An Event-Related fMRI Study of Syntactic and Semantic Violations

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We used event-related functional magnetic resonance imaging to identify brain regions involved in syntactic and semantic processing. Healthy adult males read well-formed sentences randomly intermixed with sentences which either contained violations of syntactic structure or were semantically implausible. Reading anomalous sentences, as compared to well-formed sentences, yielded distinct patterns of activation for the two violation types. Syntactic violations elicited significantly greater activation than semantic violations primarily in superior frontal cortex. Semantically incongruent sentences elicited greater activation than syntactic violations in the left hippocampal and parahippocampal gyri, the angular gyri bilaterally, the right middle temporal gyrus, and the left inferior frontal sulcus. These results demonstrate that syntactic and semantic processing result in nonidentical patterns of activation, including greater frontal engagement during syntactic processing and larger increases in temporal and temporo–parietal regions during semantic analyses.

KEY WORDS: language; syntax; semantics; fMRI; sentence processing.

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INTRODUCTION

For more than a century, aphasiologists have studied patients with various forms of neuropathology in an effort to determine how language might be implemented in the brain. This has led to the identification of the left hemisphere as the dominant hemisphere for language processing in most people, particularly right-handed individuals, and further to the identification of different regions within the left hemisphere (LH) that appear to be more or less involved in different aspects of language. Thus, damage to anterior regions of the LH usually produces a form of language dysfunction characterized by a lack of fluency and grammatical deficits in speech (e.g., in Broca's aphasia): simplified syntactic structures, including the omission or substitution of "function words" (e.g., auxiliaries, determiners) and affixes (e.g., -s or -ed in English) that play an important grammatical role. Such patients typically show similar deficits in comprehension, such as of the grammatical relations between subject and object. In contrast, more posterior LH damage, in temporal lobe or temporo–parietal (supramarginal and angular gyri) regions leaves patients fluent with relatively intact grammatical structures in their speech, while interfering with the sounds (phonology) and meanings (semantics)[5] of words (e.g., in Wernicke's aphasia) in both production and comprehension (Damasio, 1992; Goodglass, 1993; Ullman *et al.,* 1997). These findings have led to the claim that aspects of syntax depend upon left anterior structures, whereas lexical and conceptual knowledge rely largely on temporal and temporo–parietal regions (Caramazza *et al.,* 1981; Damasio & Damasio, 1992; Ullman *et al.,* 1997; Ullman, 2001; Ullman *et al.,* in press).

However, the study of lesion data is constrained by the fact that the particular brain regions that are damaged are not generally restricted to specific anatomical or functional regions and are inconsistent across patients. Moreover, a lesion limited to one structure may cause a metabolic and functional impairment in connected structures (diaschisis). These and other problems make it difficult to accurately identify the particular anatomical regions or structures whose damage has resulted in the observed linguistic impairments.

The problems associated with lesion data can largely be overcome with other methods, which permit the study of the intact and normally functioning human brain. These other approaches have both confirmed and extended

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[5] In this paper, we will use the more general term "semantics" to refer to the restricted sense of conceptual semantics, although it should be noted that this term may be used more broadly, to included other, non-conceptual aspects such as nonlexical semantics.

the conclusions derived from lesion data and, as such, provide complementary and converging evidence regarding the neurological bases of language.

One such noninvasive method is event-related brain potentials (ERPs). These are recordings of brain activity made from electrodes placed on the scalp and time-locked to specific events (e.g., stimuli). These recordings largely represent the summed electrical activity of apical dendrites of synchronously activated clusters of pyramidal neurons within the cortex (Okada, 1983). This technique offers very fine-grained temporal resolution (milliseconds), which has allowed for the development of "mental chronometry" (Posner, 1986)—the identification of different brain potentials associated with different temporal stages of processing.

ERP studies of syntactic and semantic processing have generally used a "violation paradigm" to identify indexes of different temporal stages of processing. In this paradigm, subjects read or hear correctly formed sentences intermixed with sentences that contain some sort of violation or incongruity of semantics or syntax. Semantic incongruities, such as *"*I take my coffee with milk and concrete*"[6] elicit a negative-going ERP, known as the N400, which peaks around 400 ms following the onset of the anomalous word and is largest over central–parietal electrode sites (Kutas & Hillyard, 1980, 1984). In contrast, violations of syntax, such as phrase structure or grammatical word category violations like *"*The scientist criticized Max's of proof the theorem*" often elicit a negative ERP, which peaks around 250–350 ms and is generally largest over left anterior and temporal electrodes. This ERP component is generally known as the left-anterior negativity, or LAN (Neville *et al.,* 1991; Rösler *et al.,* 1993). This early negativity is usually followed by a positivity, which usually peaks between 600 and 800 ms over central–parietal recording sites, and is referred to as the P600, or syntactic positive shift (Hagoort *et al.,* 1993; Osterhout & Holcomb, 1992). The P600 is sensitive not only to syntactic correctness, but also to syntactic complexity. Thus, it has been shown that this component is also elicited by certain correctly formed sentences relative to other, less syntactically complex well-formed sentences (Kaan *et al.,* 2000), and also by less preferred, though still well-formed, syntactic structures (Osterhout *et al.,* 1994). It is currently unclear how specific the P600 is to grammatical processing, however, as it is elicited by violations of musical structure (Patel *et al.,* 1998) and its magnitude may vary as a function of certain nongrammatical factors, such as the probability of a violation and physical

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[6] In all these examples, the word at which the sentence becomes anomalous will be shown in italics. Following the convention of theoretical linguistics, anomalous sentences are also preceded with an asterisk.

features of the word stimuli (Coulsen *et al.,* 1998; Hahne & Friederici, 1999; Osterhout *et al.,* 1996).

While ERPs are a powerful chronometric method, it is difficult to characterize the neuroanatomical loci which underlie their generation. This is due to the fact that the "inverse problem" (calculating current distributions within the brain given electrical scalp recordings) is ill-posed: the number of sources is unknown and electrical potentials may be volume-conducted through neural tissue to register at scalp recording sites distal to the source. There are thus an infinite number of current fields within the brain that could produce identical patterns of scalp potentials (Phillips *et al.,* 1997).

