal, and temporal regions. The plots of the effects of the LD task within these regions suggested that two main networks were implicated, each involved in different component processes: one recruiting the inferior parietal cortices bilaterally and the other involving LIFG BA 47 and LpITG. We attribute activity in bilateral parietal cortices to task-related effects, arising from MuR. This baseline condition involved a hi/lo decision that generated stronger bilateral inferior parietal activity than the word/nonword decision involved in the LD task. Left BA 47 and LpITG, which showed greater activation in the LD task compared with PL, showed a different pattern of responsiveness. These regions were more strongly activated for words compared with MuR. They were not activated more strongly

for words over MuR during PL nor were they activated for MuR compared with silence, even at the liberal threshold of $p < .01$ uncorrected. We suggest that, in the present study, these regions are activated in response to the requirements of making an LD to a spoken stimulus that could be a real word—that is, one which is a phonotactically legal sequence of speech sounds.

To make a decision about whether a sequence of sounds is a real word or not, sufficient information must be activated to indicate the presence of a real word. In natural speech, the automatic processes involved in the mapping from sound to lexical representations have been described as a continuous process of competitive activation involving multiple word candidates (Marslen-Wilson, 1975, 1987;

Figure 2. Brain regions showing a main effect of task (B) at voxel-level $p < .001$ uncorrected and cluster-level $p < .05$ corrected. Effects for each task are plotted for parietal regions in A and frontal/temporal regions in C, using contrast values for words-MuR. MuR = musical rain; LD = lexical decision task; PL = passive listening; R/LIPL = right/left inferior parietal lobule; RpSTG/MTG = right posterior superior and middle temporal gyri; LIFG = left inferior frontal gyrus; LpITG = left posterior inferior temporal gyrus. Error bars: *SEM*.



Marslen-Wilson & Tyler, 1975). Incoming phonological information activates a cohort of candidate words, which function as cohort competitors. As information accumulates over time, those candidates that continue to match the incoming sensory input continue to be activated, whereas the activation levels of those who do not decay over time, until only one candidate remains, which matches the sensory input. At that point, when a word has been differentiated from all its cohort competitors, it can be identified. Although the process of initiating a cohort of competitor words is activated purely on the basis of the sensory input, subsequent processes by which a single candidate emerges involve the interaction of phonology and semantics. Behavioral research has shown that both the phonological and the semantic properties of words (cohort size and imageability) affect the earliness with which a word can be recognized in terms of speeding response times in LD and repetition naming tasks (Tyler, Voice, & Moss, 2000).

This type of model, which assumes competition between activated candidates, is consistent with claims for the involvement of inferior frontal cortex in selection be-

