An Event-related Neuroimaging Study Distinguishing Form and Content in Sentence Processing

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Abstract

■ Two coordinated experiments using functional Magnetic Resonance Imaging (fMRI) investigated whether the brain represents language form (grammatical structure) separately from its meaning content (semantics). While in the scanner, 14 young, unimpaired adults listened to simple sentences that were either nonanomalous or contained a grammatical error (for example, *Trees can grew.), or a semantic anomaly (for example, *Trees can eat.). A same/different tone pitch judgment task provided a baseline that isolated brain activity associated with linguistic processing from background activity generated by attention to the task and analysis of the auditory input. Sites selectively activated by sentence processing were found in both hemispheres in inferior frontal, middle, and superior frontal, superior temporal, and temporo-parietal regions. Effects of syntactic and semantic anomalies were differentiated by some nonoverlapping areas of activation: Syntactic anomaly triggered significantly increased activity in and around Broca's area, whereas semantic anomaly activated several other sites anteriorly and posteriorly, among them Wernicke's area. These dissociations occurred when listeners were not required to attend to the anomaly. The results confirm that linguistic operations in sentence processing can be isolated from nonlinguistic operations and support the hypothesis of a specialization for syntactic processing. ■

INTRODUCTION

In this paper, we address a central issue about the processing of natural language and its neural basis. Consider the earliest communicative process that occurs when a hearer is confronted with an utterance. The question is whether the human sentence processing mechanism (the parser) has immediate access to content (meaning of the utterance) as well as form (structure of the utterance). Psycholinguistic studies demonstrate that parsing is extremely fast. The structure of a sentence is being built while the utterance is unfolding in real time, and the parser generally keeps up with the input.

One interpretation of parsing, the interactive hypothesis, supposes that there is no principled division of labor between parsing and meaning interpretation. Rather, there is continuous interaction between the listener's knowledge of the world and the structure the listener is building during the parsing process. An alternative viewpoint, the modularity hypothesis (Fodor, 1983), supposes that parsing can be fast precisely because it is initially sealed-off and encapsulated from background knowledge. The structure–building, syntactic operations of the parser are, therefore, mandatory and reflex-like, proceeding with or without conscious attention. The meaning–interpretation, semantic opera-

tions, on the other hand, may make greater demands on attention and memory because plausibility tests depend on retrieving specific pieces of knowledge about the world (Crain, Ni, Shankweiler, Conway, & Braze, 1996).

These alternative accounts of parsing continue to divide students of sentence processing. Much research effort has been expended in trying to find evidence for the primacy of syntactic over semantic processing, but the issue has proven remarkably difficult to resolve by experimentation. In a series of psycholinguistic studies of sentence processing conducted in our laboratory, it was found that listeners were significantly faster in deciding whether a sentence was ungrammatical than in deciding that it was false or absurd. But, if the listeners were attending to an ancillary task, while simultaneously hearing sentences containing syntactic or semantic anomalies, they were equally quick in registering the occurrence of a syntactic or a semantic anomaly (Fodor, Ni, Crain, & Shankweiler, 1996). Subsequent studies of the reading of sentences containing these anomalies investigated the incidence of regressive eye movements (an indicator of processing difficulty) during and after the portion of the sentence containing the anomaly. It was apparent that the two types of anomaly led to divergent behavior: Syntactic anomalies caused abrupt increases of eye regressions before returning to normal reading, whereas semantic anomalies resulted in perturbations that continued for the remainder of the sentence (Ni, Fodor, Crain, & Shankweiler, 1998). If, as these findings suggest, distinguishably different cognitive demands are posed by syntactic and semantic operations, then it is important to investigate the neurobiological basis of this dissociation.

A question thus arises in regard to the functional anatomy of language. The cortex surrounding the Sylvian fissure of the dominant hemisphere has long been regarded as the primary language zone. However, there is no consensus about whether or how this region may be partitioned with respect to the different aspects of language processing. For example, does the language cortex include dedicated structures for syntactic processing? If so, can syntactic computations be localized to particular regions within the dominant Sylvian region? Aphasia studies have yielded ambiguous answers to these questions. Broca's area in the inferior frontal region has long been implicated in speech production and morphosyntactic functions, but it has also been broadly implicated in learning and memory that is not specifically linguistic. Studies with clinical populations have not settled the question of what Broca's area does. The same can be said of Wernicke's area in the posterior temporal region.

Although studies of the effects of brain lesions have played a seminal role in suggesting hypotheses about the linguistic functions of parts of the brain, their value is limited because of the difficulties of disentangling lesion effects from physiology. Given the goal of understanding the neural basis of natural language processing, we need to know about normal, not pathological, brain function. Event-related brain potentials (ERP) offer one way to view the brain's normal workings unobscured by the difficulties of interpreting deficits resulting from lesions. Studies using this method have repeatedly yielded indications of separable processes in syntactic and semantic aspects of sentence processing. Claims have been advanced for a distinct electrophysiological signature for semantic processes, that is, the so-called N400, and for syntactic processes, the so-called P600 or the Syntactic Positive Shift (Brown & Hagoort, 1998; Friederici, Pfeifer, & Hahne, 1993; Garnsey, Tanenhaus, & Chapman, 1989; Hagoort, Brown, & Osterhout, 1998; Kutas & Hillyard, 1983; Neville, Nicol, Barss, Forster, & Garrett, 1991).

ERP, however, does not yield precise information about localization. Its localizing value is limited by the inverse transform problem, there being no satisfactory way to determine the precise point of origin of a particular waveform from surface activity alone (Hagoort et al., 1998). Functional neuroimaging methods, unlike ERP, may be capable of pinpointing sites that correspond to distinct brain specializations. Moreover, neuroimaging methods potentially avoid other ambiguities inherent in the ERP indicators. For example, N400 may be triggered by so wide a variety of stimulus events that it may not serve as an unequivocal semantic marker.

It is appropriate to acknowledge that there are also limitations associated with functional magnetic resonance imaging (fMRI). Unlike measures of the electrical activity of nerve cells, such as ERP, the fMRI signal tracks hemodynamic changes associated with neural activity. Hence, it can provide only an indirect measure of brain activation. Modulation of blood oxygen level lags considerably behind neural activity associated with perceptual and cognitive activities. So, for example, when a simple tone pulse is presented to a participant, the fMRI signal intensity begins increasing in auditory cortex within 1 sec of onset and peaks at 4–5 sec after stimulus onset (Gore, Marois, & Stevens, 1998). Because of the delay in activation, and the temporal smearing characteristic of fMRI, the technique, as it has typically been used, has very limited temporal resolution. In fact, most neuroimaging studies of cognitive function rely on averaging blocks of trials containing stimuli of the same type, using subtraction of averaged baseline trials to isolate the activity associated with the target task. In addition to the objection of unnaturalness of many repeated stimuli that are highly similar, other criticisms of the block-subtraction procedure have been discussed (D'Esposito, Zarahn, & Aguirre, 1998; Pugh et al., 1996).

Recently, an alternative procedure has come into use that overcomes some of the limitations that have dogged functional imaging studies in the past. It is now apparent

that with an event-related single-trial procedure, MRI can detect single mismatches during a run of stimuli in which the remainder are perceived to be identical (for example, Buckner et al., 1996; Friston et al., 1998a; Friston, Josephs, Rees, & Turner, 1998b; Hickok, Love, Swinney, Wong, & Buxton, 1997; Josephs, Turner, & Friston, 1997; Kang, Constable, Gore, & Avrutin, in press; McCarthy, Luby, Gore, & Goldman-Rakic, 1997; Robson, Dorosz, & Gore, 1998; and so on). The logic of such a procedure is the same as that employed in the ERP research discussed earlier. It also has the same basis as the so-called "mismatch negativity" phenomenon of the magnetoencephalogram (MEG) (Näätänen et al., 1997), which detects magnetic responses to deviant stimuli. We make use of this event-related single-trial paradigm in the present study and, moreover, we compare the results of this method with findings generated by the more conventional block-subtraction method using the same set of materials and the same participants.