This limitation is partially mitigated by magnetoencephalography (MEG), which measures the magnetic field correlates of summed brain electrical potentials and may be more accurate at localizing certain sources in the brain (Dale & Sereno, 1993), although MEG is still subject to the constraints of the inverse problem and may be blind to deep or nonoptimally oriented sources, and to closed fields. An MEG study by Simos *et al.* (1997) identified sources for the MEG correlate of the N400 to semantic anomalies in the left temporal lobe, with individual subjects showing somewhat different sources, some more lateral (middle temporal gyrus) and others more medial (hippocampal/parahippocampal gyri). Another MEG study attempted to localize the LAN elicited by syntactic phrase structure violations (Friederici *et al.,* 2000). The results suggested that the primary generators of this component may be in the middle superior temporal gyrus, with a weaker contribution from the inferior frontal gyrus. Interestingly, this study indicated that both hemispheres contribute to the LAN effect, but with a stronger contribution from LH than RH areas. However, the sources in this study were constrained to be within a centimeter of the foci of fMRI activations found in a study of a combination of syntactic violations, including, but not limited to, phrase structure violations in a separate group of subjects. This fMRI study (Meyer *et al.,* 2000, discussed in greater detail below) only examined a limited band of cortex above and below the lateral fissure, leaving open the possibility of contributions from other brain regions that were not imaged. Moreover, since MEG, ERP, and fMRI are each sensitive to different types of information, such strict use of fMRI activation foci to limit MEG source localization may be misleading.

These findings are strengthened by data from another approach: Mc Carthy, Nobre, and colleagues, using the more precise technique of recording electrical potentials directly from the brain, rather than through the scalp, identified a brain potential sensitive to semantic violations and other experimental manipulations known to modulate the N400. This potential was found to be generated in or near the anterior fusiform gyrus of the medial temporal lobes, bilaterally (McCarthy *et al.,* 1995; Nobre & McCarthy, 1995).

Lesion data have also contributed to our understanding of the sources of language-related ERP components. A patient with left frontal damage, but no evident temporal or parietal involvement, showed intact N400 and P600 effects, but no LAN (Friederici *et al.,* 1998). In a second study, three patients with damage to the left anterior cortex (including inferior and middle frontal gyri, and portions of the basal ganglia) also did not show a LAN to grammatical anomalies, but did show P600 and N400 responses (Friederici *et al.,* 1999). In contrast to these findings, a patient with damage to left parietal and posterior temporal cortex, but no discernable frontal lesion, demonstrated an intact LAN, but no measurable N400 or P600 (Friederici *et al.,* 1998). In conjunction with the findings of Simos *et al.* (1997) and McCarthy, Nobre and colleagues (1995), this suggests that lateral and medial temporal regions are both involved in the semantic processing indexed by the N400.

Functional magnetic resonance imaging (fMRI) is a noninvasive imaging technique, which offers spatial resolution superior to that of ERP or MEG, but poorer temporal resolution. One major problem with fMRI is that experimental conditions have typically been blocked, with data averaged over periods of 15 to 90 s, resulting in an inability to resolve the brain responses to individual events. Thus while fMRI has been useful in identifying regions involved in sentence processing (as well as many other cognitive processes), experimental designs have, historically, largely been limited to those which allow subjects to predict, with a high degree of certainty, the type of trial they will be exposed to next. As such, studies such as those exemplified by the violation paradigm have been impractical, because the effects elicited by violations are greatly attenuated when the violation is predictable. For example, the P600 (though not the LAN) varies in amplitude as a function of the predictability of a grammatical violation (Coulson *et al.,* 1998; Hahne & Friederici, 1999).

In spite of the limitations of these imaging techniques, a number of experiments have been conducted to identify the neuroanatomical substrates of syntactic and semantic processes. Studies in which reading or listening to well-formed sentences have been compared with control conditions in which white noise, backward spoken language, consonant strings, or pronounceable nonwords were presented, have consistently revealed activation in left perisylvian regions, particularly the superior temporal gyrus (STG) and sulcus (STS), as well as temporo–parietal and inferior frontal regions (e.g., Baveller *et al.,* 1997; Binder *et al.,* 1996; Dehaene *et al.,* 1997; Demonet *et al.,* 1992; Mazoyer *et al.,* 1993). Such studies, however, did not differentiate semantic, syntactic, phonological, and other processes involved in sentence comprehension. Other studies have attempted to examine semantic processing specifically, by task manipulations, such as having subjects make a semantic judgement (e.g., living/nonliving) about items (e.g., Demb *et al.,* 1995; Price

et al., 1997). Interpretation of the results of these studies is complicated, however, by the nature of the control task; different results are observed depending on whether semantic judgments are compared to phonological, orthographic, visual-feature, or other tasks. When subjects read sentences having relatively complex syntactic structure compared with syntactically simpler sentences, increased activity was observed in the left inferior frontal gyrus—the IFG, often referred to as Broca's area (Caplan, Alpert, & Waters, 1998; Just *et al.,* 1996; Stromswold *et al.,* 1996), as well as in left posterior superior temporal sulcus (STS) and parietal regions bilaterally (Just *et al.,* 1996).

Three recent studies implemented the violation paradigm within a blocked design. Ni *et al.* (2000, Experiment 1) compared blocks of spoken sentences containing a mixture of syntactic (verb agreement) violations and well-formed sentences, and other blocks containing a mixture of semantically incongruous and congruous sentences, with blocks of tones. Subjects judged the correctness of each sentence and the pitch of each tone. The "syntax" blocks compared to the tone blocks elicited greater activation in the left inferior frontal gyrus (IFG) than in the left posterior STS, while the "semantic" blocks compared to the tone blocks elicited equivalent (and significant) levels of activation for both of these regions. In addition, semantic blocks elicited enhanced activity in a number of other regions, including left angular gyrus, bilateral middle temporal gyrus, and the middle and superior frontal gyri bilaterally, relative to the tone condition. However, because the control condition in this experiment (tone judgments) was not well-matched with the target conditions, it is difficult to interpret the degree to which the activations observed may be due to overall differences in the processing of tones vs. language, as opposed to reflecting semantic and syntactic processing.

