Distinct Patterns of Neural Modulation during the Processing of Conceptual and Syntactic Anomalies

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Abstract

■ The aim of this study was to gain further insights into how the brain distinguishes between meaning and syntax during language comprehension. Participants read and made plausibility judgments on sentences that were plausible, morphosyntactically anomalous, or pragmatically anomalous. In an event-related potential (ERP) experiment, morphosyntactic and pragmatic violations elicited significant P600 and N400 effects, respectively, replicating previous ERP studies that have established qualitative differences in processing conceptually and syntactic anomalies. Our main focus was a functional magnetic resonance imaging (fMRI) study in which the same subjects read the same sentences presented in the same pseudorandomized sequence while performing the same task as in the ERP experiment. Rapid-presentation event-related fMRI methods allowed us to estimate the hemodynamic response at successive temporal windows as the sentences unfolded word by word, without assumptions about the shape of the underlying response function. Relative to nonviolated sentences, the pragmatic anomalies were associated with an increased hemodynamic response in left temporal and inferior frontal regions and a decreased response in the right medial parietal cortex. Relative to nonviolated sentences, the morphosyntactic anomalies were associated with an increased response in bilateral medial and lateral parietal regions and a decreased response in left temporal and inferior frontal regions. Thus, overlapping neural networks were modulated in opposite directions to the two types of anomaly. These fMRI findings document both qualitative and quantitative differences in how the brain distinguishes between these two types of anomalies. This suggests that morphosyntactic and pragmatic information can be processed in different ways but by the same neural systems. ■

GENERAL INTRODUCTION

An inherent property of language is that grammatical rules (syntax) and meaning (semantics and pragmatics) constitute different types of information (Chomsky, 1965). In order to compute higher representations of meaning as language unfolds, syntactic and conceptual information* must be combined effectively and quickly. The question of whether and how syntax and meaning are distinguished by the brain during language processing is of fundamental importance not only to our understanding of how language is processed but to how the mind and brain are organized (Fodor, 1983). This overall question has been approached from different perspectives.

Some studies have focused on the process by which noun phrases are connected to the grammatical positions that determine their thematic roles, thereby enabling us to interpret the meaning of whole sentences. There is some evidence from lesion (Grodzinsky, 2000; Caramazza & Zurif, 1976) and functional neuroimaging studies (Cooke et al., 2002; Caplan, Alpert, Waters, & Olivieri, 2000; Dapretto & Bookheimer, 1999; Inui et al., 1998; Stromswold, Caplan, Alpert, & Rauch, 1996) that the left perisylvian inferior frontal cortex (Broca's area) is engaged in such processes. On the other hand, deficits in syntactic comprehension (Caplan, Hildebrandt, & Makris, 1996) and in the performance of tasks that require access to lexico-semantics (Dick et al., 2001) follow lesions throughout the peri-sylvian cortex. Moreover, other functional neuroimaging studies suggest that such aspects of syntactic processing are mediated not only by Broca's area, but also by posterior regions (Caplan et al., 2001; Stowe et al., 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996).

Other studies have investigated the effect of lexical semantic meanings on syntactic processing. One approach focuses on the build-up of syntactic structure independently of the lexico-semantic content of individual words. Event-related potential (ERP) effects have been reported to syntactic anomalies in sentences made up of pseudowords that do not have meaning (Munte, Matzke, & Johannes, 1997) and recent functional neuroimaging studies suggest that the left inferior prefrontal cortex may be involved in syntactically parsing pseudoword sentences (Indefrey, Hagoort, Herzog, Seitz, &

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Brown, 2001; Moro et al., 2001). Another approach focuses on syntactic ambiguity resolution during online processing and suggests that lexico-semantic factors can influence the build-up of syntactic structure during the very earliest stage of parsing (MacDonald, Pearlmutter, & Seidenberg, 1994). ERP studies support the idea that, at least under some circumstances, semantic and pragmatic parameters can have an immediate (i.e. online word-by-word) influence on the build up of the structure of a sentence (Weckerly & Kutas, 1999).

A third approach, rather than focusing on the interaction between conceptual and syntactic processing (its stage or its spatial location), simply asks the question of whether or not the language processing system recognizes syntactic and conceptual information as distinct. This question can be addressed by examining the effects of introducing different types of anomalies into sentences. This approach has a long precedent in both the behavioral and event-related potential (ERP) literature. Contrasting the effects of introducing syntactic and conceptual anomalies tells us how the language processing system recognizes, integrates, or recovers from these different types of violations. As discussed below, there is evidence from ERP studies that such processes of recognition, integration, and recovery are engaged during normal on-line language processing at points of syntactic or pragmatic ambiguity or increased processing demand. The current study adopts this third approach. Below, we review behavioral, ERP, and functional neuroimaging studies that are directly relevant to this question.

Processing Anomalies: Behavioral Psycholinguistic Studies

On a behavioral level, the introduction of anomalies into sentences has been particularly helpful in determining the relative time courses of processing conceptual versus syntactic information. When subjects make explicit judgments about whether or not sentences make sense, syntactic violations are detected sooner than semantic (McElree & Griffith, 1995) and pragmatic (Fodor, Ni, Crain, & Shankweiler, 1996) violations. These findings have been taken as evidence for a temporal distinction in processing syntactic and conceptual information. This might occur because the output of conceptual processing is delayed relative to the formation of syntactic structure (which has a finite rule system). Further evidence that conceptual processing may be delayed relative to syntactic processing comes from studies that have reported distinct patterns of eye movements to syntactic and pragmatic anomalies in sentences (Fodor et al., 1996).

Processing Anomalies: Event-Related Potential Studies

The introduction of anomalies in sentences is one of the main paradigms that has been used in ERP studies of language processing. Unlike reaction times (RTs), ERPs can be similar or different along several dimensions—waveform, polarity, scalp distribution, and latency. They can thus help establish qualitative similarities or differences between on-line processing of different types of linguistic information. A distinct ERP effect has been described in association with words that are conceptually anomalous in comparison with nonviolated words. An N400 effect is not only elicited by conceptual anomalies in sentences: Its amplitude is also sensitive to semantic associations between single words (Bentin, McCarthy, & Wood, 1985), as well as to the expectancy of a word in normal sentences given its conceptual context (van Berkum, Hagoort, & Brown, 1999; Kutas & Hillyard, 1984). Two waveforms have been observed in association with a variety of syntactic violations: the left anterior negativity (LAN) occurring between approximately 300 and 500 msec with an anterior, sometimes left-lateralized scalp distribution (Friederici, 1995), and a posteriorly distributed positivity between 500 and 1200 msec after stimulus onset—the P600 (Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992). It has been proposed that the LAN reflects the initial build-up of syntactic structure (Friederici, 1997; Rayner, Carlson, & Frazier, 1983) while the P600 reflects a stage of syntactic reanalysis (Friederici, 1997) or integration (Kaan, 2000). Both the LAN and the P600 are elicited by words in normal sentences at points of increased syntactic ambiguity (Osterhout, Holcomb, & Swinney, 1994) or syntactic integration difficulty (Kaan, 2000). Although the precise operations indexed by the LAN and the P600 remain controversial (Osterhout & Hagoort, 1999; Coulson, King, & Kutas, 1998; Friederici, 1997), it is generally agreed that they are both distinct from the N400.