Past neuroimaging studies have mainly focused on single word processing, targeting the phonological and morphological levels of language processing. Neuroimaging results with sentence material are scarce, and they are equivocal as to the issue of division of labor between syntax and semantics within the language cortex. It is instructive, nonetheless, to consider three studies, one of which used the positron emission tomography technique (PET), and two exploited fMRI.

In the PET study by Stromswold, Caplan, Alpert, and Rauch (1996), a goal was to explore the effects of variations in sentence complexity on brain activity. PET scanning showed significant increases of regional cerebral blood flow (rCBR) in the posterior inferior frontal region (pars opercularis) of the left hemisphere when subjects were reading center-embedded relative clauses (for example, "The juice that the child spilled stained the rug.") compared with right-branching relative clauses (for example, "The child spilled the juice that stained the rug."). However, this study lacked a nonlinguistic baseline measure that could isolate brain activity specific to linguistic processing. Moreover, there was more than one potential source of difficulty among the test sentences. In addition to the greater syntactic complexity of center-embedded relative clauses over right-branching ones, there was also a difference in the processing demands of object relative and subject relative clauses, a difference that has been found to affect ease of comprehension (for example, King & Just, 1991; Ni, Shankweiler, & Crain, 1996). The results of the study of Stromswold et al. are, therefore, ambiguous in their implications for the issue of a specialization for syntax. As the authors themselves acknowledged, there is no way to tell whether the obtained differences between sentence types reflect differences in syntactic structure among the test sentences, or, alternatively, differences in the processing demands they impose, such as working memory requirements.

As with the study of Stromswold et al., a study by Just, Carpenter, Keller, Eddy, and Thulborn (1996), using fMRI, set out to explore the effects of variations in sentence complexity on brain activation. The authors reported a statistically significant monotonic increment in the level of activation in Broca's and Wernicke's areas, and their right-hemisphere homologue: More activation in classical language zones was observed when subjects were reading sentences containing object-relative clauses (for example, "The reporter that the senator attacked admitted the error.") than sentences with subject relatives (for example, "The reporter that attacked the senator admitted the error."). Still less activation was observed in reading conjoined active sentences (for example, "The reporter attacked the senator and admitted the error."). The comparisons were tightly controlled in this study, and there was also a baseline condition consisting of consonant strings. However, the results reflect activation associated with increases in general processing capacity, and there is no way to distinguish effects of specific aspects of sentence processing, such as syntactic processing, from effects due to other cognitive demands, such as demands on working memory.

An fMRI study by Bavelier et al. (1997) contains novel features that deserve comment. The stimulus materials consisted of a repeated alternation of blocks of sentences and blocks of consonant strings. Thus, there was a baseline that could isolate higher-level linguistic processing from low-level orthographic processing. Between-subject analyses indicated predominantly left-hemisphere activation in and surrounding classical language zones. Analyses of individual subject data showed patchy activation for sentence stimuli in small and localized regions of the cortex. While this study presented a thorough sampling of brain activity associated with reading sentence materials, it did not attempt to isolate separate processes in linguistic comprehension.

The present study is intended to circumvent the various limitations associated with the research reviewed in the preceding paragraphs. It seeks to isolate activity associated with sentence processing and to address the question of whether there are distinct patterns of brain activity representing the syntactic and semantic aspects of sentence processing. First, to insure that the obtained hemodynamic signal adequately samples activity associated with the critical information in the sentence, the linguistic material that constitutes a trial was made as brief as possible so that the critical portion of the sentence is not greatly diluted by the surrounding material. Secondly, a nonlinguistic baseline was used in Experiment 1 to isolate linguistic processing. Third, in Experiment 2, we sought to detect activity triggered by infrequent linguistic events, thereby avoiding the disadvantages of blocking trials of the same type of material. Fourth, spoken language was used as the vehicle in each experiment and, therefore, primary language processes

were tapped as compared to reading from print, which imposes an additional layer of (orthographic) structure and attendant decoding operations to the processing routine. Finally, by testing the same set of sentence materials on the same participants with both the traditional block-subtraction method and a new application of the event-related single-trial paradigm, the design allowed opportunities for results to converge on the phenomenon of central interest.

Experiment 1 (sentence anomaly detection) served to connect our study with previous research using functional neuroimaging. It was based on alternating blocks consisting of (a) nonanomalous sentences and syntactically anomalous sentences, (b) nonanomalous sentences and semantically anomalous sentences, or (c) pairs of tones of the same or different pitches. The participants' task was to monitor for the occurrence of each type of anomaly within the sentence blocks, or to detect same or different pitches in pairs of successive tones in the nonlanguage baseline condition. The primary intent of this experiment, in which participants overtly judged each sentence as acceptable or anomalous, was to unequivocally distinguish brain activity associated with linguistic computations from activity generated by associated components of the task, namely, attention, auditory perception, memory, and judgment. The activity associated with sentence processing via anomaly detection was isolated by subtraction from the pitch judgment baseline task. A secondary purpose was to compare the hemodynamic response when listeners attended to sentence form (syntax) vs. when they attended to sentence meaning (semantics). We expected maximum activation in highly circumscribed regions that are responsive to language comprehension, in comparison with regions that are responsive to nonlinguistic auditory stimuli. In addition, we expected that more regions would be active in the semantic condition than in the syntactic condition, but that both putative types of processing would be intermingled in the hemodynamic signal.

In Experiment 2 (the event-related, single-trial *oddball* paradigm), the participants were presented with isolated instances of anomalous sentences (syntactic or semantic anomaly) within a continuous sequence of nonanomalous sentences. They were instructed to judge whether each sentence contained a living object. Thus, their task was to overtly judge animacy, not anomaly. The average hemodynamic signal associated with the anomalous sentences (oddballs) was compared with the average signal associated with the nonanomalous sentences. The intent was to determine whether isolated occurrences of anomalous sentences are detectable in the hemodynamic signal, and further, whether syntactic and semantic anomalies can be differentiated in distribution of hemodynamic activity. We expected that if the *oddball* paradigm proved sensitive to isolated occurrences of anomaly, this task situation would maximize the opportunity to find differences in cortical sites that

are active as the parser carries out syntactic and semantic processing.

RESULTS

Experiment 1: Sentence Anomaly Detection

Imaging Data

Experiment 1 exploited the traditional block-subtraction method, grouping together materials displaying each anomaly type, syntactic and semantic. Sentence materials were compared with tone-pitch judgments. The tone-pitch condition provided a nonlinguistic baseline task (pitch judgments) which required the participant to make a same-different judgment on every trial. After subtracting the signals evoked by baseline pitch judgments from signals generated during sentence trials, the residual activity reflecting linguistic processes was observed. Activation was bilateral, more in the left hemisphere than in the right in regions surrounding the Sylvian fissure, including the inferior-frontal area anteriorly, and the middle and superior temporal area posteriorly. In addition, there was activity superiorly and medially in the frontal region of both hemispheres, somewhat more in the semantic condition than in the syntactic. The two anomaly conditions resulted in patterns of activity that are largely overlapping, differentiated at only a few sites, as noted below.

Reviewing the results in greater detail: Activity level during the tone condition is compared with activation during the syntactic and semantic judgments, respectively. Figure 1 shows the contrast images for six slices (arranged vertically) for the syntactic and semantic anomaly conditions. Each image (from top to bottom) corresponds to the following positions along the z-axis of the Talairach atlas: 50, 40, 32, 24, 12, and 4. Column A shows sites of activation that reveals statistical significance ($p < .05$) for the syntactic condition relative to its tone baseline; Column B shows the results for the semantic condition relative to its baseline; Column C contrasts directly the syntactic and semantic conditions. The figure legend lists every area that shows positive activation that is statistically significant.