Kuperberg *et al.* (2000) showed that relative to normal sentences, subcategorization anomalies (e.g., *"The boys giggled the nuns.")* elicited activation in the left inferior temporal/fusiform gyrus area, while semantic violations activated the right middle and superior temporal gyri to a greater degree than well-formed sentences. However, subcategorization violations may be processed differently from other forms of syntactic violation. It has been argued that semantic information also plays a significant role in subcategorization (Grimshaw, 1979; Pesetsky, 1982). Such information is expected to be stored in lexical memory and thus may involve lexical processing rather than, or in addition to, syntactic processing. Agrammatic aphasics have been found to be able to access subcategorization information (Tyler *et al.,* 1995) and in one ERP experiment neurologically intact adults showed an N400 effect indistinguishable from that elicited by lexical–semantic violations, as well as a later P600 effect (Friederici & Frisch, 2000). However, another ERP study reported a LAN for subcategorization

violations (Rösler *et al.,* 1993). Thus the processing of subcategorization violations may involve both syntactic and lexical–semantic processes.

Embick *et al.* (2000) examined the effects of grammatical and spelling errors on brain activity. The task in all conditions for this experiment involved counting; for the grammar and spelling errors, subjects counted whether each sentence contained one or two error, and, in the control task, subjects viewed an array of colored letters and counted how many involved a particular conjunction of color and letter. As with the Ni *et al.* (2000) study described above, the difference between the task and control conditions here was more than simply syntax or spelling, since the control stimuli were not even words, let alone sentences. Using a region-of-interest analysis, Embick *et al.* reported significant activity in Broca's area (IFG), Wernicke's area (posterior STS), and the angular/supramarginal gyri for both blocks of grammatical (phrase structure) violations and blocks of spelling errors, as compared to a nonlinguistic color–letter matching control task. In this same study, a "tighter" comparison, between the grammar and spelling conditions, showed that the syntactic violations were associated with greater activation than the spelling errors in all four regions of interest and, moreover, that this difference was significantly greater in the left IFG than in any of the other regions.

Thus while fMRI findings seem to be consistent with the lesion data in identifying the primacy of the left hemisphere in language function and in demonstrating a general pattern of more anterior activations for syntax and more posterior for semantics, these new techniques have also revealed that the nature of language representation in the cortex is more complex than previously described. Clearly, at least some aspects of syntax involve temporal lobe structures, certain lexical-conceptual functions appear to depend upon frontal regions, and the right, as well as left, hemisphere is observed to be active across a number of linguistic tasks. However, at present, many questions remain unanswered. Constraints on fMRI experimental design have limited the types of experiments that have been performed and prevented direct comparisons of the same paradigms under multiple modalities (e.g., ERP and fMRI).

Recent advances in fMRI image acquisition, experimental design, and analysis have opened up the possibility of performing fMRI experiments with randomly intermixed trial types—a technique known as "event-related" or "time-resolved" fMRI (e.g., Buckner *et al.,* 1996; Dale & Buckner, 1997; Josephs *et al.,* 1997; McCarthy *et al.,* 1997; Richter *et al.,* 1997; Zarahn, Aguirre, & D'Esposito, 1997; Menon & Kim, 1999). In this method, hemodynamic responses to individual stimuli or other cognitive "events" can be measured, in contrast to the more traditional method of averaging activations over longer blocks of similar stimuli. This approach has been applied to a number of different cognitive paradigms, including sensory processing

(e.g., Boynton *et al.,* 1996; Dale & Buckner, 1997), memory encoding and retrieval (e.g., Brewer *et al.,* 1998; Wagner *et al.,* 1998), motor planning and execution (e.g., Menon, Luknowsky, & Gati, 1998; Richter *et al.,* 1997, 2000), speech comprehension (Hickok *et al.,* 1997), and the sensory oddball paradigm (which elicits a P300 ERP component; McCarthy *et al.,* 1997).

Three recently published studies have used the event-related fMRI approach to characterize the effects of different types of linguistic violations. One study (Meyer *et al.,* 2000) exclusively examined syntactic anomalies (a mixture of phrase structure—word order—and agreement violations) in German. Separate groups of subjects performed one of two tasks, either simply judging the grammaticality of the sentences or both making the judgment and silently repairing the sentence. Across both tasks, left peri-Sylvian regions were more activated by grammatically incorrect than correct sentences. Somewhat surprisingly, this effect was significant all along the superior temporal gyrus (STG), but not in the IFG. The repair task additionally yielded enhanced activation in the right hemisphere IFG and middle STG, relative to simply performing the grammaticality judgment. Unfortunately, it is difficult to determine whether the pattern of activation was similar for all of the types of syntactic violations, since they were combined in the analysis and the detection and/or repair of these different types of syntactic violation could be associated with different patterns of activation. Further, this study employed a limited field of view, examining only regions of interest along the peri-Sylvian plane, excluding more superior and inferior regions.

A second study focused exclusively on semantic violations of the type known to elicit N400 ERP effects (Kiehl *et al.,* 1999). Subjects read sentences and made judgments about their semantic congruity. Enhanced activations for the violations relative to control sentences were observed along the left inferior frontal sulcus (between the middle and inferior frontal gyri) and in the anterior STS bilaterally.

In the third study, Ni *et al.* (2000, experiment 2) presented subjects with syntactically incorrect (verb agreement errors) and semantically implausible English sentences, interspersed with correctly formed sentences. Subjects judged whether each sentence contained a living thing. In comparison to control sentences, syntactic anomalies elicited activation of the left inferior, middle, and superior frontal gyri, and bilateral activation of the inferior frontal and postcentral gyri, as well as the right supramarginal gyrus. Semantic anomalies also elicited activation of the left frontal gyri and additional foci in the left superior and middle temporal sulci, relative to control sentences. Thus while Ni *et al.* found activity in the superior and middle frontal gyri for both syntactic and semantic anomalies, there was more sus-

tained inferior frontal activation for the syntactic anomalies and temporal activation exclusively for the semantic anomalies. The field of view in this study was limited and did not capture inferior temporal regions.