Processing Anomalies: Functional Magnetic Resonance Imaging Studies

There have been several attempts to use the anomaly paradigm in functional neuroimaging studies of language. Meyer, Friederici, and von Cramon (2000) and Embick, Marantz, Miyashita, O'Neil, and Sakai (2000) both introduced syntactic anomalies into sentences and compared them with normal spoken sentences and written sentences with spelling anomalies, respectively. Meyer et al. (2000) reported activation in the left superior temporal gyrus, while Embick et al. (2000) reported activation in Broca's area in association with the syntactic anomalies. Kiehl, Laurens, and Liddle (2002) introduced semantic anomalies into written sentences and reported relatively greater activation in association with the anomalies in a widespread network that included infero-medial temporal and frontal (bilateral inferior frontal and left lateral frontal) cortices.

Of most relevance in determining whether the brain distinguishes syntactic and conceptual anomalies are the studies conducted by Newman, Pancheva, Ozawa, Neville, and Ullman (2001), Kuperberg et al. (2000), Ni et al. (2000), and Kang, Constable, Gore, and Avrutin (1999), in which functional activation in association with both types of anomalies was examined in the same subjects. Each of these studies reports activity in widespread cortical regions in contrasting both conceptually and syntactically anomalous sentences with normal sentences. Yet, each study comes to different conclusions as to which brain regions are specifically involved in processing semantic/pragmatic versus syntactic information. Kuperberg et al. (2000) conclude that left and right temporal cortices are more involved in processing pragmatic and semantic (selection restriction) anomalies respectively than in processing syntactic (subcategorization) anomalies, but failed to find any brain regions that were specifically modulated in association with subcategorization anomalies. Ni et al. (2000) and Kang et al. (1999) conclude that left inferior frontal regions are more involved in processing syntactic anomalies while more posterior temporal regions play a greater role in processing semantic anomalies. Newman et al. (2001) conclude that medial and lateral superior frontal regions are involved in computing syntactic anomalies while left inferior frontal, medial temporal, and right temporal regions are involved in processing semantic anomalies.

Some of these discrepancies between studies may have arisen from differences in the types of conceptual and syntactic anomalies used—pragmatic (Kuperberg et al., 2000; Ni et al., 2000) and selection restriction (Newman et al., 2001; Kuperberg et al., 2000), subcategorization (Kuperberg et al., 2000), structural (Newman et al., 2001), and subject–verb agreement (Ni et al., 2000). Other discrepancies may have arisen from limitations and differences in experimental design. For example, in three of these studies (Kuperberg et al., 2000; Ni et al., 2000; Kang et al., 1999), conceptual and syntactic anomalies were introduced in separate scanning sessions. This might have biased subjects towards using strategies that were specific to detecting each type of violation. A third reason for discrepancies between these studies is that they each claimed distinctions and similarities in processing syntactic versus conceptual information based on different statistical contrasts. We argue that a full appreciation of how the brain responds in this paradigm requires all pairwise contrasts to be examined. A fourth limitation of functional magnetic resonance imaging (fMRI) studies that have used this paradigm is that they failed to illustrate the effect of the anomaly before and after it was presented. Kuperberg et al. (2000) integrated activity across 30-sec time blocks. Newman et al. (2001), Ni et al. (2000), and Kang et al. (1999) reported activity that correlated with idealized activation functions. Yet, as discussed above, the underlying theoretical basis of introducing an anomaly in sentences is to determine its effect during sentences parsing. We know from several studies that have compared sentences with low-level baseline control conditions, that widespread networks are activated during sentence processing (Bavelier et al., 1997). The critical question is how such activity is modulated by the presentation of different types of anomalies.

Aim and Design of the Current Study

The main aim of this study was to use rapid-presentation event-related fMRI methods to address the limitations of previous studies that have used the anomaly paradigm and to gain further insights into how the brain distinguishes between morphosyntactic and pragmatic information during language processing. First, we used rapid-presentation event-related fMRI methods (Dale & Buckner, 1997; Buckner et al., 1996; Burock, Buckner, Woldorff, Rosen, & Dale, 1998) that allowed a mixed design in which different types of sentences could be presented in a pseudorandomized order in the same experimental session. Second, we presented sentences word by word and estimated the hemodynamic response at successive temporal samples without assumptions about the shape of the underlying response function. Third, we report both increases and decreases in activity associated with the presentation of each type of anomaly in relation to normal sentences as well as in relation to one another. Fourth, subjects performed a plausibility judgment task that is known to yield a behavioral temporal distinction in processing syntactic versus conceptual anomalies. This allowed us to interpret our findings in relation to behavioral findings. In addition, the same subjects took part in a parallel ERP study (Experiment 1) that used the identical stimuli presented in the same sequence.

In both the ERP and fMRI experiments, we presented three types of 10-word sentences that differed with respect to the relationship between the subject–noun and the verb: sentences were plausible (e.g., ‘‘My parents couldn't sleep because the baby would cry''), anomalous with respect to our real-world knowledge (pragmatically anomalous, e.g., ‘‘My parents couldn't sleep because the baby would phone''), or syntactically anomalous (e.g., ‘‘My parents couldn't sleep because the baby would cries''). These sentences test important aspects of syntax (morphosyntactic subject–verb agreement) and semantics/pragmatics (the relationship between the meaning of individual words and real-world knowledge).

EXPERIMENT 1: EVENT-RELATED POTENTIALS

Introduction

Given that there are discrepancies in the literature as to which types of syntactic anomalies elicit which ERP responses and that these ERP responses may vary between different individuals (Osterhout, 1997), the main aim of this ERP study was to determine exactly which electrophysiological responses were produced by these particular stimuli in these participants. Based on numerous studies demonstrating an N400 effect in association with conceptual violations, we predicted a significant N400 effect in association with the pragmatically anomalous verbs. Previous studies of morphosyntactic violations have reported robust P600 effects (e.g., Osterhout & Mobley, 1995). Some studies (Osterhout & Mobley, 1995), although not all (e.g., Gunter & Friederici, 1999; Osterhout & Nicol, 1999; Hagoort et al., 1993), report a significant LAN in response to such violations. We, therefore, predicted that these anomalies would elicit a P600 but did not have firm expectations as to whether or not they would also elicit a LAN.