As may be seen from Figure 1, the syntactic and semantic judgment conditions display a similar activation pattern that includes the inferior frontal gyrus bilaterally (BA 44, 45, 47), the middle frontal gyrus bilaterally (BA 46, 9), the superior temporal gyrus bilaterally (BA 22, 41, 42), and the middle temporal gyrus bilaterally (BA 21, 22). Column C, which contrasts directly with the syntactic and semantic conditions, yields a few differences that represent areas that are more active in the semantic condition than in the syntactic condition. These include the inferior frontal gyrus (BA 44, 45, 47) and other frontal sites confined to superior slices; in the inferior slices more activity in the semantic condition is shown in posterior middle and superior temporal gyri (BA 21, 22,
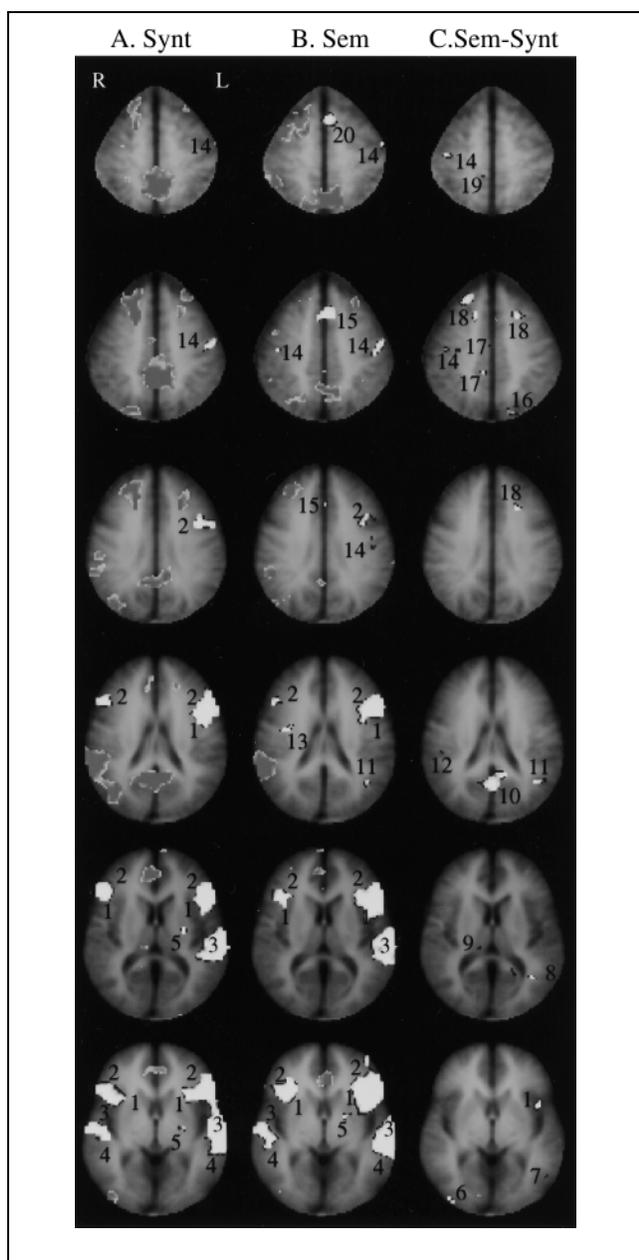
Figure 1. Contrast image maps for anomaly detection experiment. Column A is for syntactic condition minus baseline; column B is for semantic condition minus baseline; column C shows contrast between syntactic and semantic conditions. The numbers on the images indicate significantly activated regions: (1) inferior frontal gyrus (BA 44, 45, 47), (2) middle frontal gyrus (BA 46, 9), (3) superior temporal gyrus (BA 22, 41, 42), (4) middle temporal gyrus (BA 21, 22), (5) basal ganglia, (6) middle occipital gyrus (BA 18, 19), (7) posterior and inferior aspect of middle temporal gyrus (BA 21, 37), (8) posterior superior temporal gyrus near superior temporal sulcus (BA 22), (9) thalamus, (10) posterior cingulate gyrus (BA 23, 31), (11) angular gyrus (BA 39), (12) supramarginal gyrus (BA 40), (13) precentral sulcus (BA 6), (14) central sulcus (BA 4, 3, 1), (15) anterior cingulate gyrus (BA 24, 32), (16) posterior aspect of inferior parietal lobule (BA 19), (17) middle and posterior aspects of the cingulate gyrus (BA 24, 31), (18) superior frontal sulcus and adjacent superior and middle frontal gyri (BA 8, 9), (19) precuneus (BA 7), (20) medial aspect of superior frontal gyrus (BA 6). Note: In each column, section locations from top to bottom correspond approximately to the following z-axis positions of the Talairach atlas: 50, 40, 32, 24, 12, and 4.

37), the angular gyrus (BA 39), and the posterior cingulate gyrus (BA 24, 31).

A question of special interest is whether syntactic and semantic conditions give rise to different patterns of activation in and surrounding the Sylvian region. A statistical comparison was made for two regions of interest (ROIs): the inferior frontal gyrus (BA 44) and the posterior aspect of the superior temporal gyrus (BA 22). Using a number of pixels activated above threshold within each ROI as the dependent variable, ROI and anomaly condition as independent variables, analysis of variance (ANOVA) reveals no main effect of anomaly condition, nor a main effect of ROI. However, the interaction approaches significance ($F(1, 13)=4.46$, $p=.0547$): The syntactic condition induced significantly more activation in BA 44 than in BA 22 ($F(1, 13)=23.11$, $p=.0003$]; the semantic condition yielded little difference in activation in these two regions ($F(1, 13)=3.32$, $p=.0915$).

It is apparent from inspection of Figure 1 that there is more activity in the left hemisphere than in the right. A statistical analysis on activated pixels across the entire cortex confirms a significant main effect of hemisphere: Irrespective of anomaly condition, more areas in the left hemisphere are activated than their counterparts in the right hemisphere ($F(1, 13)=8.31$, $p=.0128$).

Behavioral Data From Task Performance

The accuracy of responding *Yes* or *No* to each trial and the latency of these responses were collected during each imaging session. Accuracy and latency (response time, RT) became the dependent variables in two separate one-way analyses of variance. Stimulus type (sentence vs. pitch) and judgment type (syntactic vs. semantic) were used as independent variables. For accuracy, there is a main effect of stimulus type, which establishes that pitch judgment is significantly more accurate (91.6%) than sentence anomaly judgment (89.2%) ($F(1, 11)=6.72$, $p=.0250$). For sentence anomaly judgment, there is a main effect of judgment type, which reveals that the accuracy on detecting syntactic anomaly is significantly higher (91.6%) than that on detecting semantic anomaly (86.9%) ($F(1, 11)=4.85$, $p=.0499$). The RT data shows that pitch judgment takes significantly shorter (mean=1907 msec) than that for sentence anomaly judgment (mean=2021 msec) ($F(1, 11)=7.25$, $p=.0209$]. There is a numerical trend for syntactic-anomaly judgment (mean=1996 msec) to be faster than semantic anomaly judgment (mean=2045 msec). There is no evidence of speed-accuracy trade-off.

Summary of Experiment 1

There is some behavioral difference between syntactic and semantic anomaly detection, that is, participants
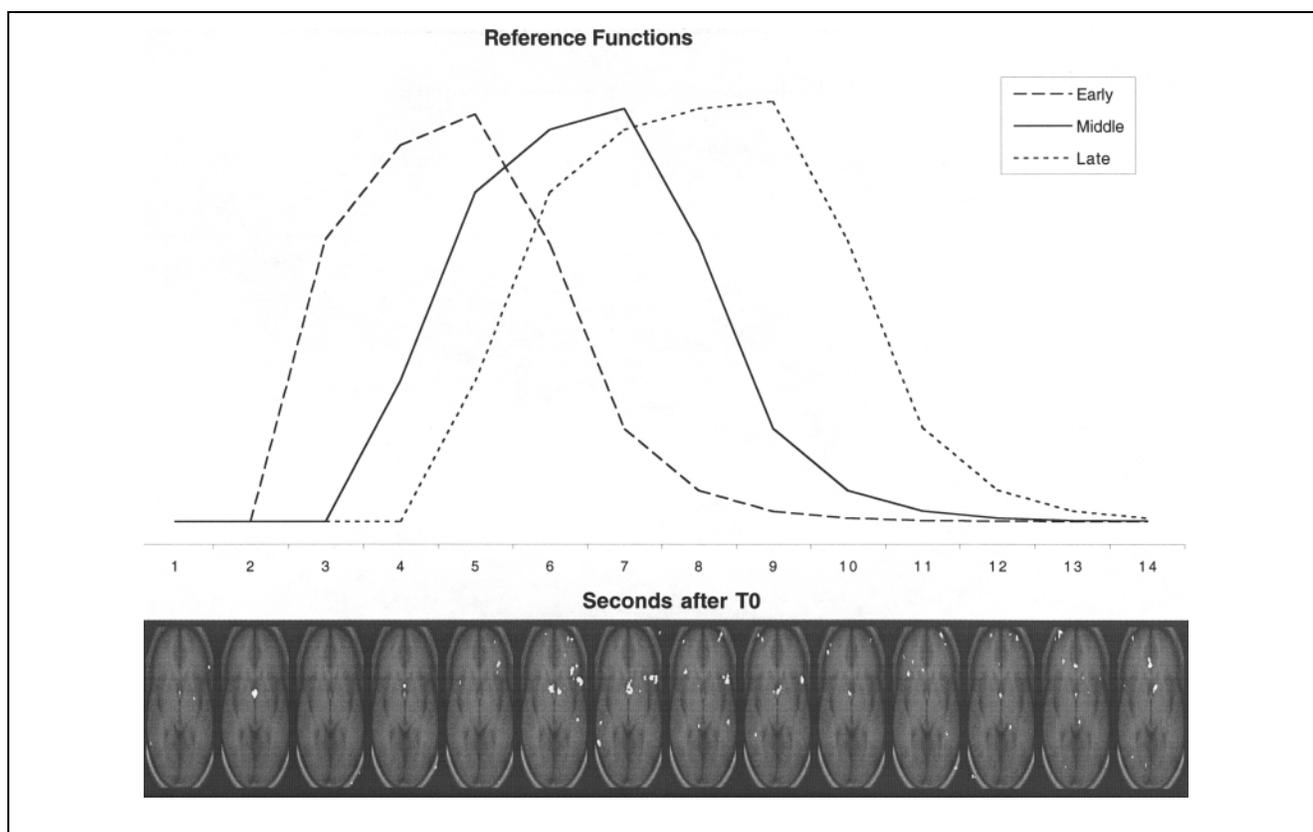
Figure 2. Reference functions—early, middle, late (upper graph) and composite images (lower graph) at successive 1-sec intervals following the onset of the sentences that contain an anomaly.

were more accurate, though not much faster, in detecting syntactic anomalies than semantic. The two anomaly conditions showed largely overlapping brain activation when subtracted from the baseline condition. Activity was observed primarily in the left hemisphere in regions surrounding the sylvian fissure, including the inferior frontal region anteriorly, the posterior superior temporal areas, and angular gyrus posteriorly. These comprise a major portion of the classical language zones identified by lesion studies of aphasic persons and electrical stimulation of the cortex (Ojemann, 1983). In addition, there was more activity superiorly and medially in the frontal region of both hemispheres, slightly more in the semantic condition than in the syntactic condition. A notable difference was the more extensive activation in the posterior sylvian area in the semantic condition.

Experiment 2: Event-related Oddball Paradigm

Imaging Data

Experiment 2 was administered before Experiment 1, and it did not require anomaly detection. Instead, participants were asked to judge whether or not each test sentence contained a living object, a judgment that was unrelated to the target anomaly. Instances of anomalous sentences occurred infrequently in the test order, interspersed irregularly among nonanomalous sentences. Hence, they were *oddballs*. About 5 sec

after onset of the oddballs, increased hemodynamic activity could be detected in and around the sylvian region and in middle and superior frontal areas. Regional activation associated with each type of sentence anomaly is clearly differentiated.

The composite brain images in the bottom part of Figure 2 represents one of six slices taken in the scanner (slice 6, $z=-4$). Fourteen images are shown, each at successive 1-sec intervals following the onset of oddball sentences, displaying residuals with activity of nonanomalous sentences subtracted out. This descriptive map shows that activation levels exceed threshold at latencies of 5–8 sec at several brain sites. The brighter spots on the images represent higher t values reflecting increases in signal strength. The increases are largely confined to known language zones in and around the sylvian region. It is apparent that the left hemisphere is more responsive than the right.

A correlation analysis was undertaken to estimate more precisely the hemodynamic responses following presentation of tokens of oddball sentences. The main purpose of the analysis was to investigate whether specific brain sites responded selectively to anomalies involving sentence form (syntax) and sentence content (semantics). Accordingly, images representing tokens of syntactic anomaly and semantic anomaly were grouped separately. Three idealized activation functions, each approximately symmetrical, were created, as shown on

the upper part of Figure 2. Raw signal intensity at each point of time postonset is correlated with each of the three reference functions. A high (or low) correlation would result if the trajectory of the activation of a particular pixel showed a good (or bad) fit with a particular function.

The results are shown in Figure 3 (syntactic oddballs) and Figure 4 (semantic oddballs). Each figure shows six serial slices through the axial plane arrayed vertically. These images (from top to bottom) correspond to the following positions along the z-axis of the Talairach atlas: 57, 46, 35, 24, 12, and −4. The images are arranged in three columns corresponding to the temporally overlapping idealized reference functions for three latency periods post-onset: early (peaking at about 4 sec postonset), middle (peaking at about 7 sec), and late (peaking at about 10 sec). The bright areas within each image represent activated pixels significantly correlated with the reference function ($p < .05$). Significance was determined by computing the false activation rate for random permutations of the data. In both figures, activity associated with oddballs is in large part limited to the middle and late periods.

In Figure 3, which shows correlated activity associated with isolated instances of syntactic anomaly, little activity is seen corresponding to the early period. Within the middle period, activity is seen predominantly in the anterior regions: inferior and middle frontal gyri on the left (BA 44, 46, 47). In addition, activity is visible in the left superior frontal gyrus (BA 8) and left middle frontal gyrus (BA 6). During the late period, additional sites of activation are seen, more on the right side. These include a portion of the postcentral gyrus, bilaterally (BA 2), and the inferior frontal gyrus and adjacent regions, bilaterally (BA 44, 45, 46, 47). Also activated are the medial aspect of the superior frontal gyrus (BA 8), the right supramarginal gyrus (BA 40), and the head of the caudate nucleus.

Figure 4 shows activity elicited by semantically anomalous sentences. In the early period, activity is found in the medial aspect of the superior frontal gyrus bilaterally (BA 9), and the middle frontal gyrus (BA 6, 9). As in Figure 3, activity during the middle period gives prominence to areas within the peri-sylvian zone long associated with language functions. Within this zone, a difference between syntax (in Figure 3) and semantics (in Figure 4) shows up clearly in slice 5 (from top, middle column). Whereas for syntactic oddballs, only the left inferior frontal region is active, semantic oddballs in Figure 4 show activity in the posterior portion of the superior temporal gyrus (BA 22) that is not seen in Figure 3. Other regions showing activity to semantic anomaly include a small portion of the inferior frontal gyrus (BA 44), the middle frontal gyrus (BA 10, 46), and the medial aspect of the superior frontal gyrus. The late period shows continuing activity in the left middle frontal gyrus (BA 10) and in the posterior aspect of left
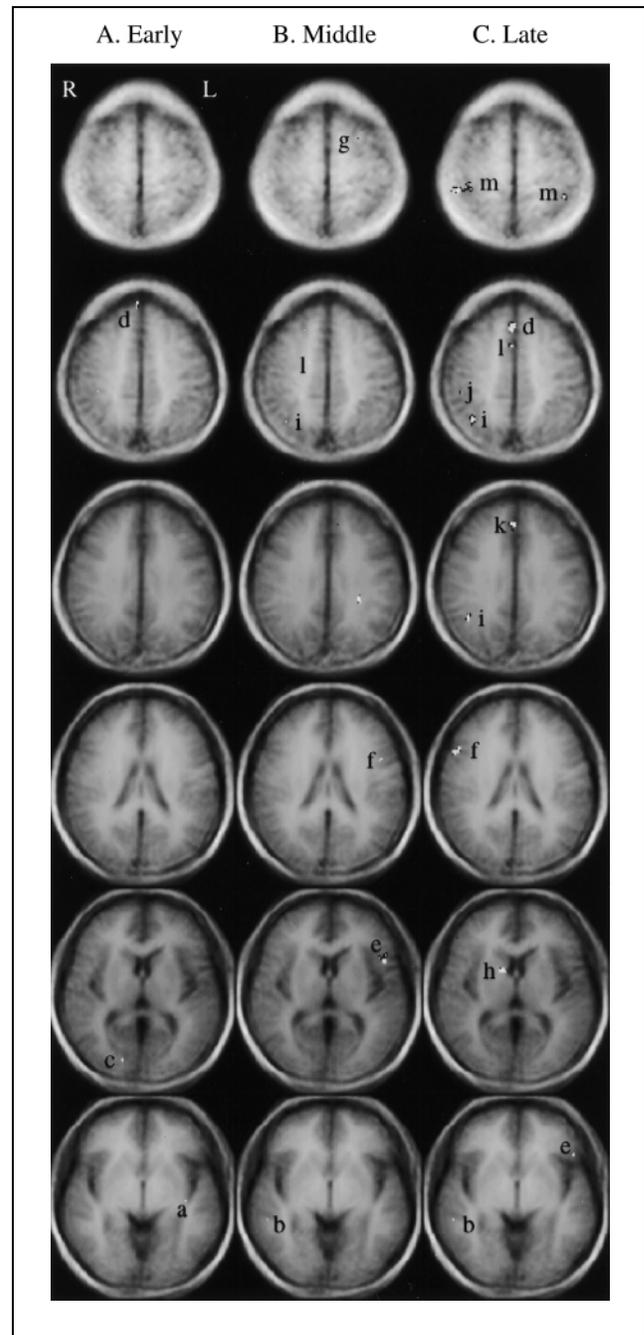
Figure 3. Correlation image maps for syntactic oddball trials. Column A shows activation correlated with the early reference function; column B shows activation correlated with the middle reference function; column C shows activation correlated with the late reference function. Letters correspond to the following regions: (a) junction of posterior insula (circular sulcus) and middle temporal gyrus (BA 21), (b) middle temporal gyrus (BA 21), (c) cuneus and calcarine fissure (BA 17, 18), (d) medial aspect of superior frontal gyrus (BA 8), (e) inferior frontal gyrus (BA 44, 45, 47), (f) inferior and middle frontal gyri (BA 44, 46), (g) superior aspect of middle frontal gyrus, adjacent to superior frontal sulcus (BA 6), (h) head of caudate nucleus, (i) angular gyrus of the inferior parietal lobule (BA 39), (j) supramarginal gyrus of the inferior parietal lobule (BA 40), (k) medial aspect of superior frontal gyrus (BA 9), (l) anterior cingulate gyrus (BA 24, 32), (m) postcentral gyrus region (BA 2). Note: In each column, section locations from top to bottom correspond approximately to the following z-axis positions of the Talairach atlas: 57, 46, 35, 24, 12, and −4.
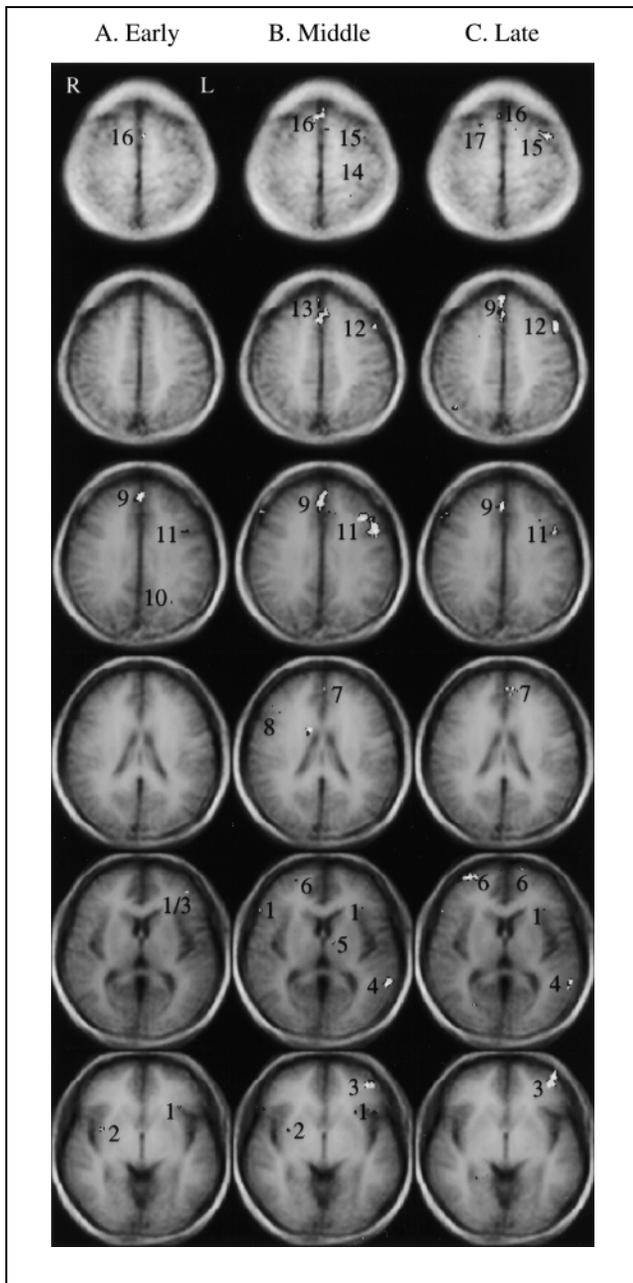
Figure 4. Correlation image maps for semantic oddball trials. Column A shows activation correlated with the early reference function; column B shows activation correlated with the middle reference function; column C shows activation correlation with the late reference function. Numbers correspond to the following regions: (1) inferior frontal gyrus (BA 44, 45, 47), (2) subinsula and claustrum region, (3) middle frontal gyrus (BA 10, 46), (4) posterior superior temporal gyrus (BA 22), (5) basal ganglia (globus pallidus), (6) superior and middle frontal gyri (BA 10, 46), (7) anterior cingulate sulcus and gyrus (BA 24, 32), (8) middle frontal gyrus (BA 46), (9) medial aspect of superior frontal gyrus (BA 9), (10) angular gyrus of the inferior parietal lobule (BA 39), (11) middle frontal gyrus (BA 9), (12) middle frontal gyrus (BA 8), (13) medial aspect of superior frontal gyrus (BA 8), (14) superior parietal lobule and postcentral gyrus regions (BA 2, 40), (15) middle frontal gyrus (BA 6), (16) medial aspect of superior frontal gyrus (BA 6), (17) superior frontal sulcus and adjacent superor and middle frontal gyri (BA 6). Note: In each column, section locations from top to bottom correspond approximately to the following z-axis positions of the Talairach atlas: 57, 46, 35, 24, 12, and −4.

superior and middle temporal gyri (BA 22). Medial and superior aspects of the left middle frontal gyri also remain active (BA 8, 9). Finally, the medial superior frontal gyrus (BA 6) continues to be active.

Behavioral Data From Task Performance

Participants' RTs to judge whether each test sentence contained an animate object were tabulated separately for nonanomalous sentences (the controls), and the isolated occurrences of anomalous sentences (the oddballs). A 2×2 ANOVA was performed with sentence type (control vs. oddball) and anomaly type (syntactic oddball vs. semantic oddball) as independent variables. The results show that RTs on the oddball sentences are significantly longer (mean=2139 msec) than RTs on the control sentences (mean=1920 msec) ($F(1, 11)=34.67$, $p=.0001$). Planned comparisons reveal that RTs are significantly longer for both the syntactic oddballs (mean=2119 msec) and the semantic oddballs (mean=2162 msec), compared with their respective nonanomalous control sentences (syntactic oddballs vs. controls ($F(1, 11)=22.48$, $p=.0006$); semantic oddballs vs. controls ($F(1, 11)=21.97$, $p=.0007$)). However, there is not a significant difference in RT between the two types of oddball sentences ($p. 120$).

Summary of Experiment 2

Although the two types of anomalous sentences did not differ in the response time to perform an unrelated task (animacy judgment), they did differ in the brain's response. Different patterns of regional fMRI activity within the left hemisphere are associated with each type of sentence anomaly. Syntactic anomalies activated the inferior frontal region strongly and posterior regions minimally. Semantic anomalies yielded more activity overall in both hemispheres, engaging both anterior (middle and superior frontal) and posterior zones (superior temporal and parietal). With regard to peri-sylvian cortex, long recognized as a critical zone for language functions, syntactic anomalies yielded a complementary pattern relative to semantic anomalies, engaging the posterior superior temporal area weakly and the inferior frontal region strongly. The findings thus support evidence from other sources implicating the left inferior frontal region in syntactic operations.

DISCUSSION

The present study yields new evidence for distinctiveness of the intact brain's response to syntax vis-a-vis semantics. This outcome was reached by way of the separate contributions of each of the two experiments. This discussion reviews the logic of the design of the experiments, the findings, and their interpretation.

The logic dictated use of the same sentence materials and the same subjects in two different paradigms. In Experiment 1, comparisons were made between a non-language control task and consecutive linguistic tasks involving detection of syntactic and semantic anomalies. The results show that hemodynamic activity specific to these linguistic operations can be isolated from activity associated with nonlinguistic aspects of the task, such as attending to and processing the auditory input. Activity during syntactic and semantic anomaly detection is largely overlapping. Sites of activation include most of those reported in earlier studies using PET or fMRI with sentence materials. Overlap between syntactic and semantic anomaly trials is not complete, however. The pattern of activity generated by the semantic condition is somewhat more widespread within the hemispheres than that associated with the syntactic condition and is more bilaterally distributed.

Experiment 1 required the participants to monitor for the well-formedness, syntactic or semantic, and actively detect specific instances of anomaly. This process could be expected to engage all portions of the language cortex, as well as areas that are active during a variety of error detection tasks. In fact, what we see in the hemodynamic record (in Figure 1) is largely combined activity for syntactic and semantic processing. The more extensive activation by semantic processing may reflect that in order to determine whether or not a sentence makes sense, the grammatical structure must be parsed and factual knowledge must be brought to bear.

Experiment 2, using an event-related approach, was designed to isolate the effects of syntactic and semantic anomaly. The results yielded evidence of separation of the effects on brain activity of each type of sentence anomaly, which did not appear in Experiment 1. Since the stimulus materials for each experiment are the same, the differences in task structure and experimental design are apparently critical. The two types of anomalous sentences occurred as infrequent events (oddballs) interspersed among the more numerous nonanomalous sentences. Regional activity shows up as significant correlations between obtained fMRI signals evoked by the oddball trials and idealized functions that track the time course of activation following the onset of each oddball. Unlike Experiment 1, where the task is explicit anomaly detection, in Experiment 2, participants' attention is drawn to a task (animacy detection) that is irrelevant to either kind of anomaly. Therefore, any activity from the anomalous oddballs, over and above the nonanomalous baseline sentences, reflects interference with the normal processing of sentence input. Since the results of this experiment yield residual effects of oddball trials subtracted from nonoddball trials, regional brain activity common to each type of anomaly and its respective baseline condition is neutralized. In consequence, the seemingly sparse activation displayed

in Figures 3 and 4 accurately reflects the isolation of syntactic or semantic interference for a given region within a given time window. Accordingly, differences in appearance between images from the anomaly detection experiment (Figure 1) and those from the oddball experiment (Figures 3 and 4) do not reflect differences in the sensitivity of the two experiments to detect relevant activity.

Inasmuch as Experiment 2 was successful in distinguishing syntactic and semantic activation, we consider the anatomic findings in some detail. In the middle period following oddball onset (Figure 3, Column B), significant activity specific to syntactic anomaly is found only in the left anterior region (with the exception of one slice). In the late period (Figure 3, Column C), there is corresponding activity on the right, and, in addition, there is right-sided activity in the superior and medial frontal and temporal sites.[1]

In comparing the differences between anomaly conditions, it is appropriate to give special weight to the pattern of activity within the peri-sylvian region. Neuropsychological theory and findings link grammatical disturbances to lesions of the dominant inferior-frontal gyrus, whereas disturbances of semantic comprehension of words and sentences are linked with temporal-lobe lesions involving, but not necessarily restricted to, the posterior portion of the peri-sylvian region (Damasio, 1992; Friederici, 1995; Goodglass, 1993). This dissociation is supported by ERP findings based on sentence processing by normal subjects (Hagoort et al., 1998). In view of these considerations, it is noteworthy that Experiment 2 yields complementarity in the distribution of activity within the peri-sylvian region for the two types of sentence anomaly. As may be seen by comparison of slice 5 (from the top middle column) in Figures 3 and 4, syntactic anomalies activated Broca's region chiefly, with smaller sites posteriorly in middle temporal and parietal regions (for example, angular gyrus) also showing some activity. Semantic anomalies yielded the reverse asymmetry, activating chiefly the posterior part of the superior temporal area (Wernicke's area) with minimal activation within the inferior frontal gyrus.

On the issue of division of labor within the left peri-sylvian region, the findings of Experiment 2 give an unequivocal indication of the involvement of Broca's area in syntactic operations. Although, as far as we are aware, the imaging literature does not offer instances of a direct comparison of the effects of syntactic and semantic processing, there have been efforts to identify sites that reflect either syntactic or semantic processing. In that respect, the results of this experiment (and Experiment 1 as well) are in keeping with indications in the existing literature pointing to the involvement of posterior temporal regions in semantically driven sentence processing. Directly pertinent is a recent result with the MEG technique by Helenius, Salmelin, Service,

and Connolly (1998) who found, with sentence materials similar to the semantic anomaly condition in the present study, that the cortical structures implicated most consistently in detecting a semantically odd final word were located in the middle and posterior portion of the superior temporal region.

Asymmetries in the activity pattern within the perisylvian zone do not exhaust the regional differences evoked by syntactic and semantic anomalies, however. Other sites within the frontal lobe, but outside the peri-sylvian region, which were differentially active, should be noted. From Figures 3 and 4, it is apparent that semantic anomaly evoked activity in middle and superior frontal regions, whereas syntactic anomaly did not activate these additional frontal sites. Parallels can be cited from the literature. Stromswold et al. (1996), whose subjects judged sentences for semantic acceptability, reported an increase in rCBF in the superior frontal lobe near the midline, when activity related to processing nonanomalous sentences was subtracted from activity evoked by sentence material containing nonsense words. Kang et al. (in press) found fRMI activity in the middle frontal region when subjects judged the semantic coherence of two-word phrases. Finally, there is evidence linking left frontal premotor activity at several sites with a variety of word judgment tasks that have a semantic dimension (Gabrieli, Poldrack, & Desmond, 1998). Thus, we can say that the results of the present experiment are in keeping with the weight of evidence in the neuroimaging literature that implicates both frontal and temporo-parietal regions in semantic activity. Whether the anterior and posterior semantically active sites form two poles of a single system will be an important question to investigate in the future.

It should be appreciated that, in part, the complexities of the task of establishing markers for syntactic and semantic aspects of linguistic processing are conceptually based. Although the idea of syntactic structure is well-circumscribed (indeed, syntax has sometimes been viewed as a self-contained processing module), the concept of semantics is so inclusive as to be vague. The variety of stimulus content and tasks that might be characterized as ''semantic'' is almost limitless. Given this diversity, it should not surprise us to find many cortical areas implicated in activities that have been called semantic. Functional groupings among them will have to be sought.

With regard to the role of task and procedure, this research raises questions that we can pose, but cannot resolve, from the data of the present study. For example, Experiments 1 and 2, alike in their stimulus materials, have two major differences: whether the critical structure is frequently occurring in the stimulus list (as in Experiment 1) or infrequently occurring (as in Experiment 2), and whether the subject's task is explicit anomaly detection (Experiment 1), or whether there is

an irrelevant task and an implicit effect of anomaly can be detected in the brain's response (Experiment 2). Additional studies will be required to evaluate whether it is the infrequent event aspect of Experiment 2 that is critical to the result, or, alternatively, whether the explicit–implicit task dimension is a critical condition for detecting a syntactic marker.

The full role of the inferior frontal region across the different dimensions of language processes remains to be clarified. There is overwhelming evidence that it is implicated in linguistic processing both at the phonological level and higher linguistic levels (Gabrieli et al., 1998).[2] Its relations with other portions of the premotor cortex and with the posterior sylvian region remain to be worked out. For one thing, Broca's area is, in all likelihood, functionally heterogeneous. It may well be too gross a region to identify as a target structure for any specific language function, without further subdivision. Already, there are findings in the research literature that support the view that Broadmann's areas 44 and 45 are morphologically and perhaps functionally distinct (Amunts et al., in press). Additional fMRI studies using techniques such as the event-related single-trial procedure will be needed to resolve questions originally posed by Broca (1861) himself concerning the optimal grain size for structure-to-function mapping.

What might be the basis for the involvement of Broca's region in syntax? Syntax has long been characterized as inherently motoric given that language is conveyed by coordinated sequences of linguistic elements (Jakobson, 1970). The region in question is, of course, a part of the premotor cortex. It has been proposed by Rizzolatti and Arbib (1998) that Broca's area is an analog in humans to a frontal region in the monkey brain where the authors find ''mirror neurons'', cells that fire when the monkey is either executing or observing communicative gestures. The hypothetical link with language, and specifically syntax, is through imitation of sequences of motor gestures, a possible mechanism for language evolution and a principle of organization of the language modality (Studdert-Kennedy, in press).

It is worth emphasizing that the indication of separate markers for syntactic and semantic processes finds a parallel in behavioral findings to which we referred earlier. These are based on eye-movement patterns in reading sentences containing the same anomalies of syntax and semantics that were studied in the scanner. Regressive eye movements during the reading of a sentence are indicators that the parser has encountered a stumbling block and must review earlier portions of the sentence to locate the source of the problem. Ni et al. (1998) found that distinctive patterns of eye movements are triggered by each type of anomaly. Syntactic anomalies caused abrupt, temporary disturbances in processing that are quickly resolved, shown by immediate but short-lived increases of regressive eye move-

ments after the point of anomaly. In contrast, semantic anomalies cause regressions that persist and increase up to the end of the sentence. Arguably, these perturbations reflect subjects' repeated attempts to find a coherent semantic interpretation. The differences related to type of anomaly suggest that syntactic and semantic information is used in a different manner during the early, automatic phase of sentence processing.

Complementing these behavioral indicators, there is neurobiological support for the hypothesis of a specialization for a specific computation, such as syntax. The timing and distribution of distinct ERP effects is one such indication that syntactic and semantic processes are isolable subsystems within the language apparatus (Neville et al., 1991). The evidence that specific brain sites are reliably active during syntactic processing constitutes further evidence for a specialized module within the language system.

In conclusion, Experiment 1 distinguishes linguistic activity in sentence processing from nonlinguistic baseline activity associated with the anomaly detection tasks. The results of Experiments 1 and 2 converge and agree with evidence from other sources in finding sites surrounding the left peri-sylvian region specifically implicated in linguistic activity associated with sentence processing. Corresponding activity in the right hemisphere was present at some locations. Evidence mainly from Experiment 2, which exploited event-related methodology, indicates that within the peri-sylvian region, syntactic computations are separately localized from semantic interpretation. Syntactic processing evokes major activity anteriorly (in Broca's area) and semantic processing evokes activity more diffusely with a focus in the posterior temporal region (Wernicke's area). The findings support the implications of psycholinguistic studies and ERP studies that syntactic parsing is encapsulated from the processes of semantic interpretation.

METHOD

Subjects

Fourteen healthy, right-handed, young adults (11 male, three female) participated in the experiments. They are all native speakers of English. The participants listened and responded to short English sentences while their brain activity was recorded using fMRI. They were tested on both the anomaly detection experiment (Experiment 1) and the oddball experiment (Experiment 2) within the same scanning session.

Materials

The stimuli comprised 44 short sentences that differed minimally between anomalous and nonanomalous items and between different types of anomaly. The anomalous sentences were equally divided between violations of syntactic form and semantic sensibility. For the syntactic anomaly condition, the stimulus sentences were meaningful, but they contained violations of verb form (for example, *Trees can grew.). For the semantic anomaly condition, the stimulus sentences were grammatical, but expressed propositions that were transparently false or absurd (for example, *Trees can eat.). Control sentences were nonanomalous, matched closely to the anomalous sentences (for example, Trees can grow.). Two types of sentence constructions were used: subject-verb (for example, Trees can grow.) and verb-object (for example, They can grow trees.). Thus, anomalous sentences of each type, and their corresponding controls, were created with the same sentence frame in matched triplets, as in ''Trees can grow/grew/eat'' and ''They can grow/ grew/eat trees.''

Procedure

Two experiments were conducted with the same set of materials. The experiments differed in arrangement of the anomalous and control sentences and in the specific task the participants were asked to perform. In the test sequence, a new sentence occurred every 4.5 sec. Presentation of stimulus materials was controlled by a Macintosh computer. The auditory stimuli were presented via an air conduction system with foam ear inserts. Headphones provided additional shielding from the scanner noise. The participants were instructed to respond to every sentence by pressing one of two buttons. Their responses and latencies were recorded using a fiber optic button box connected to the computer.

Experiment 1, sentence anomaly detection, consisted of four runs, each lasting 4 min. Within each run, 24 sentences were presented (12 anomalous, 12 controls), as well as 24 pairs of tones (12 same=same in pitch, 12 different=vary in pitch). The sentences were randomized and placed into four blocks (six sentences in each block), as were the tone pairs. Blocks of sentences alternated with blocks of tone pairs. The first two runs contained semantically anomalous sentences. The task was to press one of two buttons (''Yes'' or ''No'') after listening to each sentence to indicate whether or not the sentence made sense. The remaining two runs contained syntactically anomalous sentences. The task was to judge whether or not each sentence was grammatical. For the baseline condition of tone pairs, the response was to indicate whether each pair of tones was on the same pitch (High/High or Low/Low=''Yes'') or on different pitches (High/Low or Low/High=''No'').

In Experiment 2, the oddball paradigm, the participants completed six test runs, each lasting 3 min. In each run, 44 sentences were presented, of which seven were anomalous (oddballs). The oddballs were interspersed quasi-randomly among the nonanomalous sentences. At least six nonanomalous sentences occurred between

each instance of an oddball, so that changes in hemo-dynamic activity that resulted from the infrequent trials could return to near baseline (Robson et al., 1998). The first three runs contained semantic oddballs, and the remaining three runs contained syntactic oddballs. The participants' task was to press one of two buttons after listening to each sentence to indicate whether or not the sentence contained a "living thing". For example, a "Yes" response was expected for sentences like "Monkeys can jump" or "Snakes can glided". A "No" response was expected for sentences like "Computers can save".

Prior to going into the scanner, the participants were given examples of the test materials (sentences and tone pairs) and practice with the response button box. The oddball experiment, which did not require the partici-pant to attend to either type of sentence anomaly, was administered first. The participants were not told that there would be anomalous sentences in the first six runs of the session. Following these runs, the anomaly detection experiment began. The participants were in-structed to listen for a syntactic or semantic anomaly and make an explicit judgment on each sentence. The participants were reminded during the intervals be-tween each run which task would immediately follow. The test session for each participant, which included instructions, practice, actual test runs, and calibration and data offloads between each run, lasted approxi-mately 90 min.

The image scans were acquired with a General Electric Signa 1.5 T whole-body scanner fitted with echo planar capability. Following acquisition of sagittal T1 weighted images, six T1-weighted axial anatomical images were acquired in a plane parallel to the anterior–posterior commissural plane (flip angle $\alpha = 60°$, matrix$=128 \times 64$). Slices were positioned for maximum coverage of frontal, temporal and parietal lobes.

Echo-planar images (EPI) were acquired at the same locations as the axial anatomical images using the fol-lowing imaging parameters: Repetition time (TR): ano-maly detection experiment$=1380$ msec, oddball experiment$=1050$ msec; echo time (TE): 60 msec; slice thickness: 10 mm with a 1-mm gap; acquisition matrix: 128×64; field of view (FOV): 40×20 cm^2; in-plane resolution: 3.1×3.1 mm^2. Each scan consisted of 170 images at each of the six slice locations. Imaging time per run was 4 min for the anomaly detection experiment and 3 min for the oddball experiment..

Data Analysis

Behavioral Data From Task Performance

The accuracy of responses to each trial (accuracy) and the latency of these RT were collected. Both accuracy and RT were used as dependent variables in an ANOVA for data from the anomaly detection experiment. For the

oddball experiment, only RT data were used in the analysis, since the required responses (animacy judg-ments) were orthogonal to the targets of the study (syntactic and semantic anomalies). Due to technical failure of the response button box, behavioral data were collected from 12 of the 14 subjects.

Imaging Data

For both experiments, prior to statistical analysis, the images from each run were motion corrected for three translation directions and for the three possible rota-tions using the SPM-96 program (Friston et al., 1995). The corrected images were spatially filtered using a Gaussian filter with a full-width half-maximum value of 6.5 mm.

Experiment 1 — Anomaly detection. As a first step, brain activity associated with the tone blocks was sub-tracted from that associated with the sentence blocks for each subject. A composite map was generated showing the residuals attributed to sentence processing. Then, we conducted an analysis using statistical contrasts with the following steps. First, for each task (syntactic judg-ment and semantic judgment), a t statistic was com-puted from the comparison of the MRI signal from that task and the associated baseline task. The correction for linear drift was built into this calculation (Skudlarski, Constable, & Gore, in press). These t maps and the anatomic images from individual subjects were trans-formed by in-plane transformation and slice interpola-tion into a proportional 3-D grid defined by Talairach and Tournoux (1988). These t statistics provided a derived measure of the signal change at each voxel relative to its own intrinsic noise variability. Second, for each effect of interest, a standard linear contrast (C) (Hayes, 1988) was computed across subjects. This procedure generated a single value that was determined by the comparison of one task against another, or against zero. For instance, a contrast that identifies the areas affected by the syntactic condition was generated by computing the average t statistic across subjects, relative to its baseline condition. Under the null hypoth-esis of no effect, the expected value of the mean of this contrast (across subjects) is equal to zero.

With an appropriate error term, C can be used to generate a t statistic and a p-value for the significance of this effect. However, we chose to avoid distributional assumptions and to obtain a p-value through randomi-zation (Manly, 1997). This test was carried out by randomly selecting half of the subjects, reversing the designation given to their raw data (that is, syntactic condition or baseline), recomputing their t statistics, and recomputing the same linear contrast C' across all subjects. Since the expected value of C under the null hypothesis was zero, the expected value of C' is also zero since, on average, the randomization of task means

would cancel out any real effects. This procedure was repeated with a different randomization 10,000 times. This allowed us to generate the sampling distribution of C under the null hypothesis. The actual (observed) value of C was assigned a p-value according to its position in this distribution. In summary, the proportion of times that the observed contrast value C was more extreme than the randomized value C' is a p-value in the most direct sense: It represents the proportion of times we would expect to obtain a value of C as large or larger than the one actually obtained, if the null hypothesis were true. The resulting p-value for each voxel is overlaid upon the mean anatomic image for display. The threshold used is $p = .05$.

Experiment 2—Event-related single-trial (oddball) paradigm. First, we separated the images for anomalous sentences (the oddballs), and the remaining nonanomalous sentences. The images corresponding to the onset of each anomalous sentence (oddball) formed the time zero baseline (T0). Subsequent images corresponding to times 1–13 sec postonset were compared with this baseline. We computed a t value for each pixel as the dependent measure, comparing activation at each successive time interval with the level at T0. This approach allowed us to identify increases (or decreases) in composite signal intensity within the time window of 1–13 sec after the onset of each oddball.

For statistical demonstration of the oddball effect, a correlational analysis was carried out. Pixels that responded to the oddball trials were identified by correlating the raw signal from each scan at each successive time from onset with each of the three candidate reference functions depicted in Figure 2 (that is, early, middle, and late peaking). Each reference function represents a series of expected hemodynamic responses. Individual subject maps were created by determining the correlation with the reference function of the obtained signal for each pixel at each time point. Only those pixels responsive to the oddballs would be correlated with the reference function. Accordingly, the expected reference function for nonanomalous sentences (nonoddball trials) would be zero at all time points. Thus, a pixel responsive to the oddballs would be correlated with the reference function to the extent that it showed a hemodynamic response to oddball trials and a zero response to nonoddball trials. To assess the reliability of these activations across subjects, a permutation test was used to obtain p-values for each pixel for these correlations vs. zero in the same manner as described for the contrast maps in Experiment 1.

Notes

1. Bavelier et al. (1997) report that the only right-hemisphere site of activation associated with their study of sentence processing was in the middle temporal gyrus. It is interesting to note that in the present study, a small right middle temporal site (Figure 3B, slice 5) was found in response to syntactic oddballs.

2. In suggesting that the results of the present study argue for a privileged role for sites in inferior frontal cortex in syntactic function, we would not wish to exclude other cortical areas which may be important also, but are operating at too low a threshold for us to see them on the image maps. Needless to say, further confirmation, especially with the promising event-related single-trial method of fMRI study, is needed. It must be noted, in any case, that studies of the effects of brain lesions on language function and electrical stimulation of the open cortex during operations on the brain have each yielded evidence that additional regions are implicated in grammatical function. Thus, for example, stimulation studies reveal sites in frontal, temporal, and parietal areas that evoked syntax errors specifically (Ojemann, 1983). These sites correspond roughly to areas that when damaged may give rise to aphasias of the agrammatic type (for example, Alexander, Naeser, & Palumbo, 1990).

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