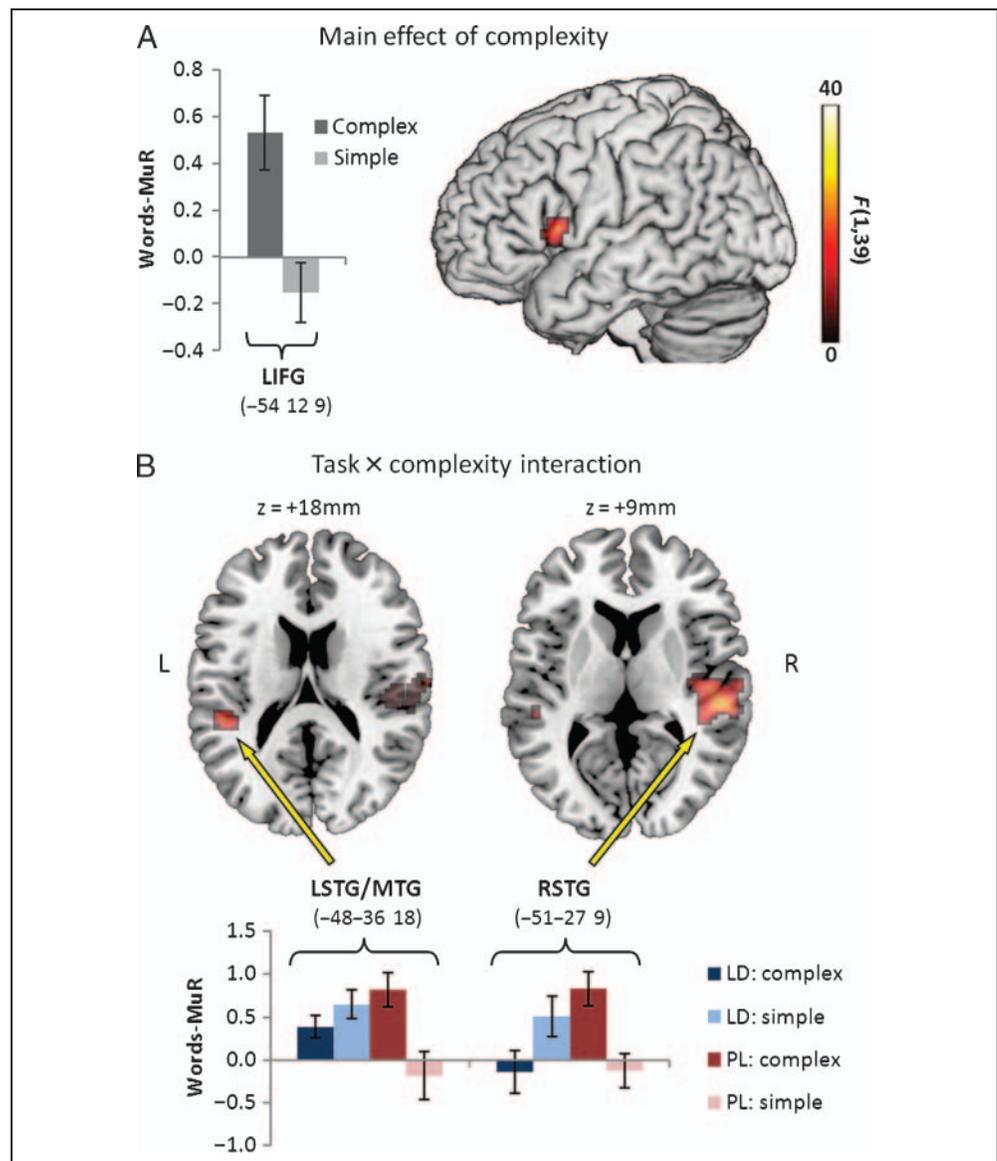
tween competing candidates in semantic tasks (Thompson-Schill, Aguirre, d'Esposito, & Farah, 1999). Recently, Badre, Poldrack, Pare-Blagoev, Inslar, and Wagner (2005) refined this hypothesis to propose a distinction between controlled retrieval processes that activate goal-relevant knowledge in a top-down biasing manner and a postretrieval selection process that resolves competition over activated candidates. Controlled retrieval of semantic information is thought to be associated with the coactivation of BA 47 and posterior temporal regions (Gold et al., 2006), whereas selection processes are thought to involve BA 45 (Badre et al., 2005). In the present study, the LD task generated increased activity in both BA 47 and LpITG, suggesting that the LD task involves processes of controlled access to semantic information. As hypothesized by Badre et al., left BA 47 may function by generating biasing signals. In the context of the LD task, this would serve to increase sensitivity to the semantic aspects of lexical processing because access to lexical meaning provides a strong cue for the existence of a real word. This may in turn boost activity in temporal cortex, known to be involved in semantic processing (Fiebach, Friederici, Smith, & Swinney, 2007; Bookheimer et al., 1998).

On this account, frontal activity is generated by processes of controlled access to semantic information, which are involved in the LD task but not in PL. Although both PL and LD involve the automatic processes of activation and competition during spoken word recognition, only LD involves the controlled retrieval of semantic information. Support for this account comes from a supplementary analysis that we carried out on the LD and PL data to determine whether left BA 47 shows greater sensitivity to a semantic variable in the LD task compared with PL. For this analysis, we calculated the number of senses for each word (obtained from WordNet; Fellbaum, 1998) and correlated this with activity in the significant clusters in left BA 47 and LpITG. The correlation with senses was calculated by including senses as a parametric modulator in the SPM model for each subject. The significance of the correlation at the group level was tested using one-sample *t* tests on contrast values for all subjects, which reflect

the strength of the modulator. This analysis showed that activity in LpITG correlated significantly with number of word senses in both tasks, LD, $t(1, 13) = -2.302, p = .038$, and PL $t(1, 13) = -2.866, p = .013$, whereas activity in left BA 47 only correlated with word senses in the LD task, left BA 47, $t(1, 13) = -2.102, p = .056$, and PL $t(1, 13) = -0.762, p = .459$.

Finally, the fact that the left pars orbitalis is not activated in PL may suggest that passively listening to speech may not involve the automatic mapping from spoken inputs onto lexical representations and the triggering of the associated linguistic operations. Two findings argue against this. First, in PL, there were strong effects associated with the processing of morphologically complex words in left pars opercularis, a process which indicates that basic processes of morphophonological and morphosyntactic analysis (Marslen-Wilson & Tyler, 2007) can be detected in the absence of an explicit task. If anything, these effects were stronger in

Figure 3. Brain regions showing a main effect of complexity (A) and a Task × Complexity interaction (B) at voxel-level $p < .001$ uncorrected and cluster-level $p < .05$ corrected. Effects for complex and simple words are plotted after collapsing across LD and PL (A) and for each task separately (B). Plots show contrast values for words-MuR. MuR = musical rain; LD = lexical decision task; PL = passive listening; R/LSTG = right/left superior temporal gyrus. Error bars: SEM.



PL than that in LD. Second, in the interaction of task and complexity, PL generated more activation than LD. Moreover, the regions activated—bilateral STG/MTG—reflect a greater effect in PL compared with LD for morphologically complex compared with simple words. These regions in left temporal and frontal cortex are very similar to those previously reported for the comparison of regularly inflected versus irregularly inflected words (Tyler et al., 2005). We have interpreted the coactivation of left BA 44 and STG in the processing of regularly inflected past tense forms as revealing the additional processing demands imposed by the decomposition of a morphologically complex spoken word into its stem and affix (Marslen-Wilson & Tyler, 2007; Tyler et al., 2005). Increased activity in BA 44 results from morphophonological parsing, whereas activity in STG reflects processes involved in the mapping of sensory inputs onto stem-based representations of morphemic form and meaning (Binder et al., 2000), which are enhanced in the case of morphologically complex words.

In conclusion, we suggest that “passive” listening offers insights into the core properties of the neural language system, separating these from the investigation of how this system is modulated by the demands for cognitive control, selection, and decision making. Although these processes may be involved in some aspects of language comprehension, it is important to be able to determine the conditions under which nonlinguistic processes routinely play a role in language and the extent to which their involvement is induced by different task manipulations. Unless we gain a better understanding of the nature of language comprehension in its “core” state, we run a serious risk of misunderstanding and misinterpreting the contribution of different regions of the LIFG to key language functions such as speech comprehension.

Acknowledgments

This research was supported by a Medical Research Council (UK) program grant to L. K. T. and an MRC-Cognition and Brain Sciences Unit funding to W. M. W. (U.1055.04.002.00001.01).

Reprint requests should be sent to Lorraine K. Tyler, Centre for Speech, Language and the Brain, Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge, CB2 3EB, UK, or via e-mail: lktyler@csl.psychol.cam.ac.uk.

REFERENCES

- Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *Neuroimage*, *26*, 839–851.
- Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*, 907–918.
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, *45*, 2883–2901.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S. F., Springer, J. A., & Kaufman, J. N. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, *10*, 512–528.
- Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T. A., Gaillard, W. D., Malow, B., & Theodore, W. H. (1998). Regional cerebral blood flow during auditory responsive naming: Evidence for cross-modality neural activation. *NeuroReport*, *9*, 2409–2413.
- Brett, M. (2001). Using the Talairach atlas with the MNI template. *Neuroimage*, *13*, S85.
- Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R., & Dale, A. M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *NeuroReport*, *9*, 3735–3739.
- 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.
- Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex*, *15*, 1768–1778.
- Fellbaum, C. (Ed.) (1998). *WordNet: An electronic lexical database*. Cambridge, MA: MIT Press.
- Fiebach, C. J., Friederici, A. D., Smith, E. E., & Swinney, D. (2007). Lateral inferotemporal cortex maintains conceptual-semantic representations in verbal working memory. *Journal of Cognitive Neuroscience*, *19*, 2035–2049.
- Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping*, *5*, 79–83.
- Giesbrecht, B., Camblin, C. C., & Swaab, T. Y. (2004). Separable effects of semantic priming and imageability on word processing in human cortex. *Cerebral Cortex*, *14*, 521–529.
- Goghari, V. M., & MacDonald, A. W. (2009). The neural basis of cognitive control: Response selection and inhibition. *Brain and Cognition*, *71*, 72–83.
- Gold, B. T., Andersen, A. H., Jicha, G. A., & Smith, C. D. (2009). Aging influences the neural correlates of lexical decision but not automatic semantic priming. *Cerebral Cortex*, *19*, 2671–2679.
- Gold, B. T., Balota, D. A., Jones, S. J., Powell, D. K., Smith, C. D., & Andersen, A. H. (2006). Dissociation of automatic and strategic lexical-semantics: Functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *Journal of Neuroscience*, *26*, 6523–6532.
- 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.
- Hampshire, A., & Owen, A. M. (2006). Fractionating attentional control using event-related fMRI. *Cerebral Cortex*, *16*, 1679–1689.
- Hayasaka, S., Phan, K. L., Liberzon, I., Worsley, K. J., & Nichols, T. E. (2004). Nonstationary cluster-size inference with random field and permutation methods. *Neuroimage*, *22*, 676–687.
- Heim, S., Eickhoff, S. B., Ischebeck, A. K., Supp, G., & Amunts, K. (2007). Modality-independent involvement of the left BA 44 during lexical decision making. *Brain Structure & Function*, *212*, 95–106.
- Marslen-Wilson, W. D. (1975). Sentence perception as an interactive parallel process. *Science*, *189*, 226–228.
- Marslen-Wilson, W. D. (1987). Functional parallelism in spoken word-recognition. *Cognition*, *25*, 71–102.
- Marslen-Wilson, W. D., & Tyler, L. K. (1975). Processing structure of sentence perception. *Nature*, *257*, 784–786.

- Marslen-Wilson, W. D., & Tyler, L. K. (1980). The temporal structure of spoken language understanding. *Cognition*, *8*, 1–71.
- Marslen-Wilson, W. D., & Tyler, L. K. (2007). Morphology, language and the brain: The decompositional substrate for language comprehension. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *362*, 823–836.
- Nagel, I. E., Schumacher, E. H., Goebel, R., & D’Esposito, M. (2008). Functional MRI investigation of verbal selection mechanisms in lateral prefrontal cortex. *Neuroimage*, *43*, 801–807.
- Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchison, E., & Britton, B. (2006). An event-related fMRI investigation of phonological-lexical competition. *Neuropsychologia*, *44*, 2209–2221.
- Rissman, J., Eliassen, J. C., & Blumstein, S. E. (2003). An event-related fMRI investigation of implicit semantic priming. *Journal of Cognitive Neuroscience*, *15*, 1160–1175.
- Ruff, I., Blumstein, S. E., Myers, E. B., & Hutchison, E. (2008). Recruitment of anterior and posterior structures in lexical-semantic processing: An fMRI study comparing implicit and explicit tasks. *Brain and Language*, *105*, 41–49.
- Snyder, H. R., Feigenson, K., & Thompson-Schill, S. L. (2007). Prefrontal cortical response to conflict during semantic and phonological tasks. *Journal of Cognitive Neuroscience*, *19*, 761–775.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Georg Thieme Verlag.
- Thompson-Schill, S. L., Aguirre, G. K., d’Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, *37*, 671–676.
- Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*, 219–224.
- Tyler, L. K., & Marslen-Wilson, W. D. (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. (2010). Preserving syntactic processing across the adult lifespan: The modulation of the fronto-temporal language system in the context of age-related atrophy. *Cerebral Cortex*, *20*, 352–364.
- Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. D. (2005). Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing. *Neuropsychologia*, *43*, 1963–1974.
- Tyler, L. K., Voice, J. K., & Moss, H. E. (2000). The interaction of meaning and sound in spoken word recognition. *Psychonomic Bulletin & Review*, *7*, 320–326.
- Uppenkamp, S., Johnsrude, I. S., Norris, D., Marslen-Wilson, W., & Patterson, R. D. (2006). Locating the initial stages of speech-sound processing in human temporal cortex. *Neuroimage*, *31*, 1284–1296.