Results

Behavioral Data

The main purpose of the plausibility judgment task was to ensure that subjects were paying attention to the sentences during the measurement of ERPs. RTs were not measured in this ERP experiment because subjects' responses were delayed in order to reduce contamination of the ERP waveform by response sensitive components such as the P300 (Donchin & Coles, 1988). There were no significant differences between the sentence types in the proportion of errors ($p > .44$): 9% of responses to the normal sentences were false positives, 13% of responses to the pragmatically anomalous sentences were false negatives, and 12% of responses to the morphosyntactically anomalous sentences were false negatives. A' scores for detecting both pragmatic and morphosyntactic anomalies were 0.96.

ERP Data: 350- to 550-msec Epoch

There was a significant ($p < .05$) main effect of sentence type at all parasagittal columns of scalp electrodes (Table 1, left). Planned simple-effects analyses were carried out to determine more specifically which sentence types differed from one another. As shown in Figure 1, there was a widespread N400 effect: The difference between the pragmatically anomalous and the nonviolated verbs reached significance ($p < .01$) at all five electrode columns (Table 2, left). As shown in the voltage map (Figure 1, top right), the N400 effect was less marked at frontal than other sites. This was reflected by Sentence Type × Electrode interactions that were significant ($p < .01$) at all electrode columns (Table 2, right). Follow-up analyses at individual electrode sites showed that N400 effects approached significance ($.01 < p < .05$) at frontal–central (FC3′/FC4′, FC5′/FC6′), central (Cz, C1/C2, C3/C4, C5/C6), central–parietal (CP3′/CP4′, CP5′/CP6′, CP1′/CP2′), parietal (Pz, P1′/P2′, P5′/P6′), temporal–parietal (TP7/TP8), temporal (T5/T6), parietal–occipital (PO1′/PO2′, PO3′/PO4′, PO7/PO8), and occipital (Oz, O1/O2) sites. There was a Sentence Type × Hemisphere interaction that approached significance at the lateral electrode column, $F(1,10) = 4.80, p < .053$, and Sentence Type × Hemisphere × Electrode interactions that approached significance at the outer medial, $F(6,60) = 5.47, p < .025$, lateral, $F(6,60) = 4.116, p < .047$, and outer lateral columns, $F(8,80) = 4.55, p < .03$, due to significantly ($p < .01$) greater N400 effects on the right than the left at some temporal (T4 > T3) sites.

In the 350- to 550-msec time epoch, there were no significant differences between the plausible and the morphosyntactically violated verbs at any of the electrode columns. Examination of the waveforms in Figure 1 indicated a slightly greater negativity to morphosyntactically anomalous than normal verbs at some central and anterior electrode sites (F5, F1, Fz, F2, FC5, FC1,

Table 1. ERP Analyses of Parasagittal Columns of Scalp Electrodes: Main Effects of Sentence Type (Three Levels) at 350–550 and 550–850 msec

	350- to 550-msec Epoch		*550- to 850-msec Epoch*	
Analysis	*df*	*F*	*df*	*F*
Midline	2,20	9.61**	2,20	14.23****
Inner medial	2,20	5.24*	2,20	13.91****
Outer medial	2,20	9.17**	2,20	14.34****
Lateral	2,20	8.69**	2,20	15.80****
Outer lateral	2,20	7.54**	2,20	16.17***

*$p < .05$.

**$p < .01$.

***$p < .001$.

****$p < .0001$.

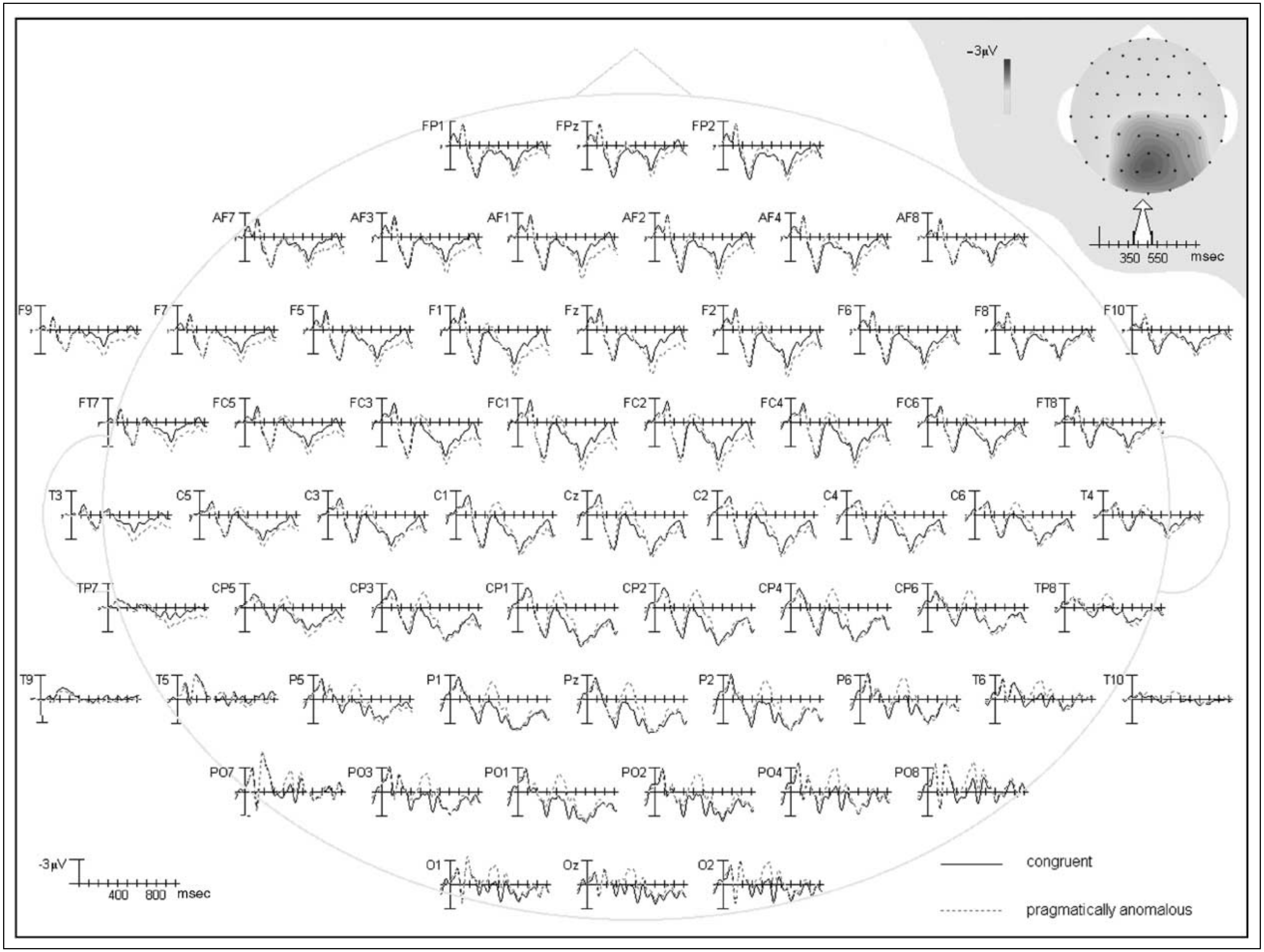


Figure 1. Averaged waveforms elicited by critical verbs of pragmatically anomalous verbs (dotted lines) versus plausible verbs (solid lines) at 63 scalp electrodes. Top right: The spatial distribution of the N400 effect (the voltage difference between 350 and 550 msec) over all electrodes at the scalp surface.

Table 2. ERP Analyses of Parasagittal Columns of Scalp Electrodes: Main Effects and Interactions in the Simple-Effects ANOVAs at 350- to 550-msec Epoch (Normal versus Pragmatically Anomalous Sentences)

	Main Effect of Sentence Type		*Interactions between Sentence Type and Electrode Site*	
Analysis	*df*	*F*	*df*	*F*
Midline	1,10	27.42****	4,40	7.12**
Inner medial	1,10	14.82**	2,20	11.67**
Outer medial	1,10	26.56****	6,60	5.66*
Lateral	1,10	31.31****	6,60	5.42**
Outer lateral	1,10	29.73****	8,80	7.26**

*$p < .05$.

**$p < .01$.

****$p < .0001$.

FC2, FC4). However, comparisons at these left anterior electrode sites (considered individually and grouped together) failed to reveal significant differences between plausible and the morphosyntactically violated verbs (i.e., the morphosyntactically anomalous verbs did not elicit a significant LAN).

ERP Data: 550- to 850-msec Epoch

During the 550- to 850-msec epoch, there were significant ($p < .01$) main effects of sentence type at all five parasagittal columns of scalp electrodes (Table 1, right). As shown in Figure 2, there was a widespread P600 effect. This was confirmed by planned simple effects analyses that revealed significant ($p < .01$) differences between normal and morphosyntactically anomalous verbs at all electrode columns (Table 3, left). Electrode × Sentence Type interactions were significant ($p < .01$) or approached significance ($p < .06$) at all columns (Table 3, right) and reflected P600 effects that were significant (all ps $< .005$) at central (Cz, C1/C2, C3/C4, C5/C6), central–parietal (CP1′/CP2′, CP3′/CP4′, CP5′/CP6′), parietal (Pz, P1′/P2′, P5′/P6′), temporal (T3/T4, T5/T6), temporal–parietal (TP7/TP8), parietal–occipital (PO1′/PO2′, PO3′/PO4′, PO7/PO8), and occipital (Oz, O1/O2) sites. The P600 effect was also slightly lateralized to the right, as reflected by Electrode × Hemisphere × Sentence Type interactions that reached significance at the and outer-medial electrode column, $F(6,60) = 8.94, p < .005$, and approached significance at the lateral electrode column, $F(6,60) = 5.30, p < .025$. In contrasting normal with pragmatically anomalous sentences in this time epoch, there was no significant main effect of sentence type. However, there were Sentence Type × Electrode interactions that reached significance at midline, $F(4,40) = 7.14$, $p < .004$, inner medial, $F(2,20) = 19.80$, $p < .001$, and outer medial columns, $F(6,60) = 9.04$, $p < .001$, and that approached significance at lateral, $F(6,60) = 3.14$, $p < .041$, and outer lateral columns, $F(8,80) = 3.31, p < .043$. These interactions reflected a significantly ($p < .01$) larger positivity to pragmatically violated than to nonviolated verbs that reached significance ($p < .01$) at temporal (T3/T4) electrode sites and approached significance ($.01 < p < .05$) at frontal (AF1′/AF2′, AF3′/AF4′, F1′/F2′), frontal–temporal (FT7/FT8), and temporal–parietal (TP7/TP8) sites.

Discussion

To summarize our ERP findings, we demonstrated a significant widespread P600 effect to morphosyntactic subject–verb agreement violations and a significant N400 effect to pragmatic violations. These findings were expected and replicate previous studies (Osterhout & Mobley, 1995; Kutas & Van Petten, 1988). In addition to the N400 and P600 effects, there were two other observations of interest. First, we detected a small but significant late positivity (within the time window of the P600) at some electrode sites to the pragmatic anomalies. This positivity may be a small late-appearing P300 that is related to the decision component of the plausibility judgment task (Donchin & Coles, 1988).

The second observation of interest was that the morphosyntactic violations failed to elicit a significant LAN—the other ERP waveform that has been associated with different types of syntactic anomalies, including morphosyntactic violations (Friederici, 1995; Kluender & Kutas, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991). This failure to elicit a LAN to morphosyntactic violations is consistent with some (Gunter & Friederici, 1999; Osterhout & Nicol, 1999; Osterhout, McKinnon, Bersick, & Corey, 1996; Hagoort et al., 1993) although not all (Hagoort & Brown, 2000; Penke et al., 1997) previous findings. It has been proposed that the LAN reflects a stage of first-pass parsing (Friederici, 1997; Rayner et al., 1983). If this is the case, our findings are consistent with the idea that morphosyntactic information does not play a significant role in the establishment of such an initial

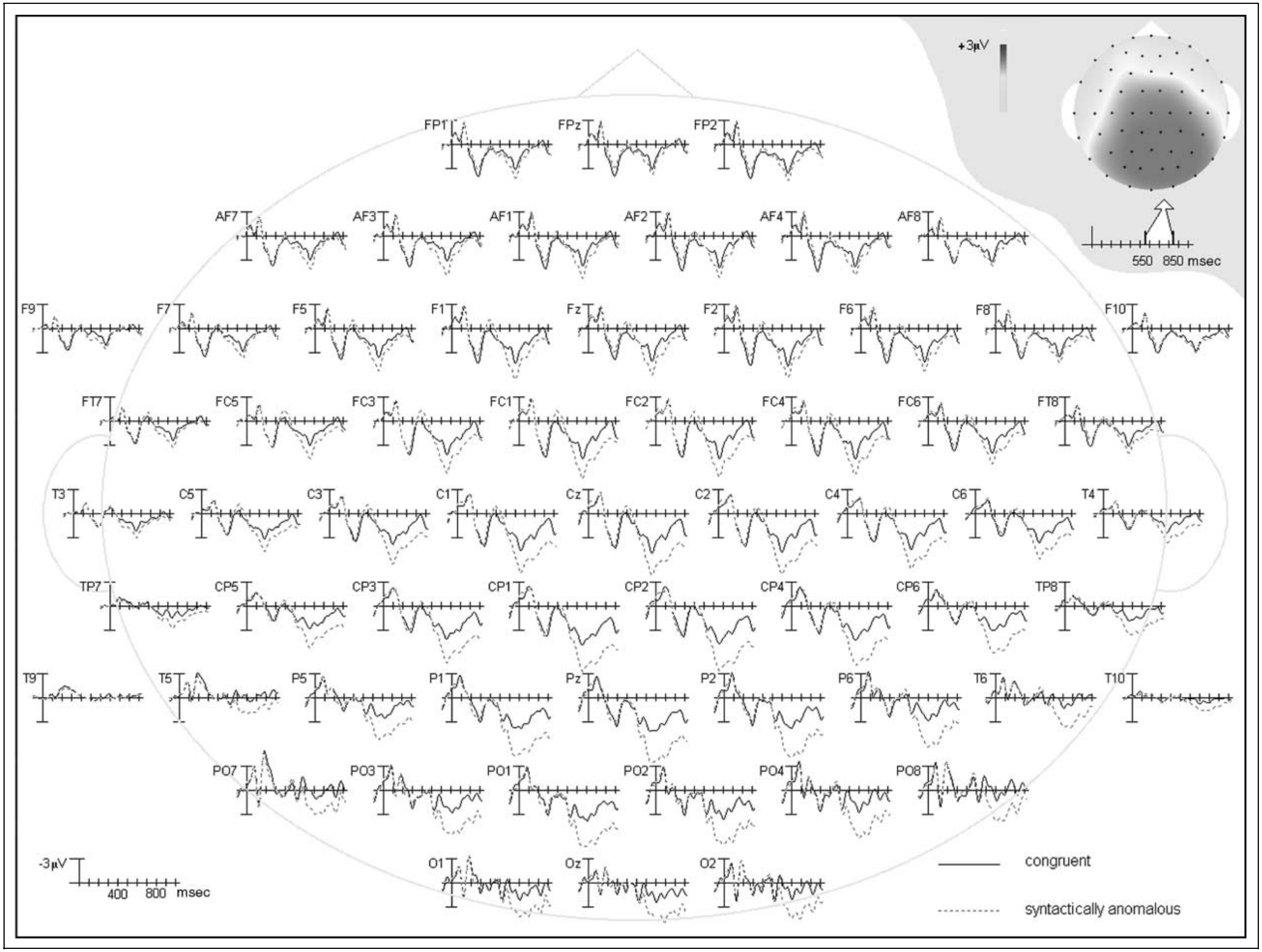


Figure 2. Averaged waveforms elicited by critical verbs of syntactically anomalous verbs (dotted lines) versus plausible verbs (solid lines) at 63 scalp electrodes. Top right: The spatial distribution of the P600 effect (the voltage difference between 550 and 850 msec) over all electrodes at the scalp surface.

Table 3. ERP Analyses of Parasagittal Columns of Scalp Electrodes: Main Effects and Interactions in the Simple-Effects ANOVAs at 550- to 850-Msec Epoch (Normal versus Syntactically Anomalous Sentences)

	Main Effect of Sentence Type		*Interactions between Sentence Type and Electrode Site*	
Analysis	*df*	*F*	*df*	*F*
Midline	1,10	17.58**	4,40	10.90***
Inner medial	1,10	18.36**	2,20	4.02
Outer medial	1,10	18.88***	6,60	6.54**
Lateral	1,10	20.18***	6,60	6.31**
Outer lateral	1,10	18.92***	8,80	5.15**

**$p < .01$.

***$p < .001$.

syntactic structure. However, future studies will need to address the question of why a LAN is elicited by morphosyntactic violations in some studies but not others.

EXPERIMENT 2: EVENT-RELATED FUNCTIONAL MAGNETIC RESONANCE IMAGING

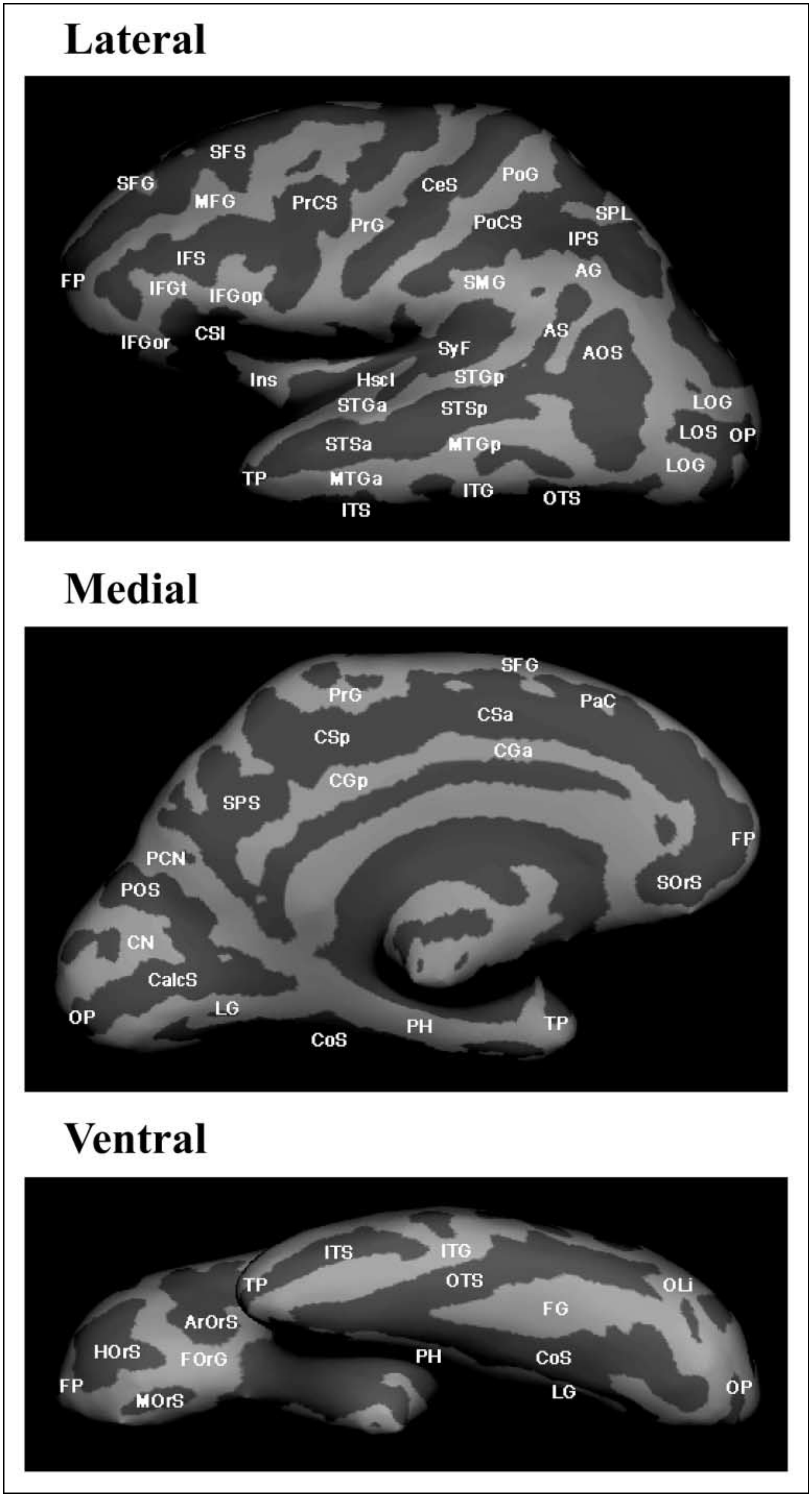
Introduction

The same subjects who took part in the ERP experiment also participated in an fMRI study in which they read the same sentences presented in the same pseudorandomized sequence while performing the same task. Unlike ERPs that were time-locked to single critical verbs, the fMRI signal indexed activity that was not only associated with the presentation of the anomalous verb itself but also that was associated with the presentation of previous and subsequent words in the sentence and with the decision process. Based on previous studies that have contrasted normal sentences with low-level "baseline" conditions such as strings of words (Friederici, Meyer, & von Cramon, 2000; Kuperberg et al., 2000; Bottini et al., 1994; Mazoyer et al., 1993), consonant letter strings (Bavelier et al., 1997), and/or a rest condition (Muller et al., 1997; Fink et al., 1996; Mazoyer et al., 1993), we expected that all types of sentences would activate a widespread language processing network that included inferior frontal and temporal regions.

We aimed to determine which parts of this language processing network would be modulated after the presentation of each type of anomaly relative to normal sentences. Below, we outline three possibilities. Previous neuroimaging studies that have examined hemodynamic activity in association with normal and anomalous sentences (Newman et al., 2001; Kuperberg et al., 2000; Ni et al., 2000; Kang et al., 1999) have not been able to distinguish between these possibilities. This is because, as discussed in the General Introduction, none of these studies addressed the critical question of how hemodynamic activity was modulated in association with the critical portions of sentences as they unfolded in time. Moreover, none of these studies reported all the relevant contrasts between different sentence types.

One possibility was that different parts of this network would be modulated in association with the presentation of the morphosyntactic versus the pragmatic anomalies. For example, if we observed more activity in left inferior frontal regions in association with the morphosyntactically anomalous sentences and more activity in left temporal regions in association with the pragmatically anomalous sentences (each relative to normal sentences), this would be strong evidence in favor of regional specialization of these types of syntactic and conceptual parsing. Note, however, that a failure to find distinct portions of the network modulated to the two types of anomaly would not rule out regional specialization of syntactic parsing (see below). A second possibility was that the same network(s) would be modulated in the same way by both types of anomaly. For example, we might observe more activity in both left inferior frontal regions and left temporal regions in association with both morphosyntactically anomalous and pragmatically anomalous sentences relative to normal sentences. Note that this finding would also not rule out the possibility of regional specialization in processing morphosyntactic versus pragmatic anomalies. However, it would suggest that these two types of information were processed in parallel.

A third possibility, in between these two extremes, was that the same networks would be recruited to a greater degree upon encountering the pragmatic relative to the morphosyntactic anomalies. As reviewed in the Introduction, it is known that syntactically anomalous sentences take less time to process than conceptually anomalous sentences when subjects perform a plausibility judgment task (McElree & Griffith, 1995). Indeed, this finding has been taken as evidence for a temporal distinction in processing these two sentence types and for models of



Lateral

Medial

Ventral

Figure 3. Inflated lateral, medial, and ventral surfaces of the left hemisphere with average folding patterns of sulci and gyri, derived using the surface-based morphing procedure (Fischl, Sereno, & Dale, 1999; Fischl, Sereno, Tootell, et al., 1999) (see Methods). Sulcal and gyral cortical folds shown in dark and light gray, respectively. a = anterior; p = posterior; AG = angular gyrus; AOS = anterior occipital sulcus; ArOrS = Arcuate orbital sulcus; AS = angular sulcus; CalcS = calcarine sulcus; CeS = central sulcus; CG = cingulate gyrus; CGa = anterior cingulated gyrus; CGp = posterior cingulated gyrus; CN = cuneus; CoS = collateral sulcus; CS = cingulate sulcus; CSa = anterior cingulated sulcus; CSp = posterior cingulated sulcus; CSI = circular sulcus of insula; FG = fusiform gyrus; FOrG = frontoorbital gyrus; FP = frontal pole; HOrS = H-shaped orbital sulcus; Hscl = Heschl's gyrus; IFGop = inferior frontal gyrus pars opercularis; IFGor = inferior frontal gyrus pars orbitalis; IFGt = inferior frontal gyrus pars triangularis; IFS = inferior frontal sulcus; Ins = insula; IPS = intraparietal sulcus; ITG = inferior temporal gyrus; ITS = inferior temporal sulcus; LG = lingual gyrus; LOG = lateral occipital gyrus; LOS = lateral occipital sulcus; MFG = middle frontal gyrus; MOrS = Medial orbital sulcus; MTG = middle temporal gyrus; MTGa = middle temporal gyrus/anterior part; MTGp = middle temporal gyrus/posterior part; OLi = inferior occipital lateral gyrus; OP = occipital pole; OTS = occipitotemporal sulcus; PAC = paracingulate cortex; PCN = precuneus; PH = parahippocampal gyrus; PoCS = postcentral sulcus; PoG = postcentral gyrus; POS = parieto-occipital sulcus; PrCS = precentral sulcus; PrG = precentral gyrus; SFG = superior frontal gyrus; SFS = superior frontal sulcus; SMG = supramarginal gyrus; SOrS= superior orbital sulcus; SPL = superior parietal lobule; SPS = subparietal sulcus; STG = superior temporal gyrus; STGa = superior temporal gyrus/anterior part; STGp = superior temporal gyrus/posterior part; STS = superior temporal sulcus.

Table 4. All Sentences versus Fixation

All Sentences > Fixation		*Fixation > All Sentences*	
Region	*BA*	*Region*	*BA*
Lateral frontal cortex		*Frontal cortex*	
L and R inferior frontal gyrus and sulcus	45, 46, 47	L and R superior frontal sulcus	8, 9
L and R orbito-frontal cortex	47, 11, 10	L and R frontal pole	9, 10
L and R middle frontal gyrus	9, 46		
		Peri-central cortex	
L and R superior frontal gyrus	9		
		L central sulcus	3, 4
Peri-central and lateral parietal cortex		R central sulcus, pre- and postcentral gyri (inferior)	3, 4
L postcentral gyrus (inferior)	4, 6		
L intraparietal sulcus	40	*Intrasylvian cortex*	
R central sulcus, pre- and postcentral gyri (superior part)	3, 4, 6	L Heschl's gyrus	42
		L insula	
		L and R circular sulcus of insula	
Temporal cortex and inferior temporal–occipital cortex			
L and R superior temporal gyrus and sulcus	22	*Lateral parietal cortex*	
L and R middle temporal gyrus (posterior)	22, 21	L and R inferior parietal lobule	39, 40
L and R inferior temporal sulcus and gyrus	21, 2	L and R superior parietal lobule	40
L and R temporal pole	38		
		Medial frontal cortex	
L and R occipito-temporal sulcus	20, 37		
		L and R superior orbital sulcus	10, 11
L and R fusiform gyrus	37, 19		
		L and R anterior cingulate sulcus and gyrus	33, 24
Occipital cortex			
		L and R paracingulate cortex	32
L and R lateral occipital gyri	17, 18		
L and R occipital pole	17, 18		
		Medial parietal cortex	
L and R calcarine sulcus	17, 18		
		L and R posterior cingulate gyrus and sulcus	23, 31, 26, 29, 30
L and R cuneus	17, 18, 19		
L and R lingual gyrus	17, 18	L and R subparietal sulcus	7, 31
		L and R precuneus	7
		L and R parieto-occipital sulcus	7, 31, 18, 19

Summary of anatomical localizations of regions that reached a significance level of $p < 10^{-12}$ (uncorrected for multiple comparisons) in comparing all sentences with fixation. Brodmann's areas (BA) are approximate. L = left; R = right.

language processing in which forming a representation of meaning requires more time than forming an initial syntactic representation (McElree & Griffith, 1995; Rayner et al., 1983). In neuroimaging studies, when the task performed by subjects remains constant, increases in hemodynamic signal within a particular region in association with stimulus type A relative to stimulus type B are often attributed to increases in processing demands that are inherently and implicitly associated with stimulus type A relative to B during the performance of that task. Behaviorally, this manifests as more time to process stimulus type A than stimulus type B (increased RTs to A vs. B). For example, when subjects perform plausibility judgment tasks, more complex sentences that take more time to process are associated with greater activity in left peri-sylvian regions than sentences that are less complex and take less time to process (Keller, Carpenter, & Just, 2001; Stromswold et al., 1996). Similarly, as subjects perform recognition judgment tasks (Buckner, Koutstaal, Schacter, & Rosen, 2000) or lexical decision tasks (Mummery, Shallice, & Price, 1999), trials that are primed and therefore take less time to process are associated with less neural activity in the same regions than trials that are not primed and take more time to process. In the current study, the plausibility judgment task remained constant throughout experimental runs in which the three sentence types were presented in pseudorandom order. Increases in RTs associated with judging pragmatically anomalous sentences relative to morphosyntactically anomalous sentences might therefore be associated with relative increases in activity within left temporal and left frontal regions. Again, this finding would not rule out the possibility of regional specialization in processing morphosyntactic versus pragmatic anomalies. It would, however, again suggest that these types of information were processed in parallel but with different time courses and would give new insights into how this temporal distinction is realized in the brain.

Results

Behavioral Results

The decision RTs to pragmatically anomalous sentences (1067 msec) were longer at the level of a trend ($p < .08$), than to plausible (972 msec) sentences that were, in turn, significantly longer than to morphosyntactically anomalous sentences (863 msec) ($p < .016$). There were no significant differences between the sentence types in the proportion of errors ($p > .32$): 10% of responses to normal sentences were false positives, 13% of responses to pragmatically anomalous sentences were false negatives, and 7% of responses to morphosyntactically anomalous sentences were false negatives. A' scores for detecting pragmatic and morphosyntactic anomalies were 0.93 and 0.95, respectively. There were no significant ($p > .1$) correlations between the proportion of errors and RTs to any of the sentence types.

fMRI: All Sentences versus Fixation

We first characterized the functional neuroanatomical networks that were modulated as subjects read all sentences in comparison with the fixation condition. Functional activation is displayed on the inflated cortical surface with average folding patterns of sulci and gyri (Fischl, Sereno, Tootell, & Dale, 1999) (see Figure 3 for annotations). The contrast of sentences minus fixation revealed activation of a widespread cortical network that was bilaterally distributed, but that appeared to be more extensive on the left (Table 4, left, shown in yellow/red in Figure 4). This reflected brain activity associated with language processing (left-lateralized temporal–frontal regions) as well as with more general processes associated with stimulus perception and response generation (occipital and motor cortex). The opposite contrast (fixation condition minus all sentences) revealed activity in a bilaterally distributed network that included the lateral and medial parietal cortex (Table 4, right, shown in blue in Figure 4). Throughout the rest of this article, we refer to the activity revealed in the ''fixation minus all sentences'' contrast as ''deactivation.''

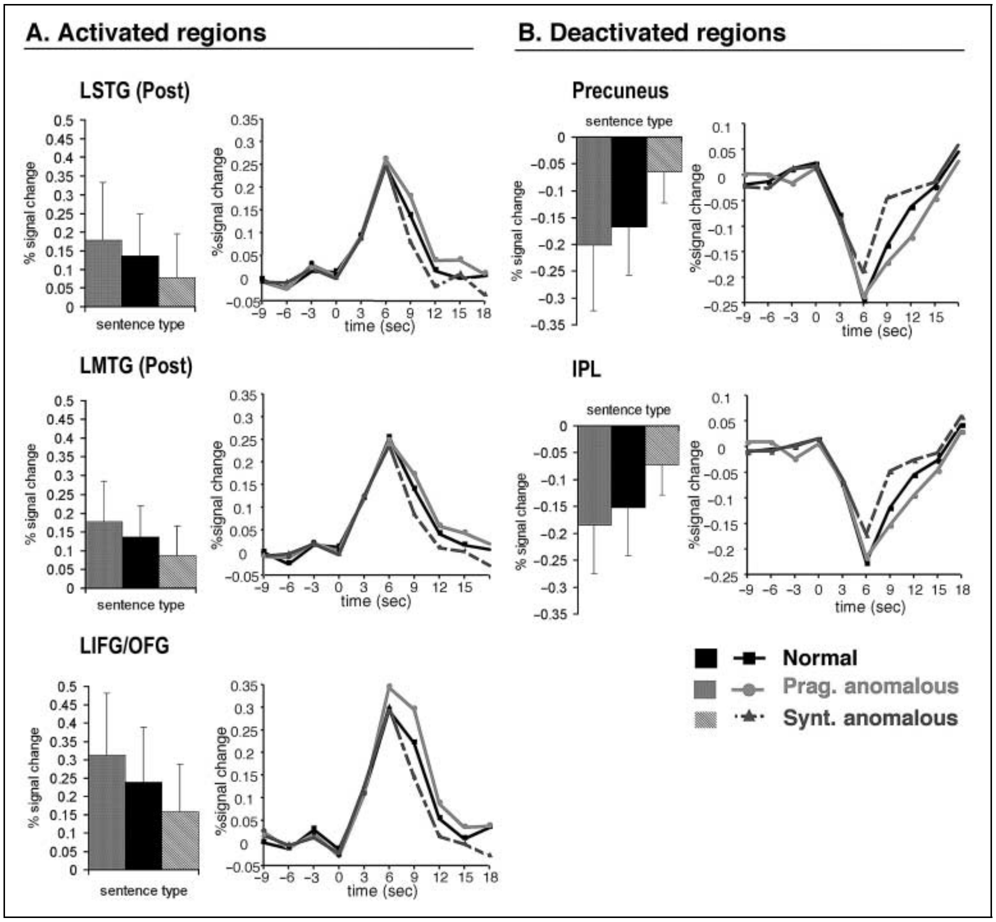
Hemodynamic Time Courses and Repeated Measures Analyses of Variance for Regions of ''Activation'' and ''Deactivation''

We selected a subset of regions that were ''activated'' and ''deactivated'' in comparing all sentences with fixation in order to examine how average hemodynamic activity within these regions was modulated at successive temporal windows as the sentences unfolded word by word. Figure 5 shows the percent signal change time courses, averaged across voxels and subjects in these regions. These time courses show that activity within the left inferior frontal/orbito-frontal gyri and the left posterior superior and middle temporal gyri showed maximal activity in association with the pragmatically anomalous sentences, less activity in association with the normal sentences, and least activity in association with the morphosyntactically anomalous sentences (Figure 5A). Conversely, in right-sided lateral and medial parietal regions, there was least deactivation in association with the morphosyntactically anomalous sentences and most deactivation in association with the pragmatically anomalous sentences (Figure 5B). In all these regions, differentiation of activity between the three sentence types appeared to be maximal during the latter part of the time course.

We next calculated the average activity for each region, in each subject, for each sentence type, at two time epochs within the hemodynamic time course 6–9 sec and 9–12 sec. For each region, we carried out repeated measures analyses of variance (ANOVAs) with sentence type and time epoch as within-subject factors. We chose these analyses to investigate possible Sentence Type × Time epoch interactions. This is because, in almost all sentences, the critical verb fell after 3 sec into a sentence (after the presentation of 7.5 words). Assuming a hemodynamic delay of at least 6 sec, the 6–9 sec time epoch mainly captured the presentation of the first half of the sentence (which was identical across sentence types) and the 9–12 sec time epoch mainly corresponded to the presentation of the second half of sentence trial—the presentation of the anomaly and the decision process—that distinguished experimental conditions.

As predicted, we observed significant Sentence Type × Time Epoch interactions in these regions: left inferior frontal/orbito-frontal gyri: $F(2,26) = 8.86$, $p < .001$, left posterior superior temporal gyrus: $F(2,26) = 10.68$, $p < .0001$, left posterior middle temporal gyrus: $F(2,26) = 10.23$, $p < .001$, right precuneus: $F(2,26) = 6.42$, $p < .005$, and the right inferior parietal lobule, $F(2,26) = 5.66$, $p < .009$. Follow-up simple-effects ANOVAs at the 6- to 9-sec time epoch revealed no significant effects of sentence type in the regions of

Figure 5. Hemodynamic time courses and responses at 9–12 sec time window for regions-of-interest that were activated with respect to fixation (A) and deactivated with respect to fixation (B). Time courses (right of A and B): Points on *x*-axis depict onset of 3-sec temporal samples in relation to trial onset (i.e., 0 corresponds to 0–3 sec, 3 to 3–6 sec, etc.). Bar charts (left of A and B): Show average percent signal change in BOLD response at the 9- to 12-sec time window; error bars show standard deviations. LSTG (post) = left posterior superior temporal gyrus; LMTG (post) = left posterior middle temporal gyrus; LIFG/OFG = left inferior frontal gyrus and orbito-frontal gyrus; IPL = inferior parietal lobule.



activation (left inferior frontal/orbito-frontal cortex, left posterior superior and middle temporal cortex) but significant effects of sentence type in the regions of ‘‘deactivation’’ (with respect to fixation): the right precuneus: $F(2,26) = 5.35$, $p < .011$, and the right inferior parietal lobule: $F(2,26) = 7.86$, $p < .002$. At the 9- to 12-sec time epoch, there were highly significant differences in activity across the three sentence types for all regions-of-interest [left inferior frontal/orbito-frontal gyri: $F(2,26) = 21.57$, $p < .0001$; left posterior superior temporal cortex: $F(2,26)$ 11.46, $p < .0001$; left posterior middle temporal cortex: $F(2,26) = 14.12$, $p < .0001$; right precuneus, $F(2,26) = 17.02$, $p < .0001$; right inferior parietal lobule, $F(2,26) = 11.19$, $p < .0001$)]. Post hoc polynomial contrasts at the late 9- to 12-sec time epoch confirmed significant linear trends in activity across the three sentence types (left inferior frontal/orbito-frontal gyri: $t = 3.24$, $p < .006$; left posterior superior temporal cortex: $t = 2.6$, $p < .022$; left posterior middle temporal cortex: $t = 3.16$, $p < .007$; right precuneus, $t = 6.52$, $p < .00002$; right inferior parietal lobule, $t = 4.9$, $p < .0003$).

Voxelwise Pairwise Contrast Maps

The above analyses revealed significant quantitative differences in the hemodynamic responses (percentage signal changes) between the three sentence types within regions-of-interest. In order to examine the regional specificity and spatial extent of hemodynamic differences in response between the sentence types over the whole brain, we generated statistical maps by contrasting each type of sentence with one another (omitting the fixation condition). We generated these maps at the 9- to 12-sec time epoch because, as discussed above, this was when we predicted and demonstrated maximal differences in the hemodynamic responses between the three sentence types.

As shown in Figure 6 and Table 5, in contrasting each type of anomalous sentence with normal sentences, some of the same brain regions that showed a greater response in association with the pragmatically anomalous sentences showed a relatively reduced response in association with the morphosyntactically anomalous sentences and vice versa. