

The Neural Bases of Sentence Comprehension: a fMRI Examination of Syntactic and Lexical Processing

Timothy A. Keller, Patricia A. Carpenter and Marcel Adam Just

Center for Cognitive Brain Imaging, Carnegie Mellon University, Pittsburgh, PA 15213, USA

One of the challenges to functional neuroimaging is to understand how the component processes of reading comprehension emerge from the neural activity in a network of brain regions. In this study, functional magnetic resonance imaging (fMRI) was used to examine lexical and syntactic processing in reading comprehension by independently manipulating the cognitive demand on each of the two processes of interest. After establishing a consistency with earlier research showing the involvement of the left perisylvian language areas in both lexical access and syntactic processing, the study produced new findings that are surprising in two ways: (i) the lexical and syntactic factors each impact not just individual areas, but they affect the activation in a network of left-hemisphere areas, suggesting that changing the computational load imposed by a given process produces a cascade of effects in a number of collaborating areas; and (ii) the lexical and syntactic factors usually interact in determining the amount of activation in each affected area, suggesting that comprehension processes that operate on different levels of language may nevertheless draw on a shared infrastructure of cortical resources. The results suggest that many processes in sentence comprehension involve multiple brain regions, and that many brain regions contribute to more than one comprehension process. The implication is that the language network consists of brain areas which each have multiple relative specializations and which engage in extensive interarea collaborations.

Introduction

Language comprehension requires the construction of coordinated representations at many levels (e.g. orthographic, phonological, semantic, thematic and syntactic) to derive the propositional content of a message. Recent research directed at determining how this integration occurs has taken one of two broad theoretical approaches to explaining its efficiency. One approach assumes that separate, informationally encapsulated modules are dedicated to the processing of different levels of linguistic representation (Fodor, 1983; Frazier, 1987). In this account, the insulation of different types of processing at early stages of comprehension allows a process, such as building the syntactic structure of the sentence, to proceed without taking into consideration other processes, such as lexical access to the semantic content of individual words. In contrast, interactive or constraint-satisfaction approaches argue that it is precisely the interaction or mutual constraints among levels that enhances efficiency (Marslen-Wilson, 1975; Just and Carpenter, 1980; McClelland, 1987). The controversy over whether modular or interactive accounts provide a better description of sentence comprehension has given rise to an accumulating body of research indicating that lexical/semantic factors do affect the speed or accuracy of syntactic/thematic processing and vice versa [for recent reviews, see (MacDonald, 1997; Tanenhaus and Trueswell, 1995)]. Although both types of models can account for such effects, the debate has led to a greater appreciation of the value of simultaneously manipulating more than one

experimental factor that influence more than one level or type of linguistic processing within language comprehension tasks. The present study combines this factorial methodology with functional brain imaging to examine how the demands made by syntactic and lexical processes are manifested in patterns of cortical activation.

A number of recent brain-imaging studies have demonstrated that, within some dynamic range, the quantitative computational demand imposed by a cognitive process modulates the amount of brain activation that occurs. In sentence comprehension (Just *et al.*, 1996), word span tasks (Grasby *et al.*, 1994), *n*-back tasks (Braver *et al.*, 1997; Rypma *et al.*, 1999) and mental rotation (Carpenter *et al.*, 1999) the amount of activation in one or more cortical regions increases with the amount of computational demand imposed by the task while the processing across conditions is kept qualitatively the same. This result was found in a study that contrasted three types of two-clause sentences—those that had conjoined active clauses (e.g. The reporter attacked the senator and admitted the error.), those with embedded subject-relative clauses (e.g. The reporter that attacked the senator admitted the error.) and those with embedded object-relative clauses (e.g. The reporter that the senator attacked admitted the error.) (Just *et al.*, 1996). While the sentence length and lexical content are equivalent, these sentences progressively increase in the amount of computational demand that they impose, whether assessed by linguistic criteria, processing time and comprehension errors, or by the processing requirements in a computational model of comprehension (Just and Carpenter, 1992). The results showed that fMRI-measured activation increased with demand in both of the classic left-hemisphere language areas, roughly Wernicke's and Broca's, and to a much lesser extent in their right-hemisphere homologues. The general suggestion is that not just one area but several participate in sentence processing and are affected by the increased processing demands imposed by the manipulation of syntactic complexity. This type of result supports the view that the allocation of cognitive processing to neural regions is not fixed but depends, in part, on task difficulty. This approach can also be used to examine how two variables that are associated with different aspects of sentence comprehension conjointly modulate the activation of each area that comprises a large-scale cortical network.

The goal of the current study was to examine the relation between syntactic and lexical processing by orthogonally manipulating two variables, syntactic complexity and word frequency, to make a sentence comprehension task more or less demanding. The general hypothesis is that increased demand will be reflected in increased activation in those regions that support the underlying processing. The focus of the current study is not just on identifying which cortical regions become activated, but on examining the distribution of activation across

regions as a function of the conjoint variations in syntactic complexity and lexical frequency.

The manipulation of syntactic complexity contrasted conjoined-active sentences (i) with object-relative clause sentences (ii) (Just *et al.*, 1996):

1. The writer attacked the king and admitted the mistake at the meeting.
2. The writer that the king attacked admitted the mistake at the meeting.

Although the contrast between sentences (1) and (2) is referred to as a difference in syntactic complexity for convenience, this structural manipulation has pragmatic consequences as well.

A second manipulation, varying the frequency of the nouns, is assumed to affect lexical access:

3. The pundit that the regent attacked admitted the gaffe at the conclave.

The less frequent nouns, such as *pundit*, *regent*, *gaffe* and *conclave*, in sentence (3) take a few hundred milliseconds longer to process than their more frequent counterparts, as in sentence (1), a robust and well-known effect (Just and Carpenter, 1980; Rayner and Duffy, 1986; Rayner and Raney, 1996; Reichle *et al.*, 1998). The time spent on a word during reading (as indexed by gaze duration) decreases with the logarithm of a word's normative frequency (Carpenter and Just, 1983). The effect typically is attributed to an access process that gradually raises to threshold the activation level of the mental representation of the word meaning from its resting level (which is lower for infrequent words), to make it accessible to other comprehension processes. Less frequent words also have a number of associated properties, including less common orthography, phonology, etc., so the manipulation of word frequency may also impact the access and manipulation of word-form representations.

Evidence that syntactic processes are supported at least in part by the left inferior frontal gyrus (Broca's area) has come from both neuropsychological and neuroimaging findings (Berndt and Caramazza, 1980; Schwartz *et al.*, 1980, 1987; Caplan 1983; Linebarger *et al.*, 1983; Grodzinsky, 1986). Patients with lesions in the pars opercularis or pars triangularis of the left inferior frontal gyrus make more comprehension errors on reversible sentences that lack semantic or pragmatic cues indicating the thematic role assignments (e.g. The girl that the boy is chasing is tall.), than on sentences with such cues (e.g. The dog that the boy is petting is tall.) (Caramazza and Zurif, 1976). Such patients also display deficits in the processing of function words that are necessary for determining syntactic phrase boundaries and assigning thematic roles to lexical items (Bradley *et al.*, 1980). However, patients with lesions outside of Broca's area also display similar patterns of deficits (Caplan and Hildebrandt, 1988; Caplan *et al.*, 1996; Dronkers *et al.*, 1996). In addition, positron emission tomography (PET) studies of resting state glucose metabolism in unselected aphasic patients with comprehension deficits have demonstrated that temporal and parietal areas, but not necessarily Broca's area, show hypo-metabolism regardless of the site of the structural lesion (Karbe *et al.*, 1989; Metter *et al.*, 1990; Kempler *et al.*, 1991). Such findings argue that the correlation between damage to Broca's area and syntactic comprehension deficits is not sufficient for localizing syntactic processing to Broca's area.

Several PET studies that have used task subtraction to attempt

to localize syntactic processing have not converged on a single region of the inferior frontal area. A plausibility judgement task contrasted syntactically simpler right-branching sentences (e.g. The child spilled the juice that stained the rug.) with more difficult center-embedded sentences (e.g. The juice that the child spilled stained the rug.) (Stromswold *et al.*, 1996). The latter condition showed a regional cerebral blood flow (rCBF) increase in the left pars opercularis region (BA 44) of Broca's area, and in the supplementary motor area, cingulate gyrus and the right middle temporal gyrus. These findings were generally replicated in another study (Caplan *et al.*, 1998), although the location within Broca's area was somewhat superior and anterior to that found elsewhere (Stromswold *et al.*, 1996), and no differences were found in the right temporal gyrus. A similar effect was found with auditory presentation, comparing the plausibility judgements of cleft-subject (e.g. It was the child that enjoyed the juice.) and more difficult cleft-object sentences (e.g. It was the juice that the child enjoyed.), although the activation was in the pars triangularis (BA 45) rather than the pars opercularis of the inferior frontal gyrus (Caplan *et al.*, 1999). These studies do implicate the inferior frontal gyrus, although there is no convergence on a particular location, perhaps in part because of the differences in particular tasks and subtractions.

Other neuroimaging studies have argued that an interactive perspective must be considered when attempting to localize syntactic processing. For example, Mazoyer *et al.* (Mazoyer *et al.*, 1993) presented participants with lists of words and with syntactically correct speech (stories) that was either meaningful, semantically anomalous or contained pseudowords. These authors reasoned the three conditions involving syntactic processing should show areas of common activation when compared with a rest condition, and should differ from a word-list condition. However, the only common areas of activation across the story conditions that did not activate in the word-list condition were the right and left temporal poles. Rather than conclude that the temporal poles were the sites of syntactic processing, these authors suggested that without the collaborative processing carried out in normal speech comprehension with meaningful stimuli, areas specialized for processes such as syntactic processing may not activate above threshold. Thus there is considerable uncertainty about which cortical areas are involved in syntactic processing, although the inferior frontal and posterior temporal areas seem strongly implicated.

The mapping of visual lexical access to cortical regions is beset by analogous uncertainties. One line of neuropsychological evidence comes from patients diagnosed with pure alexia, a disorder in which individuals read words on a letter-by-letter basis, without other related language deficits. A localization argument has been made based on the correlation of this deficit with occipital lesions in left ventral extrastriate cortex (Damasio and Damasio, 1983). However, the interpretation of this area as supporting access to the orthographic lexicon is inconsistent with studies showing that patients with pure alexia and a left extrastriate lesion are still sensitive to manipulations of orthographic structure (Bub *et al.*, 1989; Reuter-Lorenz and Brunn, 1990; Bowers *et al.*, 1996). In addition, patients with surface dyslexia, characterized by a specific deficit in reading words with irregular spelling-to-sound correspondences, such as 'pint', have been found to have lesions not in extrastriate cortex, but rather in the left superior and middle temporal gyri (Vanier and Caplan, 1985). Such patients show no corresponding deficit in reading regular words such as

Table 1

Brodman's areas activated in selected studies designed to isolate semantic processing in response to visually presented items

Study	Task comparison	Cortical region activated				
		Inferior frontal	Superior/middle temporal	Inferior parietal	Middle frontal	Extrastriate/fusiform
(Beauregard <i>et al.</i> , 1997)	read words silently versus view + signs		21/22, 19/37		B. 46	+
(Bookheimer <i>et al.</i> , 1995)	silent word reading and silent object naming versus viewing abstract drawings	47/13		39		20/21, 18/19
(Damasio <i>et al.</i> , 1996)	naming of animals, tools or famous persons versus fixation	44/45				20, B. 18/19
(Herbster <i>et al.</i> , 1997)	read words silently versus read non-words silently					20, 28, 30, 37
(Howard <i>et al.</i> , 1992)	read word aloud versus view false font string and say 'crime'		21/22			20
(Kapur <i>et al.</i> , 1994)	category judgement versus orthographic judgements	47				R. 17
(Petersen <i>et al.</i> , 1989)	generate verbs aloud versus repeat nouns	13, 47, 45			46	
(Petersen <i>et al.</i> , 1990)	activation for silent word reading versus fixation but not silent pseudoword reading versus fixation	10				
(Price <i>et al.</i> , 1994)	living/non-living judgements versus syllable judgements of real words		21	39		20, 28/38
(Pugh <i>et al.</i> , 1996)	category judgement — rhyme judgement		38, 42, 22, 21	37, 39		
(Vandenberghe <i>et al.</i> , 1996)	conjunction of activation for category judgements of words and pictures versus size	45, 11/47	21	39		20, 21/37, 19

Activation locations are in the left hemisphere unless otherwise noted. B, bilateral; R, right hemisphere.

'hint', suggesting that they have lost access to the orthographic lexicon and depend on a phonological representation of word form for lexical access.

Neuroimaging research on the location of orthographic, phonological and semantic components of lexical access also yields conflicting conclusions. When silent reading of single words is compared with viewing non-words, some studies report left-lateralized activation in inferior occipital/temporal extrastriate cortex (Petersen *et al.*, 1988, 1989, 1990; Posner *et al.*, 1988), others report bilateral activation (Price *et al.*, 1994; Bookheimer *et al.*, 1995) and others report no activation in this area (Howard *et al.*, 1992). Similarly, activation in the left posterior superior and middle temporal gyri has been reported in some silent word-reading studies (Howard *et al.*, 1992; Price *et al.*, 1994; Bookheimer *et al.*, 1995; Beauregard *et al.*, 1997), while others report no activation in this area (Posner *et al.*, 1988; Petersen *et al.*, 1989, 1990), or bilateral deactivation (Rumsey *et al.*, 1997), depending on the specific task comparisons.

Neuroimaging findings suggest a role for the inferior frontal gyrus and frontal insula in at least the phonological aspects of word reading. PET-measured changes in rCBF in this area are similar for phonological discrimination tasks involving either visual or auditory stimuli, but orthographic discrimination tasks performed on these same stimuli do not activate the region (Fiez *et al.*, 1995), and fMRI studies report activation for phonological, but not orthographic or semantic decisions (Pugh *et al.*, 1996). Additional neuroimaging work has implicated Broca's area and the left insula in the processing of words with irregular spelling-to-sound correspondences (e.g. 'cocoa') and pseudowords that can only be phonologically represented by assuming spelling-to-sound consistency. Rumsey *et al.* (Rumsey *et al.*, 1997) found activation in BA 44 for a lexical decision task, with greater activation when the decision required phonological as opposed to orthographic processing. When the task required overt pronunciation, however, activation was not found in BA 44, and was found in the insula only when the items were irregular real words. In contrast, other authors (Herbster *et al.*, 1997; Fiez and Petersen 1998) have reported activation of the inferior frontal gyrus for overt pronunciation of both pseudowords and low-frequency irregular words, but not for low-frequency regular words, suggesting that this area plays a role in not just phonologically mediated but also semantically mediated access to articulatory representations.

Table 1 summarizes a selected set of neuroimaging studies that have examined the cortical locus of semantic aspects of

lexical access. As the table indicates, there is little evidence for a one-to-one mapping of lexical semantic processing onto cortical region. It suggests instead that the relation between the component processes and regional cortical activation is complex, and that the current conceptions may not capture the underlying principles of brain organization.

The cumulating evidence suggests that language processing is accomplished by large-scale, variable and distributed patterns of activity among cooperating and interactive cortical areas. It tends not to support the hypothesis that the components of the standard psycholinguistic taxonomy of processes (e.g. phonetic, phonological, orthographic, lexical, semantic, syntactic) map onto distinct and local regions of the cortex. The data, along with the findings from other high-level tasks, suggest that multiple regions of cortex are activated by a number of different hypothetical component processes, and conversely, that single processes are associated with activation in multiple regions. When more naturalistic language-processing tasks, such as sentence comprehension, are examined relative to a baseline task that involves none of the component processes, activation is observed in numerous cortical sites that appear to collaborate in performing the comprehension (Just *et al.*, 1996; Bavelier *et al.*, 1997; Binder *et al.*, 1997). Such findings are consistent with recent reassessments of behavioral data from patient populations with lesions to well-specified cortical areas, in that the site of the lesion is poorly correlated with the behavioral deficits (Caplan and Hildebrandt, 1988).

In addition, the results seem more compatible with interactive models of language processing that stress the mutual influence and cascaded interaction of component linguistic processes (McClelland, 1987) than with models that postulate modularity of component processes. Interactive models suggest that one might expect to find interactive effects of task demand within cortical areas. For example, differences in activation resulting from the manipulation of the difficulty of one process, such as lexical access, might be expected to modulate differences in activation resulting from manipulation of the difficulty of another process, such as syntactic processing. An emerging perspective is that sentence comprehension has a number of neural bases the underlying organization of which may consist of a network of only relatively specialized and highly collaborative areas. When a brain area must deal with an additional computational demand, the impact of that extra demand may be propagated to many of its collaborating areas.

Materials and Methods

Sentence Materials

The conjoined active and object-relative constructions in the present study were based on the stimuli in a previous study (Just *et al.*, 1996). These sentences were constructed initially to have a similar structure, consisting of two clauses and a final prepositional phrase, and the same set of verbs. In half of the sentences, chosen at random, the nouns were replaced with similar words of high lexical frequency [>70 per million according to Kucera and Francis (Kucera and Francis, 1967)], and in the other half, with similar low-frequency words (<3 per million). Sentences that we judged to be either semantically anomalous or bizarre were eliminated.

Procedure

The participants' task was first to read a sentence and then to press a button to terminate the sentence presentation and initiate the presentation of a probe question, to which the participants responded by pressing one of two buttons to indicate true or false. A sentence like 'The writer that the king attacked admitted the mistake at the meeting' might be followed by a probe like 'The king admitted the mistake'. Half of the probes interrogated the first clause and half interrogated the second. Each sentence and question was self-paced, and the behavioral data included the sentence reading time, probe reading and answering time, and accuracy.

Four experimental conditions were formed by the two levels of syntactic complexity (conjoined active and object-relative sentence types) crossed with two levels of noun frequency (high and low lexical frequency). Five sentences of the same type were presented sequentially in an epoch, and there were four epochs of each of the four conditions, in addition to six epochs of a baseline condition to which all of the experimental conditions were compared. During the baseline epochs, participants fixated a centered x for 24 s. The experimental and baseline epochs were presented in a pseudo-randomized order to control for practice effects. Epochs were separated by 6 s of rest, during which participants looked at a fixation point.

Before the study began, the participants in the functional imaging study were familiarized with the task, the scanner and the fMRI procedure. During the fMRI scanning, the sentences were projected onto a translucent plastic screen attached to the roof of the bore of scanner. Participants viewed the screen through a pair of mirrors attached to the top of the head coil, with the total distance between the eyes and the screen being ~ 20 cm. The sentences subtended an angle of $\sim 30^\circ$.

An ancillary follow-up study was run to better understand how reading times were distributed across the sentences. The same sentences were presented in this study, but they were presented word-by-word on a monitor using a moving-window paradigm (Just *et al.*, 1982). The participant controlled the duration of presentation for each word by clicking a microswitch to advance to the next word in the sentence. The final word in the sentence was followed by the probe, which was displayed in full until the participant pressed one of two buttons to respond true or false.

Participants

The participants were 30 (13 females) college students or staff members at Carnegie Mellon University, with a mean age of 21.8 years ($SD = 3.4$ years). All participants, native speakers of English, were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), with a mean score of 78.1 ($SD = 16.3$). Data from eight additional participants were discarded because of excessive estimated head motion (see below) or poor comprehension performance. Each participant gave signed informed consent approved by the University of Pittsburgh and the Carnegie Mellon Institutional Review Boards. The participants in the ancillary behavioral reading-time study were 32 (16 female) right-handed college students drawn from the same population.

fMRI Acquisition Parameters

The imaging was carried out at the University of Pittsburgh Magnetic Resonance Research Center on a 3.0 T whole body General Electric Signa scanner (Thulborn *et al.*, 1996) retrofitted for echo-planar imaging (EPI) by Advanced NMR Systems (Wilmington, MA). The images were acquired

with a GE quadrature birdcage head coil. For the functional imaging, a T_2^* -sensitive gradient echo EPI pulse sequence was used with $TR = 3000$ ms, $TE = 25$ ms and a flip angle of 90° . Fourteen adjacent oblique-axial slices were acquired in an interleaved sequence, with 5 mm slice thickness, 1 mm slice gap, a 40×20 cm FOV and a 128×64 matrix size, resulting in in-plane resolution of 3.125×3.125 mm. Two sets of structural images acquired for each participant and were used to parcellate the functional images into anatomically predefined ROIs. A 124-slice axial T_1 -weighted 3D Spoiled GRASS volume scan was acquired for each participant with $TR = 25$ ms, $TE = 4$ ms, flip angle = 40° , FOV = 24 cm and a 256×256 matrix size, resulting in $0.9375 \times 0.9375 \times 1.5$ mm thick voxels. In addition, a 14-slice T_2 -weighted gradient echo EPI two-shot Instascan Multi-Echo Multi-Planar (ISMEMP) pulse sequence was acquired with the catch-and-hold option and with $TR = 10$ s, $TE = 112$ ms, flip angle = 90° , FOV = 40×20 cm and a 512×128 matrix. The slice locations and thickness were the same as those for the functional single-shot EPI data; however, this sequence provides an in-plane resolution of 0.78125×1.5625 mm and shows susceptibility artifacts similar to those in the functional acquisition sequence.

Anatomical Regions of Interest

Regions of interest (ROIs) were defined using the parcellation method originally described by Rademacher *et al.* (Rademacher *et al.*, 1992) and further refined by Caviness *et al.* (Caviness *et al.*, 1996). For each participant, a mean of the functional images was registered to the high-resolution, T_1 -weighted structural volume scan and placed in parallel alignment with the anterior commissure–posterior commissure (AC-PC) line. Limiting sulci and cerebral landmarks defining coronal planes were identified by viewing the structural images simultaneously in the three orthogonal planes. The functional images were then segmented in the axial plane by manually delineating the ROIs on each slice. Because the echo-planar functional images are more susceptible to anatomical distortions than the T_1 -weighted SPGR volume image, the ROIs were edited by superimposing them on T_2 -weighted high-resolution EPI images in order to compensate for the distortions of sulcal boundaries and anatomic landmarks introduced by the rapidly oscillating read gradient.

Figure 1 displays a schematic representation of the ROIs. In the Caviness *et al.* (Caviness *et al.*, 1996) nomenclature, the inferior parietal ROI corresponded to inferior portions of the posterior supramarginal gyrus (SGp; BA 40) and the angular gyrus (AG; BA 39). The extrastriate occipital/inferior temporal ROI included the fusiform gyrus regions (TOF and TfP; BA 36, 37 and 20) and the inferior temporal gyrus areas (TO3 and T3p; BA 37 and 20). The superior temporal ROI corresponds to the superior temporal gyrus (T1a and T1p; BA 22) and the middle temporal gyrus regions (T2a, T2p, and TO2; BA 21 and 37). The inferior frontal ROI consisted of the orbital, pars triangularis and pars opercularis portions of

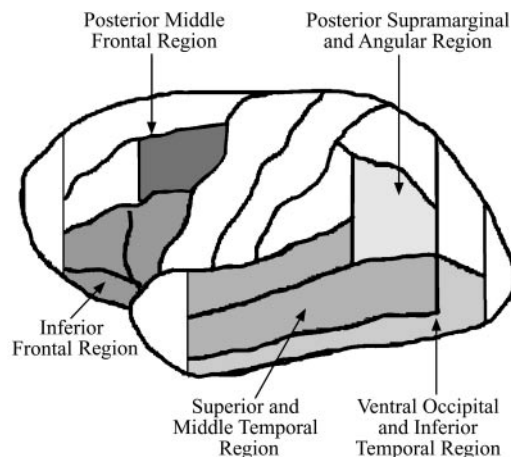


Figure 1. Schematic diagram indicating the regions of interest which were individually parcellated for each participant in the current study. The parcellation scheme follows that described elsewhere (Caviness *et al.*, 1996), but collapses a number of parcellation units into single broad ROIs (see Materials and Methods).

the inferior frontal gyrus (FOC, F3t and F3o; BA 47, 45 and 44), and also included the frontal insula region (INS; BA 13).

The anatomically defined posterior middle frontal ROI included roughly the posterior half of the middle frontal gyrus and the portion of the precentral sulcus that is superior to the inferior frontal gyrus. This area corresponds approximately to the inferior portions of Brodmann's areas 6 and 8 within the middle frontal gyrus and area 6 within the precentral sulcus. A pilot study using similar sentences suggested very little activation in the middle frontal gyrus anterior to the genu of the corpus callosum in any participant, and therefore the ROI was restricted to that portion of the gyrus posterior to this landmark. In addition, consistent with the pilot data, little reliable activation was found in any subject in the present study in the more anterior areas of dorso-lateral prefrontal cortex associated with executive processes in working memory (i.e. in areas BA 10, 9 or 46).

Data Analysis

The image preprocessing corrected for head motion and signal drift (Eddy *et al.*, 1996). The in-plane slice-wise maximum estimated displacement (an average of translations in the *x*- and *y*-dimensions and rotations around the *z*-axis) of the 30 participants never exceeded 0.2 voxels (0.625 mm), and the mean estimated displacement across participants was <0.1 voxels. The data analysis quantified the changes in the fMRI-measured signal by using a dependent measure which takes into account both the volume of activation and the percentage change in signal relative to a baseline level (Xiong *et al.*, 1998). For each voxel in the *a priori* defined ROIs, the distribution of signal in an experimental condition was compared with that for the rest condition using a *t*-test with a threshold of $t > 6.0$. This threshold was selected to give a Bonferroni-corrected alpha level of 0.01 given ~5000 voxels per participant in all ROIs and four comparisons with the baseline condition for each voxel. The integral of the percentage change in signal intensity was then calculated for each ROI and each condition by summing the change in signal intensity relative to the baseline estimate across voxels that reached the critical threshold for that condition. The data from each ROI were then submitted to a 2 (lexical frequency) by 2 (syntactic complexity) repeated-measures analysis of variance (ANOVA).

Because the experiment was participant-paced (to measure reading times and to provide a realistic sentence-processing situation), longer reading times as a function of task difficulty were expected. To ensure that any differential effects of trial times would not affect the means or variances across conditions, the analyses reported for most of the regions were applied to the activation obtained after the condition block durations were truncated to an equal length across all four combinations of conditions on an individual participant basis. The cost of this procedure is that the number of stimuli presented per condition will be slightly less for the more difficult conditions, which could end up

minimizing the contribution of the lower-level processes, such as word encoding. Because such perceptual processes are likely to influence the amount of activation in the occipital/inferior temporal extrastriate regions, the analyses for these regions involved the full condition blocks.

To reduce the possible influence of larger vessels, we excluded from analysis any voxels showing a percentage change in signal intensity >6.0% relative to the fixation condition. This constituted <1% of the voxels in all ROIs except for the inferior temporal/occipital extrastriate regions. For the left extrastriate ROI an average of 2.6% (SD = 3.4) of the voxels per participant were excluded, and an average of 2.8% (SD = 4.6) of the voxels were excluded for the right.

In the ancillary behavioral study, the data for each subject were first fit to a linear regression equation, in order to calculate the expected reading time at each word length as a function of word length, and the residual reading times were then submitted to ANOVAs (Ferreira and Clifton, 1986).

Results

Behavioral Measures: Response Times and Errors

As predicted and shown in Figure 2a, the mean sentence reading time and the question answering times both increased for more complex sentence types and sentences with less frequent nouns [$F(1,29) = 19.29, P < 0.01$ and $F(1,29) = 47.69, P < 0.01$ for sentences; $F(1,29) = 86.63, P < 0.01$ and $F(1,29) = 8.00, P < 0.01$ for probes]. Although each of the factors showed the predicted effect, their interaction was reliably under-additive for sentence reading times [$F(1,29) = 27.11, P < 0.01$], although not for the probe reading times [$F(1,29) = 2.53, n.s.$]. The overall error rates (Fig. 2b) were very low, and also showed effects of syntactic complexity [$F(1,29) = 66.86, P < 0.01$], noun frequency [$F(1,29) = 14.78, P < 0.01$] and their interaction [$F(1,29) = 15.54, P < 0.01$]. Thus, sentence complexity and noun frequency influence both the time and accuracy of sentence comprehension.

Functional Activation Results

To foreshadow the overall results, Figure 3 shows, for a single participant, the thresholded *t*-maps for two oblique axial slices for each of the four conditions relative to fixation, superimposed on the corresponding structural images. The figure shows an increase in the volume of activation in the classic left perisylvian language areas as a function of increasing syntactic complexity, particularly for the object-relative sentences containing low-frequency words. Figure 4 displays a *t*-map in Talairach space

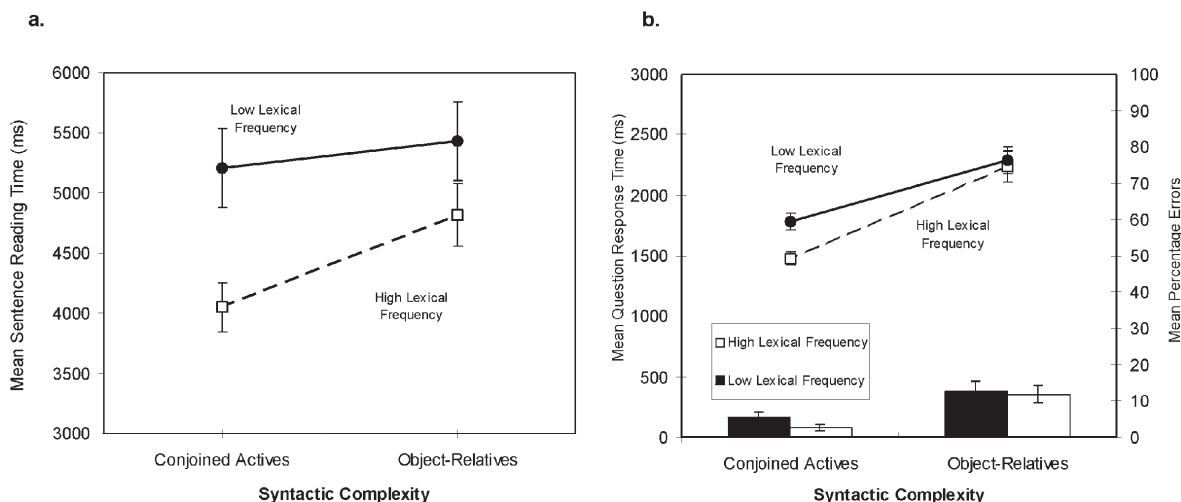


Figure 2. Behavioral results for sentence reading times, question response times and percentage of errors for the sentence comprehension task performed in the scanner. Error bars represent the standard error of the mean.

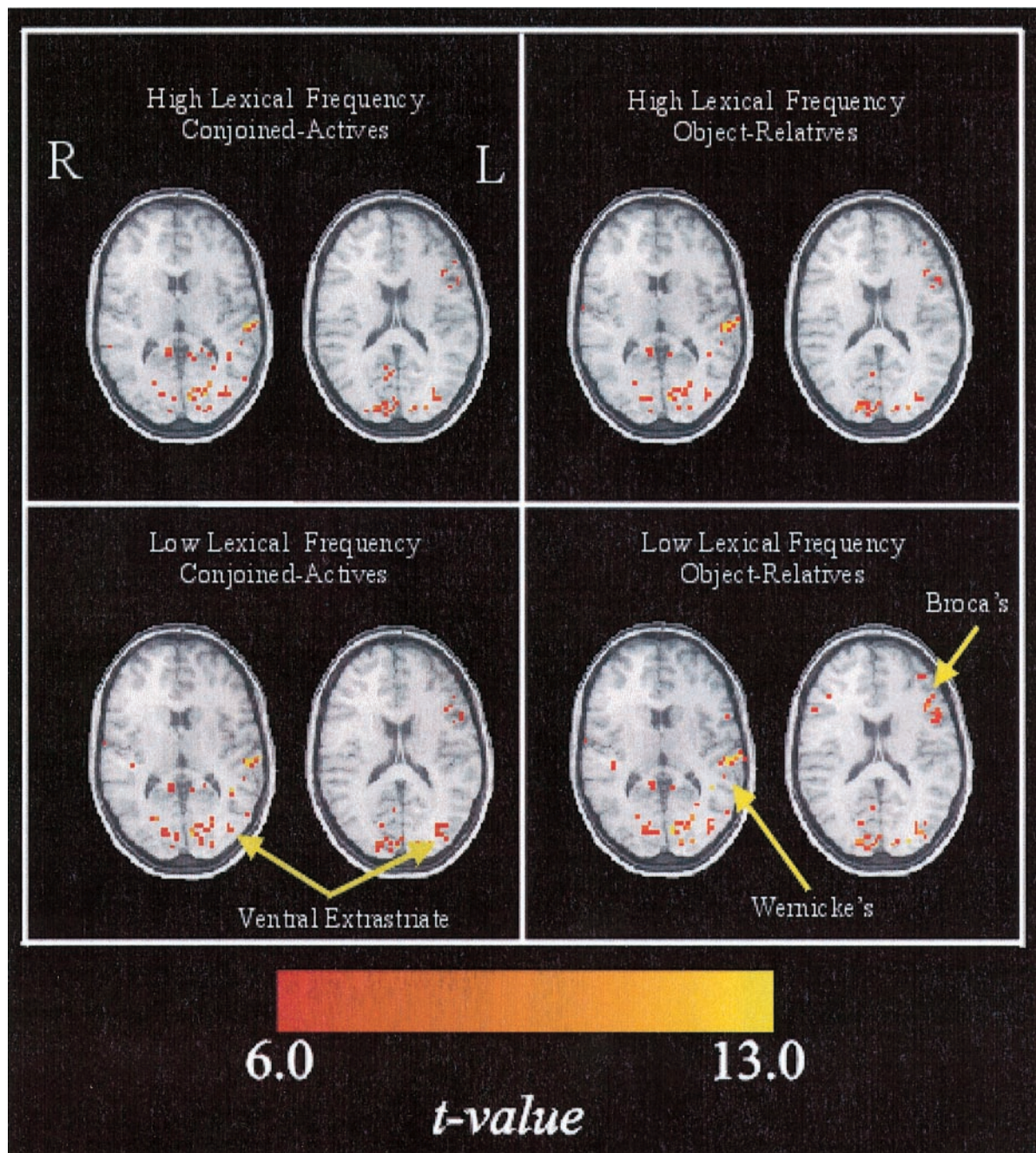


Figure 3. Functional activation results (thresholded t -maps for the comparison between individual conditions and the fixation condition) from a single participant, overlaid on the corresponding structural slices. The slice displayed on the left in each panel is more inferior.

averaged across participants for the most demanding condition (object-relative sentences, low-frequency words), along with plots of the mean integral of percentage change in signal for the four conditions for the relevant ROIs. As the figure suggests, the major result is that several of the left-hemisphere areas displayed an interaction between lexical frequency and syntactic complexity. Moreover, within each of these regions, a substantial proportion of the activated voxels was responsive to both factors, and very few voxels were responsive specifically to the effect of either factor alone. The consistency of this effect across the left-hemisphere regions argues against any simple cortical localization of either lexical access or syntactic processing.

At the very least, it suggests that if there is some degree of cortical specialization for each of the processes, the grain size of such specialization is below the spatial and temporal resolution of current functional imaging, or that the reciprocal interactions between these two types of processes prevent detection of such specialization in normal sentence comprehension. We now report on the results for each region.

Left Inferior Frontal Region (Broca's Area)

For this region, the amount of activation in response to the processing of a syntactically complex sentence was disproportionately increased by the presence of infrequent content words,

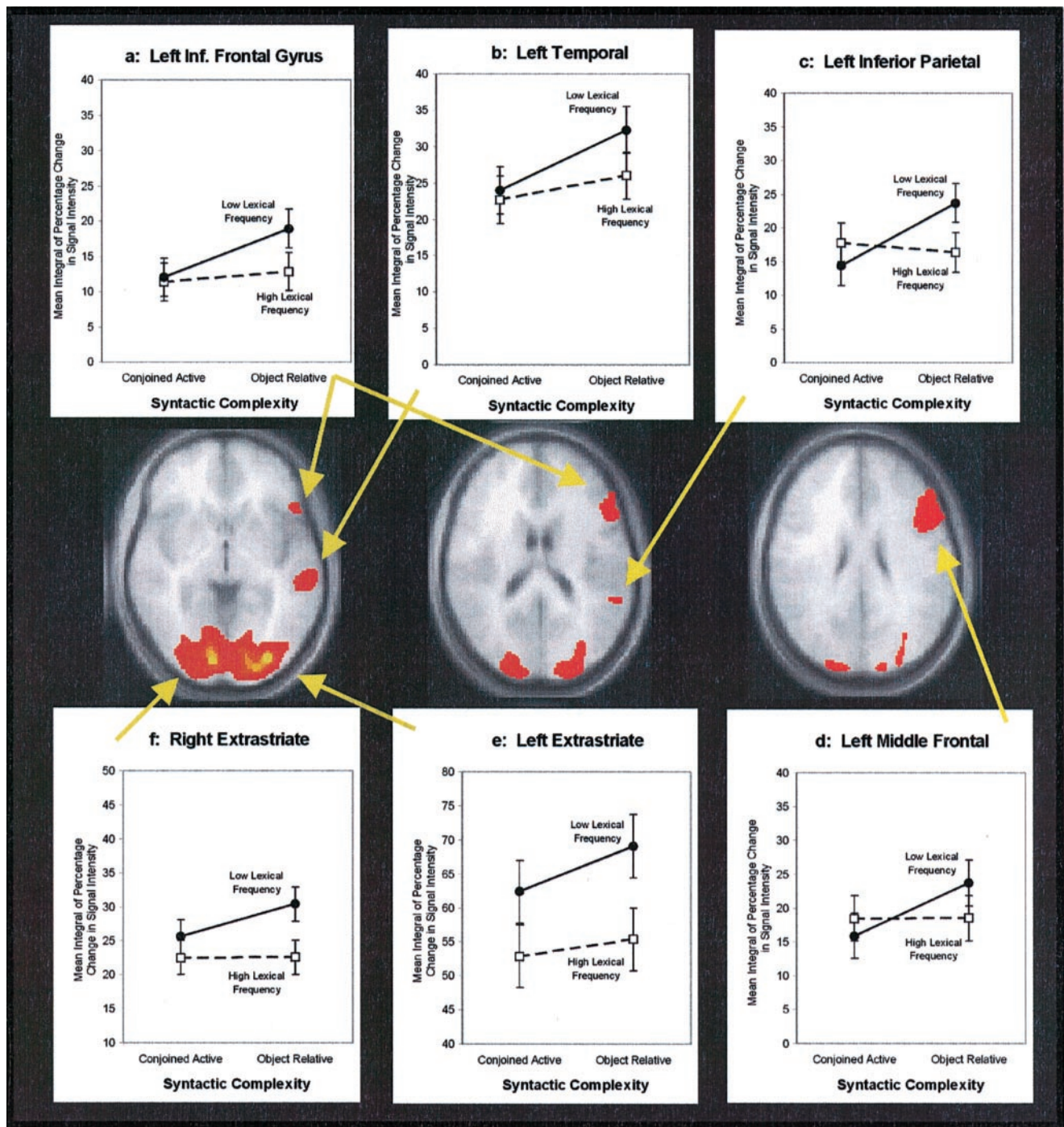


Figure 4. Across-participant paired *t*-map for the subtraction of mean signal intensity in the fixation condition from that in the condition involving sentences with object-relative syntactic structure and low lexical frequency words. The *t*-map was calculated after spatially smoothing (4 mm root mean square Gaussian filter) each participant's mean signal intensity for each condition and transforming it to a standardized space (Talairach and Tournoux, 1988) using MCW-AFNI software (Cox, 1996). The activation map is thresholded at $t(29) = 2.46$ ($P < 0.01$, uncorrected for multiple comparisons) and overlaid upon an averaged image of the 30 participants' structural volume scans. From left to right, the three images correspond to Talairach z-coordinates of 0, 18 and 26 mm. These images are intended only to convey common areas of activation across participants in the most difficult combination of conditions; the statistical analyses of the effect of syntactic complexity and lexical frequency were carried out upon data from each participant within the individually delineated ROIs. The plots indicate the mean integral of percentage change in signal across participants for the ROIs. Error bars represent 95% confidence intervals based on the pooled *MSe* values from the corresponding ANOVA in Table 2 (Loftus and Mason, 1994).

resulting in reliable interaction between the two factors, as shown in Figure 4a. Additional tests of simple main effects indicated that the effect of noun frequency was reliable only for the object-relative sentences [$t(29) = 2.73$, $P < 0.05$], and that the effect of sentence complexity was reliable only when the

sentences included low-frequency nouns [$t(29) = 3.37$, $P < 0.005$]. Table 2 presents the numerical values of the interaction and the two main effects of syntactic complexity and lexical frequency, along with the associated statistical results for this region and the other ROIs. Not only did both sources of

Table 2

Lexical frequency by syntactic complexity ANOVAs for the mean integral of percentage change in signal intensity in the regions of interest

Region of interest	Lexical frequency effect				Syntactic complexity effect				Frequency by complexity interaction			
	Diff.	<i>F</i> (1,29)	<i>MSe</i>	<i>P</i> <	Diff.	<i>F</i> (1,29)	<i>MSe</i>	<i>P</i> <	Int.	<i>F</i> (1,29)	<i>MSe</i>	<i>P</i> <
Left inferior frontal (Fig. 4a)	3.38	4.66	73.55	0.05	4.16	10.21	50.69	0.005	5.44	4.86	45.68	0.05
Left super/mid. temporal (Fig. 4b)	3.79	4.68	92.25	0.05	5.86	11.52	89.31	0.005	4.99	3.13	59.56	0.10
Left inferior parietal (Fig. 4c)	1.94	2.13	52.88	0.20	3.94	9.55	48.67	0.005	10.81	9.75	89.87	0.005
Left post. mid. frontal (Fig. 4d)	1.32	0.30	175.91	0.60	3.92	11.61	39.77	0.005	7.77	11.00	41.06	0.005
Left extrastriate (Fig. 4e)	11.59	16.21	248.56	0.0005	4.60	6.31	100.15	0.05	4.20	0.96	139.07	0.5
Right extrastriate (Fig. 4f)	5.44	15.50	57.36	0.0005	2.38	7.56	22.52	0.05	4.76	2.77	61.11	0.5
All 5 left hem. ROIs (Fig. 5a)	28.45	11.02	1717.04	0.005	23.73	30.19	559.11	0.0001	33.65	9.34	909.32	0.005
All 5 right hem. ROIs (Fig. 5b)	6.80	7.24	191.29	0.05	3.87	3.92	114.49	0.10	4.01	0.76	159.78	0.5

Diff. = Low-frequency mean minus high-frequency mean for the lexical frequency effect and object-relative mean minus conjoined-active mean for the syntactic complexity effect. Int. = interaction between high-frequency/conjoined-active minus high-frequency/object-relative minus low-frequency/conjoined active plus low-frequency/object-relative.

processing difficulty affect the activation in this region, but some facet of the interaction occurs in most of the left-hemisphere areas.

Left Superior and Middle Temporal Region (Wernicke's Area)

In this region, the pattern was remarkably similar to that found in the inferior frontal gyrus (see Fig. 4b). Although the interaction of lexical frequency and syntactic complexity was only marginally reliable, planned contrasts indicated that the frequency effect was reliable for the object-relative sentences [$t(29)=2.23, P < 0.05$], but not for the conjoined-active sentences [$t(29) = 0.88, P > 0.3$]. Similarly, sentences containing low-frequency nouns showed a reliable effect of complexity [$t(29) = 3.99, P < 0.0005$], but sentences composed of familiar high-frequency nouns showed no corresponding effect [$t(29) = 1.43, P > 0.2$]. Overall, this area showed a robust increase in activation for the more syntactically complex sentence, replicating previous results (Just *et al.*, 1996). Also, there was reliably more activation for sentences with low-frequency nouns than sentences with high-frequency nouns, largely the result of a difference in activation only for the more difficult object-relative sentences. Thus, as was found with Broca's area, the pattern of results are indicative of some interdependence between the effect of lexical frequency and syntactic complexity for the amount of activation seen in Wernicke's area.

Left Inferior Parietal Cortex: Supramarginal and Angular Gyri

This region is sometimes considered to be part of Wernicke's area, although there are cytoarchitectonic differences among the superior temporal gyrus, supramarginal gyrus and angular gyrus, and there is no clear evidence for their functional equivalence (Bavelier *et al.*, 1997). As shown in Figure 4c and Table 2, syntactically more complex sentences produced reliably more activation than less complex sentences, and this effect interacted with the effect of lexical frequency, producing a cross-over interaction. For the conjoined-active syntactic structure, sentences containing high-frequency nouns actually showed reliably more activation than those constructed from low-frequency nouns [$t(29) = 2.15, P < 0.05$], while for the object-relative construction the frequency effect is in the predicted direction [$t(29) = 2.79, P < 0.01$]. Furthermore, there was no reliable change in the activation as a function of syntactic complexity when the sentences contained high-frequency nouns, but there was when the sentences contained low-frequency nouns [$t(29) = 3.57, P < 0.005$]. Lexical frequency did not have a significant main effect, unlike the results for the inferior frontal and superior/middle temporal regions.

Left Dorsolateral Prefrontal Cortex: Posterior Middle Frontal Gyrus

As shown in Figure 4d and in Table 2, the pattern of results for this region was similar to that found for the three perisylvian regions already examined: a robust effect of syntactic complexity along with an over-additive interaction between syntactic complexity and lexical frequency. As in the inferior parietal region, the main effect of frequency was not reliable. Neither simple main effect of frequency reached significance, although there was a marginal effect suggesting greater activation for sentences with low-frequency nouns relative to those with high-frequency nouns for object-relative sentences [$t(29) = 1.84, P < 0.1$]. There was a robust simple main effect of syntactic complexity for sentences that contained low-frequency words [$t(29) = 4.45, P < 0.001$], but no effect for sentences that contained high-frequency words.

Inspection of the individual participants' *t*-maps indicated that the vast majority of activated voxels within this region consistently fell within or near the precentral sulcus. Previous neuroimaging studies of saccadic eye movements have suggested this area as the location of the frontal eye fields in humans (Sweeney, *et al.*, 1996; Luna *et al.*, 1998). Eye movement responses may be sufficient to activate this area but not necessary, since our laboratory and others (Binder *et al.*, 1997) have found left-lateralized activation in this region associated with auditory sentence comprehension. For most participants, the activation in the precentral sulcus extended continuously along the posterior boundary of the middle frontal region and inferior frontal region, thus providing no evidence for a functional dissociation between these areas.

Ventral Extrastriate Cortex: Left and Right Inferior Occipital and Inferior Temporal Regions

Given previous neuroimaging and neuropsychological evidence pointing to the role of left extrastriate occipital and inferior temporal cortex in the processing of visual word form, one might expect an effect of lexical frequency in this area. On the other hand, one would not expect that syntactic complexity would modulate activation in this region. In fact, the pattern of results for both the left and right ventral extrastriate areas was similar to that found in the other areas examined, with the suggestion of an interaction between the two factors (Figure 4e,f). Although the interaction is not reliable for either hemisphere (Table 2), both ventral extrastriate regions show reliable main effects of lexical frequency and syntactic complexity.

Laterality Effects

As expected, the overall activation was strongly left-lateralized

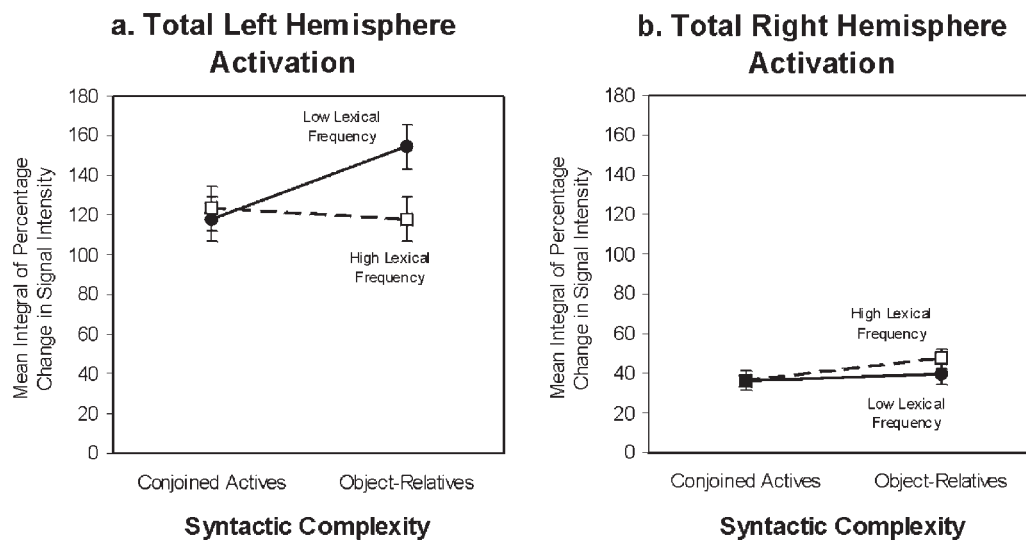


Figure 5. The mean integral of percentage change in signal across the five regions within a hemisphere. Error bars represent 95% confidence intervals based on the pooled *MSE* values from the corresponding lexical frequency \times syntactic complexity ANOVA for each hemisphere.

for our sample of right-handed participants. To assess the degree of lateralization, we first conducted an overall hemisphere (left versus right) by lexical frequency (low versus high) by syntactic complexity (easy versus difficult) repeated-measures ANOVA for the mean integral of percentage change in signal by summing across the five ROIs within a hemisphere of each participant. These data, presented in Figure 5, show main effects of hemisphere [$F(1,29) = 80.04$, $MSe = 5055.9$, $P < 0.0001$], lexical frequency [$F(1,29) = 11.21$, $MSe = 1360.4$, $P < 0.005$] and syntactic complexity [$F(1,29) = 23.15$, $MSe = 493.2$, $P < 0.0001$]. There were interactions between hemisphere and both language factors [$F(1,29) = 32.77$, $MSe = 180.5$, $P < 0.0001$ for the interaction with lexical frequency; $F(1,29) = 7.62$, $MSe = 698.6$, $P < 0.01$ for the interaction with syntactic complexity], in addition to a reliable three-way interaction [$F(1,29) = 8.89$, $MSe = 370.5$, $P < 0.01$]. The three-way interaction can be interpreted in terms of an over-additive frequency by complexity interaction in the left hemisphere but not in the right hemisphere (see Table 2). For the left hemisphere, there was a significant simple main effect of syntactic complexity within the low-frequency trial types [$F(1,29) = 26.59$, $MSe = 927.5$, $P < 0.0001$], but not within the high-frequency trial types. The left hemisphere also showed a significant simple main effect of word frequency within the object-relative sentence types [$F(1,29) = 13.86$, $MSe = 1901.4$, $P < 0.001$], and no corresponding difference in the frequency effect for active sentences.

Although the left hemisphere was clearly more responsive to the manipulation of linguistic factors, the right hemisphere nevertheless showed a reliable main effect of lexical frequency and a marginal main effect of syntactic complexity. The modulation of activation by lexical frequency is consistent with data from patient populations suggesting lexical access functions of the right hemisphere (Zaidel, 1990), and the trend toward an effect of syntactic complexity is consistent with previous reports of a role for the right hemisphere in some aspect of structural processing (Just *et al.*, 1996).

Individual Voxel Response Profiles

The spatial resolution of fMRI makes it possible to assess the effects of lexical frequency and syntactic complexity in terms of

their impact on individual voxels. To quantify these effects, we examined the entire set of voxels that were activated in any of the four conditions and classified them with respect to which of the four conditions they displayed a reliable difference in activation relative to the fixation condition. For example, a voxel could reliably activate only in the condition in which both factors impose the larger demand (low-frequency/object-relative syntax), only in the two conditions involving low-frequency words, only in the two conditions involving the object-relative syntactic structure or in all four conditions. [Of course, if a voxel failed to significantly activate in some condition, this does not imply that its activation was at a baseline level, but rather that it was not quite as high as when it crossed the threshold.] With four conditions, there are 15 ($2^4 - 1 = 15$) mutually exclusive ways that an activated voxel could behave. The voxels were sorted into these 15 possible subsets, and the size of each subset, expressed as a percentage of the entire set, was computed within each ROI for each participant. These means are presented in Table 3 for the main subsets for the five left-hemisphere regions.

A consistent finding across all five of the left-hemisphere regions was that two of the possible subsets were disproportionately large. The first (Set 1 in Table 3), voxels that responded to all four conditions, accounted for ~10% of the activated voxels in Broca's area to nearly 30% in the extrastriate occipital/temporal region. The percentage of this set differed significantly among regions [$F(4,116) = 5.25$, $MSe = 3.1$, $P < 0.001$], and post-hoc tests indicated that the proportions were greatest and statistically equivalent in the four left-hemisphere regions other than the inferior frontal region. The finding that many voxels are activated in all four conditions may reflect the fact that many aspects of sentence processing are common across conditions, although it is surprising that this percentage was relatively lower for Broca's area.

The second largest set (Set 2 in Table 3) was composed of voxels that became significantly activated only when both the lexical and syntactic demands were simultaneously high. A one-way repeated measures ANOVA indicated no reliable differences among the five left-hemisphere regions in the percentages classified within this subset [$F(4,116) = 2.00$, $MSe =$

Table 3

Percentage of voxels in each region that are activated in particular combinations of conditions

Conditions in which the voxels are significantly active	Left-hemisphere region of interest				
	Inferior frontal	Superior/middle temporal	Inferior parietal	Middle frontal	Ventral extrastriate
1. All four conditions	9.9	22.3	25.5	24.4	29.4
2. Low-frequency/ object-relative cond.	23.4	18.7	16.0	14.3	12.8
3. Low-frequency/ conjoined-active cond.	10.7	6.8	6.3	5.7	9.3
4. High-frequency/ object-relative condition	10.6	13.6	8.3	7.0	6.2
5. High-frequency/ conjoined-active cond.	8.0	8.9	9.7	9.6	10.9
6. Two low-frequency conditions	7.9	5.6	3.3	9.9	4.7
7. Two high-frequency conditions	4.1	1.9	5.1	5.1	5.3
8. Two object-relative conditions	5.8	4.4	4.0	3.3	1.2
9. Two conjoined-active conditions	0.7	1.3	0.8	0.3	2.0

The six subsets that are omitted have small percentages and their theoretical interpretation is less clear (e.g. voxels that activate only in the high-frequency/conjoined-active and low-frequency/object-relative condition).

2.6, $P > 0.1$). This set mirrors the over-additive lexical frequency by syntactic complexity interaction in the analysis of the overall amount of activation within the left-hemisphere regions. The significance of this finding is that it localizes the dual sensitivity to both the lexical frequency and the syntactic complexity manipulations to a large number of individual voxels across multiple left-hemisphere areas, indicating that they must in some way be integrating the processing effects of the two variables.

Under a simple null model, in which the probability of a voxel activating in a particular condition is assumed to be equivalent across conditions, the percentage of voxels activated in Set 2 would be expected to equal that in Sets 3–5 (Table 3). One-way repeated measures ANOVAs conducted for each of the five left-hemisphere regions indicated that this null model could be rejected for the inferior frontal region [$F(3,87) = 3.36$, $MSe = 4.3$, $P < 0.05$] and for the superior/middle temporal region [$F(3,87) = 3.32$, $MSe = 2.5$, $P < 0.05$]. Additional pairwise comparisons indicated that for the inferior frontal region, the percentage of voxels responding only to the conjunction of low lexical frequency and high syntactic complexity was greater than that for any of the other sets in which activation was restricted to one condition [i.e. Sets 3–5 in Table 3; all $F_s(1,29) > 4.5$, all $P_s < 0.05$]. For the superior/middle temporal region, similar pairwise comparisons indicated that the percentage of voxels in Set 2 was reliably greater than that for either of the sets involving the simple conjoined active syntactic structure [i.e. Sets 3 and 5 in Table 3: $F(1,29) = 9.28$, $MSe = 4.6$, $P < 0.005$ for the difference from Set 3; $F(1,29) = 5.71$, $MSe = 5.2$, $P < 0.05$ for the difference from Set 5].

The subset analysis also provided very limited evidence of areas within the left-hemisphere ROIs that are specialized for lexical access or syntactic processing. First, Set 8 (Table 3), voxels that respond above threshold only in the two conditions involving object-relative sentences, had very small percentages, ranging from 1.2% in the extrastriate region to 5.8% in the inferior frontal gyrus, with no reliable differences among the five ROIs [$F(4,116) = 1.63$, $MSe = 0.5$, $P > 0.15$]. This percentage (Set 8) was greater in most regions than the percentage for Set 9, voxels responding only to conjoined active sentences; thus, the greater demand of the more complex sentences had effects on individual voxels. Slightly greater, but also small in absolute size, were the percentages for Set 6, the voxels that are significantly active only for sentences containing low-frequency nouns, with no differences in this percentage of activated voxels among the five ROIs [$F(4,116) = 1.33$, $MSe = 0.016$, $P > 0.25$]. Comparisons within each ROI of the percentage of voxels responding to low-frequency (Set 6) versus high-frequency (Set 7) conditions

revealed that the difference only approached significance in the left superior/middle temporal region [$F(1,29) = 3.69$, $MSe = 1.1$, $P < 0.1$]. The analysis of the subset relations suggests that the characterization that applies to entire regions, namely being subject to interactions across regions and showing syntactic complexity effects, also applies at the level of individual voxels in multiple regions.

Ancillary Behavioral Study

In the imaging study, the under-additive interaction in the response times did not match over-additive activation results in some of the ROIs. The under-additivity of the response times may reflect an implicit limit on the time a reader wants to invest on a sentence, such that they are more likely to hurry through the end of a more difficult sentence. Although this hypothesis could not be tested directly with the fMRI data, it received modest support from the self-paced, word-by-word reading study. Figure 6 shows the mean reading times separately for the nouns and verbs in the four conditions. First, lexically infrequent nouns took longer than frequent nouns in the first three positions [all $P_s < 0.01$], but not for the fourth noun at end of the sentence, accounting for an interaction of frequency and noun position [$F(1,31) = 9.26$, $MSe = 10700.58$, $P < 0.0001$]. There was also a significant interaction between sentence complexity and noun position in these data [$F(1,31) = 13.31$, $MSe = 11557.13$, $P < 0.0001$], which appears to have resulted from a main effect of complexity on noun 2 [$F(1,31) = 19.32$, $MSe = 29278.83$, $P < 0.0001$] but no reliable effect of complexity on the nouns in other sentence positions (all $P_s > 0.1$). The longer reading times on noun 2 in the conjoined active condition can be explained by the fact that for conjoined active sentences the second noun comes at the end of the first clause, but in object-relative sentences it does not.

The verb times show sentence complexity effects for both verbs [$F(1,31) = 71.06$, $MSe = 138061.56$, $P < 0.0001$] and individually for each verb [both $P_s < 0.01$], and the expected interaction with verb position [$F(1,31) = 20.18$, $MSe = 65153.38$, $P < 0.01$], replicating previous findings that increases in reading time for object-relative sentences occur primarily on the verbs (Ford, 1981; Holmes and O'Reagan, 1983; King and Just, 1991). However, it must be noted that the word-by-word paradigm did not reproduce the overall smaller frequency effect for the more complex sentences, although the means were in that direction [the mean total reading times were 6382 ms (SD = 1815) for the high-frequency active sentences, 6922 ms (SD = 1961) for the high-frequency object-relative sentences, 7052 ms (SD = 1900) for the low-frequency actives and 7470 ms (SD = 1912) for the

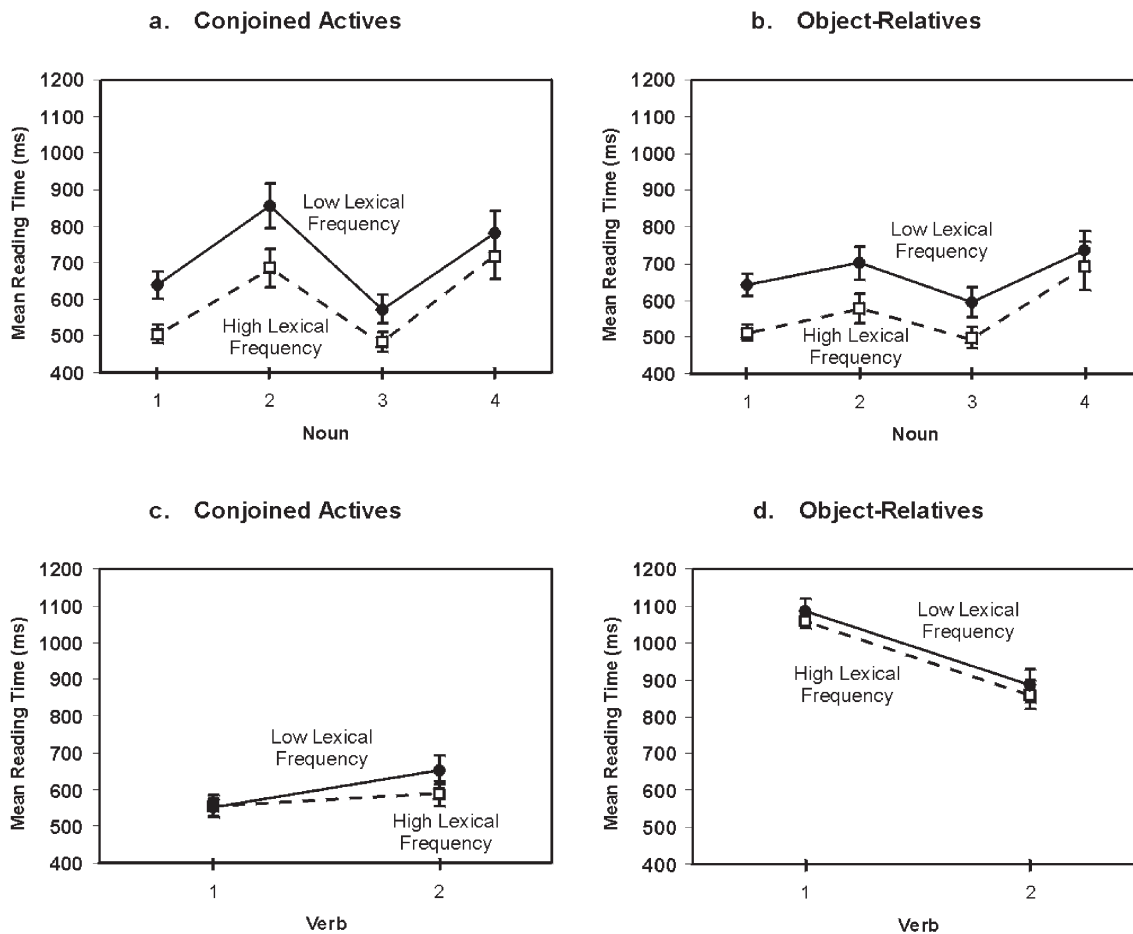


Figure 6. Mean reading times for the content words in the ancillary word-by-word behavioral study. Error bars represent the standard error of the mean.

low-frequency object-relatives]. Thus, these data provide only modest information relevant to the main study.

The divergence between the patterns of response times and fMRI-measured activation in the main study suggests that these two types of measures reflect related, but different aspects of processing (Carpenter *et al.*, 1999). Specifically, fMRI-measured activation appears to be sensitive to processing demands in a number of areas (Just *et al.*, 1996); such increased demand typically is reflected in increased processing duration, but a correlation is not always found (Carpenter *et al.*, 1999) and it was not present in the current study. It is possible that participants limited their processing time for sentences in the hardest condition by skimming its latter parts, particularly the ending phrase, which was not interrogated by the probe. Skimming might imply the execution of more processes within a shorter period, which could increase the workload that is reflected by fMRI-measured activation and could even contribute to the over-additive interaction. Whether this detailed explanation of the response time pattern is correct, it is clear that the over-additive interaction was present in the fMRI-measured activation in several ROIs. Indeed, the central result of the study is that this fMRI activation pattern is not isolated to one area but is present in multiple ROIs, and is present in the analysis of individual voxels in several ROIs.

Discussion

The advantage of the factorial design and common baseline

methodology employed in the present experiment is that the modulation of activation due to one type of process, such as lexical access, can be evaluated as a function of the influence of another type of processing, such as syntactic/thematic processing. The results showed two important phenomena. First, the two variables interacted, providing evidence for the collaborative effect that each type of processing has on the other in terms of the recruitment of regional neuronal activity. Second, this interaction was qualitatively similar across a number of left-hemisphere regions, including the inferior frontal, the inferior parietal, the posterior middle frontal and marginally the superior/middle temporal regions. These two main results can be accounted for by at least two mutually compatible explanations.

One explanation for the interaction within a cortical region is that a single region may subserve the two processes, lexical access and syntactic/thematic analysis. If the resources available to support processing is finite, as it surely is, and both processes are particularly demanding, then their conjoint demand may be manifested by greater neural recruitment than when only one or the other process is particularly demanding. That the same pattern of interaction occurred in multiple cortical regions may be evidence that the processes are subserved by multiple cortical regions. The possibility of functional overlap across cortical regions runs contrary to the common assumption that cortical regions have distinct specializations; nevertheless, as we discussed in the introduction and Table 1, some version of this

general hypothesis is consistent with other neuroimaging and neuropsychological evidence as well. The functional-overlap explanation is compelling when adjacent cortical regions show contiguous activation, which occurred for most participants in this study for the inferior frontal and posterior middle frontal regions. However, nothing limits this hypothesis to adjacent cortical regions, particularly because different regions need not use the same 'style' or algorithm, or have the same efficiency in achieving a similar functional outcome.

A second interpretation is that theoretically separable processes are so highly interactive that altering the demands placed on one process indirectly alters the demands placed on the other. Specifically, lexical processes may feed into and affect the thematic/syntactic processes and vice versa. For instance, the ease of accessing and maintaining a representation of a noun might influence the ease with which its referent can be assigned to two different thematic roles, a syntactic/thematic process that is needed to represent an object-relative embedded clause. Two functionally and anatomically separable but highly interactive processes might appear to be subserved by the same cortical regions by virtue of highly interdigitated collaboration. This second interpretation is consistent with constraint-based models and a growing body of research showing the effects of the frequency of lexical features on the resolution of syntactic ambiguity (Taraban and McClelland, 1988; Trueswell *et al.*, 1993, 1994; MacDonald *et al.*, 1994; Trueswell, 1996; Garnsey *et al.*, 1997; Trueswell and Kim, 1998).

This second interpretation brings into relief an important aspect of the debate concerning modularity and interaction. Framing the scientific discourse in terms of the search for modules may misleadingly suggest that these processing units are absolutely modular. However, a module is only 'modular' with respect to a given time span because ultimately the information from various sources usually comes together. A scientifically more useful framing might be in terms of the duration over which a process is non-interactive (if at all), and the way in which it then interacts. Of course, the temporal resolution of current neuroimaging methods provides a rather wide window, particularly in blocked designs like that used in the current study. The present evidence of interaction could be consistent with fast-acting lexical and syntactic modules; however, the fact that the same regions and multiple cortical regions are affected by both factors argues against a search for specific locations that have exclusive modular functions. Functional brain imaging methods that combine greater temporal resolution with high spatial resolution, such as event-related fMRI (Buckner *et al.*, 1996; Rosen *et al.*, 1998) or magnetoencephalography (Helenius *et al.*, 1998), will provide better tools for investigating the temporal relations among neural processes at the same spatial location. Nevertheless, even with this interpretation, the existence of the interactions across multiple cortical regions would still suggest that these processes are highly distributed.

The Possible Roles of the Participating Areas

It is useful to characterize the computational functions of some of the various areas, assuming that the current effects primarily reflect processing collaboration. For example, previous studies have found activation in the inferior frontal region for effects of syntactic demands (Just *et al.*, 1996; Stromswold *et al.*, 1996; Caplan *et al.*, 1998), semantic versus non-semantic decisions (Wagner *et al.*, 1998) (see also Table 1), phonological factors affecting lexical access (Herbster *et al.*, 1997; Rumsey *et al.*,

1997; Fiez and Petersen, 1998) and the generation of subvocal speech (Paulesu *et al.*, 1993; Awh *et al.*, 1996). The present results go further, suggesting that some aspects of syntactic and lexical processing are closely interrelated. Luria (Luria, 1962) and Mesulam (Mesulam, 1990, 1998), on the basis of anatomical connectivity with the temporal region and aphasic language-production deficits, suggested that Broca's area represents a bottleneck in the transformation of sequential neural representations. We propose a generalization of this characterization, namely that Broca's area may contribute to generating various serial-order-based representations that serve as the input to other linguistic processes carried out in other cortical regions, such as the construction of temporally ordered motor speech plans in speech production, and the generation of representations of abstract sequential syntactic structures that are elaborated with semantic information.

Wernicke's area has been described as a coordinator in the lexical/semantic pole of the language processing network (Mesulam, 1990, 1998), as well as having a role in phonological processing and retention (Petersen and Fiez, 1993; Fiez *et al.*, 1995). More abstractly, this region could subservise interpretive and elaborative functions involving the coactivation of distributed semantic representations which are required in lexical access, in the mapping of thematic roles and in syntactic parsing. This interpretive function would presumably collaborate extensively with the generative functions attributed to more anterior regions.

The inferior parietal region has not been consistently associated with activation in functional studies of single word reading, although it has been implicated in developmental dyslexia (Horwitz *et al.*, 1998), semantic processing of auditory words (Demonet *et al.*, 1992) and neuropsychological studies of orthographic processing (Damasio and Damasio, 1983; Henderson, 1986). The present study found robust left-lateralized activation (Bavelier *et al.*, 1997). Although some participants showed discrete clusters of activation in the angular and supramarginal gyri, other participants showed a continuous cluster of activation extending from the temporal region into the inferior parietal region. If this area were solely devoted to the transformation of orthographic information into a format that could be used by Wernicke's area for semantic access, one might expect an effect of lexical frequency, but no effect of syntactic complexity. In fact, there was a complexity effect and an interaction of complexity and frequency. This pattern may reflect a larger role for the maintenance of phonological representations of the surface structure of the sentence and only a more minor role related to recoding visual information into a phonological form. When demands on phonological processing and storage are simultaneously increased in the low-frequency/object-relative condition, the limited capacity of the region reveals itself in the additional activation. Such an interpretation is consistent with studies that have associated activation in this region with the short-term retention of linguistic information, suggesting that it has a role related to the storage of phonological information (Paulesu *et al.*, 1993; Awh *et al.*, 1996).

Studies of the role of the ventral extrastriate inferior temporal/occipital region provide evidence of its role in both orthographic and semantic processes related to lexical access. Event-related potential (ERP) recordings taken directly from the inferior temporal lobe during surgery suggest that the fusiform gyrus is involved in both letter-level orthographic processing and word-level semantic processing (Nobre *et al.*, 1994, 1998). The posterior portion of the left-hemisphere region has also

been associated with pure alexia (Damasio and Damasio, 1983). In addition, a role for the left inferior temporal region as an intermediary in bridging conceptual and phonemic representations has been supported by PET rCBF picture-naming studies as well as patient studies (Damasio *et al.*, 1996). The current study found no differences in the overall pattern of activation between more posterior and more anterior portions of this region, and both the left and right hemisphere showed modulation by frequency and syntactic complexity. One possible reconciliation of the current results with these other studies is that the processing of object-relative constructions places a greater premium on the maintenance of information about the individual words. If this maintenance is facilitated by more extensive lexical semantic and/or orthographic processing, then an area with no syntactic processing might nevertheless show modulation.

In summary, frontal areas may be relatively specialized for the generation of linguistic representations, while parietal and temporal areas may be relatively specialized for the interpretation, elaboration and storage of such representations. Distinctions among types of representations at the linguistic level (syntactic, semantic, phonological, orthographic), however, do not neatly correspond to anatomical locations. Syntactic processing and maintenance appears to require coordinated communication between at least Broca's and Wernicke's areas, and may involve right-hemisphere areas as well. Semantic processing and maintenance involve the collaboration of multiple regions in a language-processing network. Phonological processing and maintenance may require interactive communication among Broca's area, Wernicke's area and the left inferior parietal lobule. Orthographic computations seem to be carried out in the bilateral ventral extrastriate pathway, but the available evidence suggests that the participation of other areas in the left-hemisphere language-processing network is necessary in achieving lexical access on the basis of orthographic information.

It has been suggested that functional neuroimaging studies may provide evidence concerning the degree to which the language comprehension system is characterized by a modular versus interactive architecture (Posner and Carr, 1992). Implicit in the early promise may have been the assumption that small, localized cortical regions that respond selectively to just one or another component linguistic process would be evidence of modularity; by contrast, large, multiple or overlapping regions that respond to various component processes would support an interactive account. Our interpretation of the results of the present study and of other neuroimaging and patient studies is that they are more consistent with an interactive account that posits that different linguistic processes influence each other as they unfold. Perhaps the most notable contribution of the current study is its demonstration that the evidence of interaction among processes becomes more evident as the demands are increased at multiple linguistic levels. The characterization of the language-processing network that emerges from the present study is that, despite relative specialization of function within cortical regions, there also is evidence of extensive collaboration and perhaps even overlapping functions. These characteristics result in the distribution of effects across widely distributed cortical regions.

Notes

This research was partially supported by the National Institute of Mental Health Grant MH 29617, and by the National Institute of Mental Health Research Scientist Awards MH00661 and MH00662. The authors thank Vladimir Cherkassky, Vaibhav Divadkar, Robert Mason, Erica Michael,

Sharlene Newman, Erik Reichle and two anonymous reviewers for helpful comments on this manuscript.

Address correspondence to Timothy A. Keller, Department of Psychology, 5000 Forbes Avenue, Carnegie Mellon University, Pittsburgh, PA 15213, USA. Email: tk37@andrew.cmu.edu.

References

- Awh E, Jonides J, Smith EE, Schumacher EH, Koeppel RA, Katz S (1996) Dissociation of storage and rehearsal in verbal working memory: evidence from positron emission tomography. *Psychol Sci* 7:25–31.
- Bavelier D, Corina D, Jezzard P, Padmanabhan S, Clark VP, Karni A, Prinster A, Braun A, Lalwani A, Rauschecker JP, Turner R, Neville H (1997) Sentence reading: a functional MRI study at 4 Tesla. *J Cogn Neurosci* 9:664–686.
- Beauregard M, Chertkow H, Bub D, Murtha S, Dixon R, Evans A (1997) The neural substrate for concrete, abstract, and emotional word lexica: a positron emission tomography study. *J Cogn Neurosci* 9: 441–461.
- Berndt RS, Caramazza A (1980) A redefinition of the syndrome of Broca's aphasia: implications for a neuropsychological model of language. *Appl Psycholing* 1:225–278.
- Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T (1997) Human brain language areas identified by functional magnetic resonance imaging. *J Neurosci* 17:353–362.
- Bookheimer SY, Zeffiro TA, Blaxton T, Gaillard W, Theodore W. (1995) Regional cerebral blood flow during object naming and word reading. *Hum Brain Map* 3:93–106.
- Bowers JS, Bub D, Arguin M (1996) A characterization of the word superiority effect in pure alexia. *Cogn Neuropsychol* 13:415–441.
- Bradley DC, Garrett MF, Zurif EB (1980) Syntactic deficits in Broca's aphasia. In: *Biological studies of mental processes* (Caplan D, ed.), pp. 269–286. Cambridge, MA: MIT Press.
- Braver T, Cohen JD, Jonides J, Smith EE, Noll DC (1997) A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage* 5:49–62.
- Bub D, Black S, Howell H (1989) Orthographic context effects and word recognition in a letter-by-letter reader. *Brain Lang* 36:357–376.
- Buckner RL, Bandettini PA, O'Craven KM, Savoy RL, Petersen SE, Raichle ME, Rosen BR (1996) Detection of cortical activation during averaged single trials of a cognitive task using functional magnetic resonance imaging. *Proc Natl Acad Sci USA* 93:14878–14883.
- Caplan D (1983) A note on the 'word order problem' in agrammatism. *Brain Lang* 20:155–165.
- Caplan D, Hildebrandt N (1988) *Disorders of syntactic comprehension*. Cambridge, MA: MIT Press.
- Caplan D, Hildebrandt N, Makris N (1996) Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension. *Brain* 119:933–949.
- Caplan D, Alpert N, Waters G (1998) Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *J Cogn Neurosci* 10:541–552.
- Caplan D, Alpert N, Waters G (1999) PET studies of syntactic processing with auditory sentence presentation. *NeuroImage* 9:343–351.
- Caramazza A, Zurif EB (1976) Dissociation of algorithmic and heuristic processes in language comprehension: evidence from aphasia. *Brian Lang* 3:572–582.
- Carpenter PA, Just MA (1983) What your eyes do while your mind is reading. In: *Eye movements in reading: perceptual and language processes* (Rayner K, ed.), pp. 275–307. New York: Academic Press.
- Carpenter PA, Just MA, Keller T, Eddy WF, Thulborn KR (1999) Graded functional activation in the visuospatial system with the amount of task demand. *J Cogn Neurosci* 11:9–24.
- Caviness VS Jr, Meyer J, Makris N, Kennedy DN (1996) MRI-based topographic parcellation of human neocortex: an anatomically specified method with estimate of reliability. *J Cogn Neurosci* 8:566–587.
- Cox RW (1996) AFNI: software for visualization and analysis of functional magnetic resonance neuroimages. *Comp Biomed Res* 29:162–173.
- Damasio A, Damasio H (1983) The anatomic basis of pure alexia. *Neurology* 33:1573–1583.
- Damasio H, Thomas JG, Tranel D, Hichwa RD, Damsio AR (1996) A neural basis for lexical retrieval. *Nature* 380:499–505.
- Demonet JF, Chollet F, Ramsay S, Cardebat D, Nespoulous JL, Wise R,

- Rascol A, Frackowiak R (1992) The anatomy of phonological and semantic processing in normal subjects. *Brain* 115:1753–1768.
- Dronkers NF, Wilkins DP, Van Valin RD, Redfern BB, Jaeger JJ (1996) A reconsideration of the brain areas involved in the disruption of morphosyntactic comprehension. *Brain Lang* 47:461–463.
- Eddy WF, Fitzgerald M, Genovese CR, Mockus A., and Noll DC (1996) Functional imaging analysis software – computational olo. In: *Proceedings in computational statistics* (Prat A, ed.), pp. 39–49. Heidelberg: Physica-Verlag.
- Ferreira F, Clifton C (1986) The independence of syntactic processing. *J Mem Lang* 25:348–368.
- Fiez JA, Petersen SE (1998) Neuroimaging studies of word reading. *Proc Natl Acad Sci USA* 95:914–921.
- Fiez JA, Raichle FM, Miezin FM, Petersen SE, Tallal P, Katz WF (1995) PET studies of auditory and phonological processing: effects of stimulus characteristics and task demands. *J Cogn Neurosci* 7: 357–375.
- Fodor JA (1983) *The modularity of mind*. Cambridge, MA: Bradford.
- Ford M (1983) A method for obtaining measures of local parsing complexity throughout sentences. *J Verbal Learn Verbal Behav* 22:203–218.
- Frazier L (1987) Theories of sentence processing. In: *Modularity in knowledge representation and natural-language understanding* (Garfield JL, ed.), pp. 291–307. Cambridge, MA: MIT Press.
- Garney SM, Pearlmuter NJ, Meyers E, Lotocky MA (1997) The contributions of verb bias and plausibility to the comprehension of temporarily ambiguous sentences. *J Mem Lang* 37:58–93.
- Grasby PM, Frith CD, Friston K, Simpson J, Fletcher PC, Frackowiak RSJ, Dolan RJ (1994) A graded task approach to the functional mapping of brain areas implicated in auditory-verbal memory. *Brain* 117: 1271–1282.
- Grodzinsky Y (1986) Language deficits and the theory of syntax. *Brain Lang* 27:135–159.
- Helenius P, Salmelin R, Service E, Connolly JF (1998) Distinct time courses of word and context comprehension in the left temporal cortex. *Brain* 121:1133–1142.
- Henderson VW (1986) Anatomy of posterior pathways in reading: a reassessment. *Brain Lang* 29:119–133.
- Herbster AN, Mintun MA, Nebes RD, Becker JT (1997) Regional cerebral blood flow during word and nonword reading. *Hum Brain Map* 5: 84–92.
- Holmes VM, O'Regan JK (1981) Eye fixation patterns during the reading of relative clause sentences. *J Verbal Learn Verbal Behav* 20:417–430.
- Horwitz B, Rumsey JM, Donohue BC (1998) Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proc Natl Acad Sci USA* 95:8939–8944.
- Howard D, Patterson K, Wise R, Brown WD, Friston K, Weiller C, Frackowiak R (1992) The cortical localization of the lexicons: positron emission tomography evidence. *Brain* 115:1769–1782.
- Just MA, Carpenter PA (1980) A theory of reading: from eye fixations to comprehension. *Psychol Rev* 87:329–354.
- Just MA, Carpenter PA (1992) A capacity theory of comprehension: individual differences in working memory. *Psychol Rev* 99:122–149.
- Just MA, Carpenter PA, Woolley JD (1982) Paradigms and processes in reading comprehension. *J Exp Psychol Gen* 111:208–238.
- Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR (1996) Brain activation modulated by sentence comprehension. *Science* 274: 114–116.
- Kapur S, Rose R, Liddle PF, Zipursky RB, Brown GM, Stuss D, Houle S, Tulving E (1994) The role of left prefrontal cortex in verbal processing: semantic processing or willed action? *NeuroReport* 5:2193–2196.
- Karbe H, Herholz K, Szeliess B, Pawlik G, Wienhard K, Heiss WD (1989) Regional metabolic correlates of token test results in cortical and subcortical left hemispheric infarction. *Neurology* 39:1083–1088.
- Kempler D, Curtiss S, Metter EJ, Jackson CA, Hanson WR (1991) Grammatical comprehension, aphasic syndromes, and neuroimaging. *J Neuroling* 6:301–318.
- King J, Just MA (1991) Individual differences in syntactic processing: the role of working memory. *J Mem Lang* 30:580–602.
- Kucera F, Francis WN (1967) *Computational analysis of present-day American English*. Providence, RI: Brown University Press.
- Linebarger MC, Schwartz MF, Saffran EM (1983) Sensitivity to grammatical structure in so-called agrammatic aphasics. *Cognition* 13:361–392.
- Loftus GR, Mason MEJ (1994) Using confidence intervals in within-subject designs. *Psychol Bull Rev* 1:476–490.
- Luna B, Thulborn KR, Strojwas MH, McCurtain BJ, Berman RA, Genovese CR, Sweeney JA (1998) Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. *Cereb Cortex* 8:40–47.
- Luria AR (1962) *Higher cortical functions in man*, 2nd edn. New York: Basic Books.
- MacDonald MC (1997) Lexical representations and sentence processing: an introduction. *Lang Cogn Processes* 12:121–136.
- MacDonald MC, Pearlmuter NJ, Seidenberg MS (1994) The lexical nature of syntactic ambiguity resolution. *Psychol Rev* 101:676–703.
- Marslen-Wilson WD (1975) Sentence perception as an interactive parallel process. *Science* 189:226–228.
- Mazoyer BM, Tzourio N, Frak V, Syrota A, Murayama N, Levrier O, Salamon G, Dehaene S, Cohen L, Mehler J (1993) The cortical representation of speech. *J Cogn Neurosci* 5:467–479.
- McClelland JL (1987) The case for interactionism in language and processing. In: *Attention and performance, XII. The psychology of reading* (Coltheart M, ed.), pp. 3–36. London: Lawrence Erlbaum.
- Mesulam M-M (1990) Large-scale neurocognitive networks and distributed processing for attention, language and memory. *Ann Neurol* 28:597–613.
- Mesulam M-M (1998) From sensation to cognition. *Brain* 121:1013–1052.
- Metter EJ, Hanson WR, Jackson CA, Kempler D, Van Lancker D (1990) Temporoparietal cortex in aphasia: evidence from positron emission tomography. *Arch Neurol* 47:1235–1238.
- Nobre AC, Allison T, McCarthy G (1994) Word recognition in the human inferior temporal lobe. *Nature* 372:260–263.
- Nobre AC, Allison T, McCarthy G (1998) Modulation of human extrastriate visual processing by selective attention to colours and words. *Brain* 121:1357–1368.
- Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Paulesu E, Frith CD, Frackowiak RSJ (1993) The neural correlates of the verbal component of working memory. *Nature* 362:342–345.
- Petersen SE, Fiez JA (1993) The processing of single words studied with positron emission tomography. *Annu Rev Neurosci* 16:509–530.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988) Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331:585–589.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1989) Positron emission tomographic studies of the processing of single words. *J Cogn Neurosci* 1:153–170.
- Petersen SE, Fox PT, Snyder AZ, Raichle ME (1990) Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science* 249:1041–1044.
- Posner MI, Carr TH (1992) Lexical access and the brain: anatomical constraints on cognitive models of word recognition. *Am J Psychol* 105:1–26.
- Posner MI, Petersen SE, Fox PT, Raichle ME (1988) Localization of cognitive operations in the human brain. *Science* 240:1627–1631.
- Price CJ, Wise RJS, Watson JDG, Patterson K, Howard D, Frackowiak RSJ (1994) Brain activity during reading – the effects of exposure duration and task. *Brain* 117:1255–1269.
- Pugh KR, Shaywitz BA, Shaywitz SE, Constable RT, Skudlarski P, Fulbright RK, Bronen RA, Shankweiler DP, Katz L, Fletcher JM, Gore JC (1996) Cerebral organization of component processes in reading. *Brain* 119:1221–1238.
- Rademacher J, Galaburda AM, Kennedy DN, Filipek PA, Caviness VS Jr (1992) Human cerebral cortex: localization, parcellation, and morphometry with magnetic resonance imaging. *J Cogn Neurosci* 4:352–374.
- Rayner K, Duffy SA (1986) Lexical complexity and fixation times in reading: effects of word frequency, verb complexity, and lexical ambiguity. *Mem Cogn* 14:191–201.
- Rayner K, Raney GE (1996) Eye movement control in reading and visual search: effects of word frequency. *Psychon Bull Rev* 3:245–248.
- Reichle ED, Pollatsek A, Fisher DL, Rayner K (1998) Toward a model of eye movement control in reading. *Psychol Rev* 105:125–157.
- Reuter-Lorenz PA, Brunn JL (1990) A prelexical basis for letter-by-letter reading: a case study. *Cogn Neuropsychol* 7:1–20.
- Rosen BR, Buckner RL, Dale AM (1998) Event related fMRI: past, present, and future. *Proc Natl Acad Sci USA* 95:773–780.
- Rumsey JM, Horwitz B, Donohue BC, Nace K, Maisog JM, Andreason P (1997) Phonological and orthographic components of word recognition: a PET-rCBF study. *Brain* 120:739–759.
- Rypma B, Prabhakaran V, Desmond JE, Glover GH, Gabrieli JDE (1999)

- Load-dependent roles of frontal brain regions in the maintenance of working memory. *NeuroImage* 9:216-226.
- Schwartz MF, Saffran EM, Marin OSM (1980) The word order problem in agrammatism. I. Comprehension. *Brain Lang* 10:249-262.
- Schwartz MF, Linebarger MC, Saffran EM, Pate DS (1987) Syntactic transparency and sentence interpretation in aphasia. *Lang Cogn Processes* 2:85-113.
- Stromswold K, Caplan D, Alpert N, Rauch S (1996) Localization of syntactic comprehension by positron emission tomography. *Brain Lang* 52:452-473.
- Sweeney JA, Mintun MA, Kwee S, Wiseman MB, Brown DL, Rosenberg DR, Carl JR (1996) A positron emission tomography study of voluntary saccadic eye movements and spatial working memory. *J Neurophysiol* 75:454-468.
- Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. New York: Thieme Medical Publishers.
- Tanenhaus MK, Trueswell JC (1995) Sentence comprehension. In: *Speech, language, and communication* (Miller JL, Eimas PD, eds), pp. 217-262. San Diego, CA: Academic Press.
- Taraban R, McClelland J (1988) Constituent attachment and thematic role assignment in sentence processing: influences of content-based expectations. *J Mem Lang* 27:1-36.
- Trueswell JC (1996) The role of lexical frequency in syntactic ambiguity resolution. *J Mem Lang* 35:566-585.
- Trueswell JC, Kim AE (1998) How to prune a garden path by nipping it in the bud: fast priming of verb argument structure. *J Mem Lang* 39: 102-123.
- Trueswell JC, Tanenhaus MK, Kello C (1993) Verb-specific constraints in sentence processing: separating the effects of lexical preference from garden-paths. *J Exp Psychol Learn Mem Cogn* 19:528-553.
- Trueswell JC, Tanenhaus MK, Garnsey SM (1994) Semantic influences on parsing: use of thematic role information in syntactic ambiguity resolution. *J Mem Lang* 33:285-318.
- Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ (1996) Functional anatomy of a common semantic system for words and pictures. *Nature* 383:254-256.
- Vanier M, Caplan D (1985) CT scan correlates of surface dyslexia. *Surface dyslexia: neuropsychological and cognitive studies of phonological reading*. London: Lawrence Erlbaum.
- Wagner AD, Schacter DL, Rotte M, Koutstaal W, Dale AM, Rosen BR, Buckner RL (1998) Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. *Science* 281:1188-1191.
- Xiong J, Rao S, Gao J-H, Woldorff M, Fox PT (1998) Evaluation of hemispheric dominance for language using functional MRI: a comparison with positron emission tomography. *Hum Brain Map* 6:42-58.
- Zaidel E (1990) Language functions in the two hemispheres following complete cerebral commissurotomy and hemispherectomy. In: *Handbook of neuropsychology*, Vol. 4 (Boller F, Grafman J, eds), pp. 115-150. Amsterdam: Elsevier Science Publishers B.V.