In the present experiment, we sought to compare, within subjects, regions involved in syntactic and semantic processing, extending the results of previous studies while overcoming their limitations. We conducted an event-related fMRI experiment structured exactly the same way, with exactly the same stimuli and task demands, as a previously conducted ERP experiment (Newman *et al.,* 1999; Ullman *et al.,* 2000). In addition to well-formed (control) sentences, subjects read sentences with syntactic phrase structure violations (e.g., *"Yesterday I cut Max's <u>with</u> apple caution"*) and semantically implausible sentences (e.g., *"Yesterday I sailed Todd's <u>hotel</u> to China"*). These anomalies have been shown to elicit strong, distinct ERP effects in a number of experiments by a number of different laboratories (e.g., Hahne & Friederici, 1999; Kutas & Hillyard, 1984; Neville *et al.,* 1991). In particular, these are two of the same conditions used by Neville *et al.* (1991), with very similarly structured sentences. Moreover, as indicated above, the set of sentences used here were exactly those previously used in an ERP experiment, in which the phrase structure violations were shown to elicit a LAN and P600, while the semantic violations elicited an N400 (Newman *et al.,* 1999; Ullman *et al.,* 2000).[7] In this experiment, all of the experimental parameters (timing and mode of stimulus presentation, task performed by subjects, etc.) were identical to those used in the ERP version of the experiment, so that a direct comparison of results could be made. The task directed subjects' attention to the content and structure of the sentences without biasing them toward syntactic or semantic strategies, by simply asking them to determine whether each was a "well-formed English sentence." This overcomes problems of task demands inherent in some previous studies. In addition, our fMRI scanning covered the entire brain, including the cerebellum, ensuring that no region of activation would be missed—a problem which has, no doubt, led to inconsistencies among the findings of previous studies. We chose, furthermore, to focus on regions of the brain in which the difference in activation between violation and control conditions was significantly greater for one than the other type of violation (syntactic or semantic). This latter point is important both because the distinction between syntax and semantics is based on extensive theoretical and empirical work and because the ERP effects to these two types of violations have been demonstrated to be distinct and independent (Hagoort,

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[7] The ERP study also included other violation types (of inflectional morphology) that were not used in the present study.

1999; Hagoort & Brown, 1999; Osterhout & Nicol, 1999). Thus by identifying brain regions that are more active in response to one or the other type of violation, we are quite likely to identify the neural generators of the ERP effects—regions which are preferentially involved in one or the other linguistic subsystem.

We hypothesized, based on the lesion, MEG, PET, and fMRI literature reviewed above, that we would find activation of frontal, and perhaps temporal, cortex for syntactic violations, and activation along the STS/STG, in medial temporal regions, and perhaps in frontal structures for semantic violations. However, we also remained open to the possibility that other brain regions might be activated by these violations—regions which had not previously been detected due to the lack of spatial resolution inherent in lesion and MEG studies, the constraints of blocked designs, the restricted field of view employed in previous event-related fMRI studies, and, for the syntactic condition, the type of violation examined.

METHOD

Subjects

Sixteen subjects participated in this experiment. However, data from two subjects were excluded due to errors in data acquisition. All subjects were right-handed males with no left-handed parents or siblings. Subjects gave informed consent and were paid for their participation.

MR Scanning Procedures

The study was conducted on a Siemens Vision 1.5T whole-body MR systemat Georgetown University. Echo-planar functional images were collected in five scanning runs, using the following parameters: TE = 40 ms; TR = 3 s; matrix = 64 $\times$ 64 voxels; field of view = 32 cm (giving an in-plane spatial resolution of 5 mm); slice thickness = 4 mm with a 1-mm interslice gap (treated as 5-mm thick in reconstruction, to account for signal rolloff between slices). Slices were acquired in the axial plane; 27 slices were used (acquired in ascending slice order), which afforded coverage of the entire brain, including the cerebellum. In addition, a whole-brain structural image was obtained for each subject, using a 3D MP-RAGE pulse sequence. For 10 subjects, these images were acquired in the axial plane (matrix = 256 $\times$ 256; field of view = 25.6 cm; slice thickness = 1 mm; 150 slices). For the remaining 6 subjects, the images were acquired in the sagittal plane (with otherwise the same scanning parameters), which eliminated "wrap" artifacts seen in some of the axially acquired data.

Stimuli

The stimuli consisted of 128 simple declarative English sentences. These sentences were also used in a previous ERP experiment (Newman *et al.,* 1999; Ullman *et al.,* 2000). Their structure was based on the stimuli used in an ERP study by Neville *et al.* (1991). Sixty-four of these sentences belonged to the syntactic condition, in which phrase structure anomalies were created by reversing the order of the object noun and the closed-class function word following it (e.g., "*Yesterday I cut Max's [apple with / *with apple] caution*"). For the other 64 sentences, in the semantic condition, the anomalous version of each was created by replacing the object noun with another noun that was semantically incongruent, given the preceding context (e.g., "*Yesterday I sailed Todd's [boat / *hotel] to China.*"), but had a similar frequency in English (Kucera & Francis, 1967). All sentences in both conditions had similar structures, consisting of two words (including the grammatical subject), followed by a verb, followed by a proper noun (except in the case of phrase structure violations, where the violation was produced by swapping the positions of this noun and the following, closed-class, word). In both violation conditions, the anomaly became apparent at this position in the sentence, so subjects could not predict which condition a given sentence was in nor the type of violation (if any) it contained until the word at which the sentence became anomalous. Following the critical word at which the sentence could become anomalous was a predicate of two or three words, which completed the sentence. The number of sentences ending in two vs. three words was balanced across sentence types. For each sentence, a well-formed and anomalous (syntactic or semantic) version were created. Two orthogonal stimulus sets were created, each containing 32 anomalous and 32 correct sentences from each condition (syntactic and semantic); each sentence appeared in each set, but only in either its correct or anomalous form in a given set. Stimulus set was counterbalanced across subjects. The stimuli were presented visually by a notebook computer running the Presentation software package (Neurobehavioral Systems, Davis, CA), in a randomized order that differed for each subject. For the first 8 subjects, the notebook was connected to an LCD projector, whose output was projected to a small screen positioned atop the MR head coil, which subjects viewed via a mirror mounted on the MRI head coil. For the remaining 8 subjects, the computer was connected to a binocular LCD goggle system (Avotec, Jensen Beach, FL), which was positioned atop the head coil. This latter system was employed due to a failure of the LCD projector. The timing of the stimuli were controlled by the timing of the acquisition of MR images, via pulses sent from the MR scanner to the parallel port of the stimulus presentation PC.

Procedure

The stimulus timing and the task performed by the subjects were identical to those employed in our previous ERP study (Newman *et al.,* 1999; Ullman *et al.,* 2000). Subjects were told that some sentences would appear odd in some way, but were not told the exact nature of the anomalies nor were they given examples. Each scanning run began with a 35-s period in which subjects focused their eyes and attention on a fixation cross in the center of the screen. Following this fixation period, the outline of a box subtending half of the screen replaced the fixation cross, indicating the impending onset of a sentence. One second after the appearance of this box, the sentence was presented, one word at a time (duration $=$ 300 ms; SOA $=$ 500 ms), in the center of the screen. Following the end of each sentence, the screen was blank for 1 s, and then a question prompt, which read "Good or Bad?," appeared on the screen for 2 s. At this point, subjects indicated their response by pressing a button with either the right or left hand (correspondence between hand and response was counterbalanced across subjects and stimulus sets). Responses were made via a fiber optic response pad (Current Designs, Philadelphia, PA); however, due to technical limitations, these responses were not actually recorded. This was not a serious shortcoming, as in an ERP experiment using the same stimuli (Newman *et al.,* 1999), we found that subjects were consistently very accurate (84–97% correct responses). Debriefing further confirmed that all subjects had understood the task and had been able to correctly discriminate good from anomalous sentences. Following the question prompt, the fixation cross again appeared, followed after 4500 ms by the box outline indicating the imminent appearance of the next sentence. Thus the time between the onset of each sentence totaled 12 s, allowing for the acquisition of four complete whole-brain functional images for each sentence. Since the hemodynamic response to brief stimuli returns to baseline after approximately 12–15 s (Boynton *et al.,* 1996; Dale & Buckner, 1997; Zarahn *et al.,* 1997), we thus ensured that fMRI response to each sentence would not overlap to any significant degree with those of the preceding or subsequent sentences.

Image Preprocessing and Analysis

The reconstructed structural MR images for each subject were normalized to the International Consortium on Human Brain Mapping (ICBM) standard stereotaxic space based on the Montreal Neurological Institute's averaged T1 template, using the Statistical Parametric Mapping (SPM) software package (Wellcome Department of Cognitive Neurology, London, UK). For the functional images, the first 12 time points from each run (during

which subjects had viewed the fixation cross) were discarded to eliminate artifacts arising from magnetization inhomogeneities and subject arousal. The remaining reconstructed functional images first had slice timing adjusted to match the middle slice of each time point, using a fast fourier transform method implemented in the SPM package. The functional volumes were all realigned to the first image of the first set, using the Automated Image Registration (AIR) software package (Woods *et al.,* 1998a, b) to remove artifacts due to subject head motion and then a mean functional image was created using AIR, which was then normalized to the ICBM / Montreal Neurological Institute EPI template using SPM. The normalization parameters thus defined were then applied to each of the individual, realigned functional volumes.

Statistical analyses were performed using the AFNI software package (Analysis of Functional Images; Cox, 1996; Cox & Hyde, 1997). The first step used multiple regression (Courtney *et al.,* 1998; Neter *et al.,* 1985; Rencher, 1995; Ward, 2000) to fit each subject's data to two regression models modeling predicted impulse response functions, one having a greater level of activation for syntactically anomalous as compared to correct sentences and the other having greater signal for semantically anomalous than correct sentences. The estimated impulse response functions for voxels, which showed a significant correlation with either of these models, were then used to calculate the area under the curve for the hemodynamic response to anomalies for these voxels, defined as the difference between the average level of activation at time points 3 and 4 (corresponding to 5.5 and 8.5 s, respectively, after the onset of the target word, after slice timing correction) and time point 1 (1.5 s after the beginning of the sentence, prior to the presentation of the target word). These calculated values were then submitted to a 2-way analysis of variance, with subjects as a random-effects variable and condition (syntactic vs. semantic) as a fixed-effect variable. Planned comparisons showing voxels, which showed a significantly greater bad–good effect for syntactic than semantic conditions, and vice versa, were then examined.

RESULTS

Figures 1 and 2 show the averaged activations of all 14 subjects, superimposed on a structural image taken from a single subject and normalized to the standard stereotaxic space as described above. The activations shown are those for which a violation elicited a greater BOLD fMRI response than the control condition and where, moreover, this response was significantly ($p <$ 0.005, two-tailed *t*-test) greater for one violation type than the other (i.e., syntax bad–syntax good > semantics bad–semantics good, and semantics
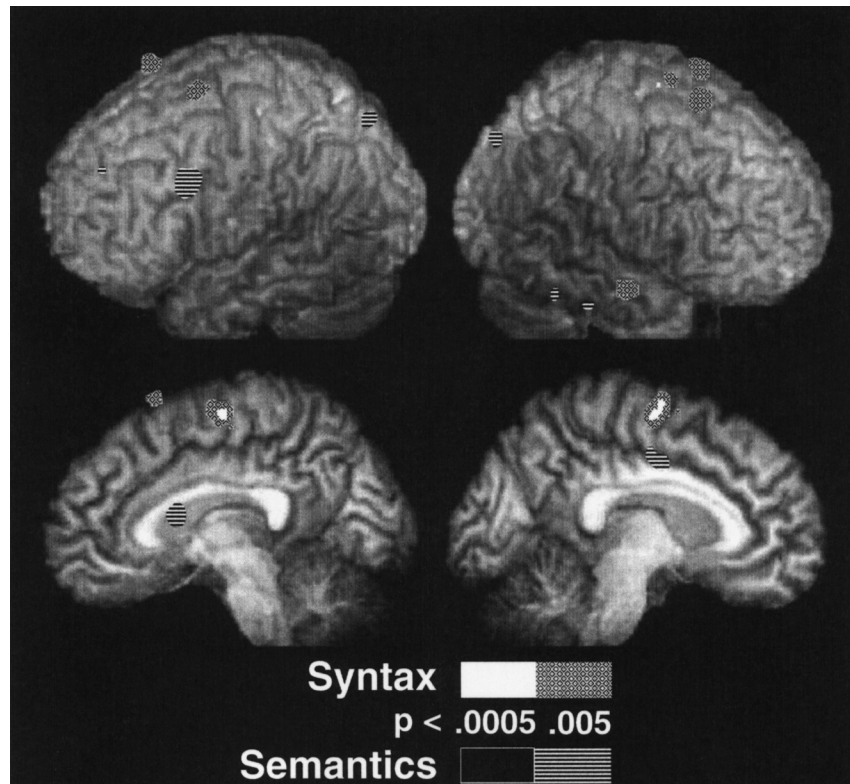
Fig. 1. Activations (threshold at $p <= 0.005$) for syntactic and semantic anomalies on the lateral (top) and medial (bottom) surfaces of each hemisphere. The data have been averaged over all 14 subjects following stereotaxic normalization, resampled to 1 mm³ voxels using cubic interpolation, and superimposed on a stereotaxically normalized anatomical image (1 mm³ resolution; the exact number of significant voxels in each cluster, sampled at the original resolution of $5 \times 5 \times 5$ mm, may be found in Table I). The structural image used is from one subject, chosen for its particularly high quality (in terms of clarity and grey-white matter contrast). This anatomical image was used rather than an averaged anatomical image of all subjects due to its greater clarity. Since all subjects' individual structural images are effectively anatomically equivalent after normalization, the choice of one anatomical image over another does not alter the localization of the results—the differences are purely aesthetic.

bad–semantics good > syntax bad–syntax good). Each cluster of contiguous, significantly activated voxels is listed in Table I, with three-dimensional ICBM coordinates, approximate Brodmann's areas, *t*-values, and significance levels (*p* values) given for the most significantly activated voxel of that cluster.
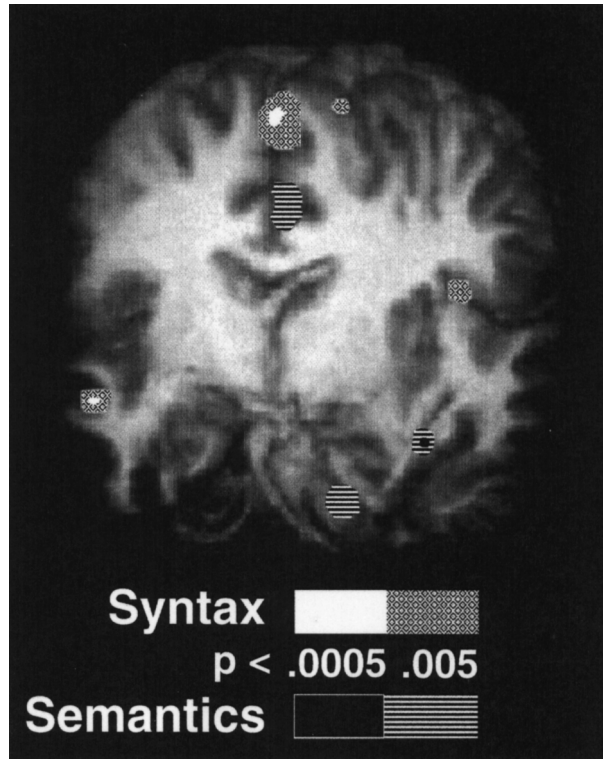
Fig. 2. Activations for syntactic and semantic activation shown on a coronal section of brain with the anterior portions removed, to demonstrate medial activations in prefrontal and middle temporal structures, and the right superior temporal sulcus. Position of the cut is approximately −20 in the *y* dimension of ICBM stereotaxic space. All other display parameters are identical to those in Fig. 1.

Syntactic Violations

Table I and Figs. 1 and 2 show that syntactic violations elicited greater activation than semantic anomalies in a number of regions of the superior frontal gyrus, in both hemispheres. These activations were distributed on both the dorsal surface of the superior frontal gyri and in medial regions of these gyri within the central fissure. Their locations correspond to Brodmann's areas (BA) 6 and 8, including regions which likely correspond to the supplementary motor area (Wise *et al.,* 1996). Additional syntactic activations were observed in two other regions. One was in the left posterior insula (medial BA 41/43), very close to Heschl's gyrus (see Fig. 2). The other was found at the base of the right anterior

Table I. Activations for Syntactic and Semantic Anomalies, Averaged Across all 14 Subjects[a,b]

	Location	Coordinates (x, y, z)	t	p (<=)	Size (# voxels)	Brodmann's area
Syntax						
LH	SFG dorsal	−20,4,74	3.52	0.001	2	6/8
	SFG dorsal	−21,−6,67	3.41	0.005	1	6
	SFG dorsal	−15,−16,67	3.66	0.005	1	6
	SFG medial	−5,−6,69	4.22	0.001	3	6
	Insula (posterior)	−45,−26,19	3.99	0.005	1	41/43
Medial	SFG medial	0,−6,64	4.67	0.001	4	6
RH	SFG dorsal	21,19,69	4.33	0.001	2	6/8
	SFG medial	5,−11,59	3.53	0.005	3	6
	STS anterior	55,−6,−15	5.17	0.001	1	21/22
Semantics						
LH	SFG anterior	−20,49,34	3.65	0.005	1	6/8
	IFG anterior	−50,34,5	3.37	0.005	1	49
	Frontal pole	−35,48,0	3.51	0.005	1	10
	MFG/IFS	−50,14,39	4.28	0.001	5	9/46
	Middle cingulate gyrus	−5,−6,39	4.54	0.001	2	24/31
	Medial Infero-frontal cortex	−5,49,−5	3.44	0.005	1	10
	Hippocampus	−39,−16,−20	3.88	0.005	1	—
	Parahippocampal gyrus	−20,−6,−36	5.33	0.0001	1	—
	Angular gyrus	−35,−76,60	3.69	0.005	1	—
RH	MTG (middle)	70,−36,−15	3.78	0.005	1	21
	MTG (middle)	70,−21,−21	3.50	0.005	1	21
	Angular gyrus	45,−76,50	3.80	0.005	1	39
	Caudate head	10,9,15	4.02	0.005	1	—

[a] LH, left hemisphere; RH, right hemisphere; SFG, superior frontal gyrus; STS, superior temporal gyrus; MFG, middle frontal gyrus; IFS, middle frontal sulcus; MTG, Middle temporal gyrus.

[b] Regions shown are those which showed greater activation for the anomalous condition as compared to the control condition and, further, where this difference in activation was significantly greater ($p <= 0.005$) for the syntactic than semantic condition, or vice versa. Each subject's data were stereotactically normalized to a standard template prior to averaging; the *xyz* coordinates given are in the International Consortium on Brain Mapping (ICBM) space.

STS, at the border between the superior and middle temporal gyri (BA 21/22; see Figs. 1 and 2).

Semantic Violations

Semantic anomalies yielded a different pattern of activation, with substantially more temporal and temporo–parietal involvement than syntactic

anomalies. Figure 1a shows that reading semantically anomalous sentences caused increased activity in the angular gyri bilaterally (BA 39), and in two foci along the right middle temporal gyrus (BA 21). In the left hemisphere, two medial temporal foci were observed—one in the hippocampus and the other in the parahippocampal gyrus (see Fig. 2). Additional activations were found in two left prefrontal regions, one in the inferior frontal sulcus/middle frontal gyrus (BA 9/46) and the other in the anterior portion of the SFG (BA 9/10; see Fig. 1). In addition to these lateral activations, Fig. 1b shows that more medial foci were found in the left middle cingulate gyrus (BA 24/31), the head of the caudate nucleus, and medial inferofrontal cortex (BA 10).

DISCUSSION

Syntactic Violations

Our findings suggest that the superior frontal gyri, including not only premotor cortex, but those portions of it which likely correspond to the supplementary motor area, are involved in the processing of syntactic phrase structure violations. While this is an unusual finding, and the intersubject stereotaxic normalization process used can result in a reduction in the accuracy of activation localization, it is not unique: Ni *et al.* (2000, Experiment 2) found superior frontal gyrus activation in response to morphosyntactic violations. This is a particularly stimulating finding in light of the hypothesis that grammatical computation may be subserved by the same "procedural memory" frontal/basal-ganglia system (for studies on this memory system, see Cohen & Squire, 1980; Gabrieli *et al.,* 1993; Heindel *et al.,* 1989; Squire *et al.,* 1993) that also underlies motor and cognitive skills, such as how to use a tool or ride a bicycle (Ullman, 2001; Ullman *et al.,* 1997). The procedural system, including the basal ganglia and the supplementary motor area, may be specialized for computing sequences (Graybiel, 1995; Willingham, 1998). The activation of bilateral premotor areas to syntactic violations may represent increased demand on this procedural/sequencing system as it attempts to process sentences, which violate the expected syntactic sequence.

A number of current models of sentence parsing suggest that as each word in a sentence is read, the reader is building expectations about what words will come next, based on the existing sentence context and knowledge of the phrase structure rules of the language (e.g., Chomsky, 1965; Fodor, 1989; Gibson, 1998). Friederici (1995) has suggested that parsing of this kind occurs very early in the time course of processing each word and that it is indexed by the LAN. Such structure building may be thought of as one of the procedural/sequencing aspects of grammar (Izvorski and Ullman, 1999, 2000; Ullman, 2001; Ullman *et al.,* in press). As described above, patients with damage to left anterior cortex (but not posterior cortex) fail to

show a LAN to grammatical anomalies, although they show a normal P600 response (Friederici *et al.,* 1998, 1999). One or more of the prefrontal activations observed in the present study may thus be considered as candidates for the generator(s) of the LAN. The bilaterality of the activations is somewhat surprising, given that the LAN has been shown to be eliminated by a left hemisphere lesion. However, to our knowledge, right hemisphere-damaged patients have not been tested for the presence or absence of a LAN.

It is perhaps surprising that we did not observe activation of Broca's area in response to syntactic anomalies. It may be that this region is activated, but to an equal degree in processing sentences, which have the same basic grammatical structure, regardless of whether they contain an anomaly (syntactic or semantic) or not. Our findings are consistent with those of Meyer *et al.* (2000) and Kuperberg *et al.* (2000), neither of which showed left IFG activation for syntactic anomalies. While Ni *et al.* (2000) did report activation of the inferior, middle, and superior frontal gyri, they also found these regions to be active for semantic anomalies, indeed, to a greater degree than for the syntactic ones. Consistent with this finding, our data do show increased activation for semantic anomalies in frontal structures adjacent to Broca's area, both within the IFG, anterior to the pars orbitalis, and immediately dorsal to the IFG. Embick *et al.* (2000) found enhanced activity in Broca's area for phrase structure violations; however, the task, control condition, stimuli, and design (i.e., blocked) all different from our methodology, making direct comparison difficult. It may be the case that an electrophysiological brain response as transient as the LAN (~100 ms) does not produce a measurable change in the fMRI BOLD signal and that more sustained changes in activation, such as occur in blocked designs, are required to see Broca's area activation in response to syntactic errors. As well, MEG data implicate the anterior temporal lobe as a more significant generator of the LAN than the IFG (Friederici *et al.,* 2000), although we did not find significant activity in this region either. Another possibility is that any activity within Broca's area was sufficiently sparse and variable in location across subjects that it was "averaged out" by the spatial normalization process. Such a possibility will be the focus of future analyses treating Broca's area as a specific region of interest. Overall, the data that have been generated by fMRI studies of syntactic violations call into question speculation that the left IFG is a generator of the LAN and should motivate further work to consider other loci, such as more superior frontal regions, in modeling such a generator or generators.

Correctly interpreting phrase structure violations may require the reader to mentally repair the sentence according to the language's phrase structure rules. It has been suggested that such later, more consciously controlled processes are indexed by the P600 ERP effect (Friederici, 1995, 1996; Hahne &

Friederici, 1999). For example, the revisions of predicted sentence structure necessitated by garden-path sentences elicit P600 effects (Hagoort *et al.,* 1993; Osterhout & Holocomb, 1992). Such a "repair" task compared to judgment only was associated with enhanced activation of the right inferior temporal gyrus and middle STS using fMRI (Meyer *et al.,* 2000). We also found RH STS activation and, although it was more anterior than that reported by Meyer *et al.,* this may stem from differences in spatial normalization (stereotactic warping in our study vs. ROI identification in Meyer *et al.*). In the present study, subjects only performed the judgment task and were given no instruction regarding sentence repair. Nevertheless, it is conceivable that subjects attempted to patch up the violations in spite of the lack of instruction to do so.

Another region activated more for syntactic than semantic anomalies in the present study is the left posterior insula/Heschl's gyrus region, in or near auditory cortex. There has been speculation that part of syntactic reanalysis may involve revising the prosodic contour of the sentence (Bader, 1998; Steinhauer *et al.,* 1999; Steinhauer & Friederici, 2001), and central positivities not unlike the P600 are observed at prosodic contour breaks when sentences are presented to subjects auditorily (Steinhauer *et al.,* 1999) and at commas when sentences are read (Steinhauer & Friederici, 2001). Thus we might tentatively hypothesize that this region would be activated, even by written sentences, if such prosodic revision was occurring.

In summary, the effects of reading syntactic anomalies were seen primarily in prefrontal regions, although more superior to those classically thought to be involved in syntactic processing. In addition, syntactic anomalies yielded activation in peri-Sylvian regions, which may be involved in the reanalysis of the sentences, possibly including prosodic recoding as well structural revision.

Semantic Violations

In the semantic condition, we found enhanced activity compared to the syntactic condition in a number of regions, including some that have previously been shown to be involved in the storage (posterior temporal and temporal-parietal) and encoding and/or retrieval of semantic information (medial temporal regions and the left prefrontal cortex).

The temporal lobe is known to be involved in semantic processes, both in language (Damasio, 1992; Damasio & Damasio, 1992; Goodglass, 1993) and in semantic memory, more generally (for a recent review, see Tulving *et al.,* 1999). Activations in these regions are also predicted for lexical and semantic processing by the Declarative Procedural Model of language (Ullman, 2001; Ullman *et al.,* 1997). Although the exact roles of the medial

temporal structures are not clear, the majority of data converge on a general model of more anterior medial temporal lobe (hippocampal) regions being involved in encoding and more posterior (parahippocampal) regions in retrieval (Dolan & Fletcher, 1999; Lepage *et al.,* 1998; see, however, Schacter & Wagner, 1999). The activity of these left medial temporal regions is enhanced by increased semantic encoding demands (Martin, 1999; Wagner *et al.,* 1998). Reading semantically incongruent sentences, such as the anomalies in the present study, doubtless requires greater encoding effort and perhaps greater retrieval effort, than easily-interpretable sentences; the medial temporal activations found in the present study may reflect this. The medial temporal activations we observed, also support McCarthy *et al.*'s (1995) and Simos *et al.*'s (1997) findings that the medial temporal cortex is a generator of the N400 ERP. Curiously, McCarthy *et al.*'s data indicate bilateral medial temporal activity, whereas our data show only left hemisphere activation (Simos *et al.* did not examine the right hemisphere). This may represent a difference between the sensitivity of, and/or the physiological index measured by, the different techniques.

Additional temporal and temporo–parietal sites of activation for semantic anomalies were found in the angular gyri and the right middle temporal gyri. Damage to the left angular gyrus may lead to impairments in the association of written words with their meanings (Goodglass, 1993), suggesting its role in processing written semantic information. It was also activated by semantic violations in the blocked-design study of Ni *et al.* (2000). The additional (and equivalent) involvement of the right angular gyrus found here, along with right middle temporal gyrus, is not altogether surprising, given that fMRI studies of language have quite consistently revealed activation of right hemisphere homolog of left hemisphere language structures (e.g., Demonet *et al.,* 1992; Just *et al.,* 1996; Mazoyer *et al.,* 1993; Wise *et al.,* 1991). Right posterior middle temporal regions have also been implicated in the storage of semantic information (Wiggs *et al.,* 1999) and were activated by semantic violations in the Kuperberg *et al.* (2000) and Ni *et al.* (2000) blocked-design studies.

Finally, the activation we observed for semantic violations in prefrontal cortex may be related to the encoding and/or retrieval of semantic information. Such a role for prefrontal cortex has been shown in a number of studies (e.g., Buckner & Koustall, 1998; Demb *et al.,* 1995; Grabowski *et al.,* 1998; Nyberg *et al.,* 1996; Wagner *et al.,* 1998). In addition, this region yielded activation in a study of semantic sentence anomalies not unlike those in the present experiment (Kiehl *et al.,* 1999).

In summary, the neural responses to semantic anomalies involve regions that are known to underlie semantic memory more generally, both in the encoding and retrieval of information, and in its long-term storage.

CONCLUSION

The findings of the present study both confirm previous findings using fMRI and other imaging techniques and extend these findings by presenting intriguing patterns of activation that warrant further investigation. For syntactic violations, we found extensive bilateral activation of the superior frontal gyrus. This region is more dorsally located than the inferior frontal gyrus, which has traditionally been identified as a major substrate of grammatical processing—although dorsal frontal activations have been shown in other recent fMRI studies of syntax. Furthermore, such activation, particularly in premotor cortex, and especially in the supplementary motor area, follows from the predictions of the Declarative/Procedural Model of language, which aligns grammatical computations with nonlinguistic procedural processing, and sequencing in particular (Ullman, 2001; Ullman *et al.,* 1997). In addition, syntactic violations yielded right-lateralized activity in the anterior superior temporal sulcus, which may relate to reanalysis of anomalous sentences, as may the activity in the left Sylvian fissure, which we speculate may be involved in the use of prosodic information in processing syntactic anomalies.

For semantic violations, we found a pattern of activity implicating the same network of cortical systems known to underlie semantic processing, including both structures involved as a repository of semantic information (e.g., posterior temporal and temporo–parietal), and those known to subserve the encoding and/or retrieval of semantic information. Again, this is supportive of the Declarative/Procedural Model of language, in which lexical/ semantic processing in language is hypothesized to rely upon similar neural systems as does conceptual-semantic knowledge more generally.

Overall, our findings indicate that syntactic and semantic processing depend upon distinct neurolinguistic processes, which involve nonidentical neural substrates, and, further, that these processes depend upon neural circuits whose function extends beyond that of language, indicating a degree of domain-generality in the neurocognitive processes that subserve language.

Finally, this study further demonstrates that we can exploit the spatial resolution of fMRI, in combination with the temporal resolution of ERPs, using identical cognitive paradigms, to yield a deeper understanding of the neurocognitive processes involved in sentence processing.

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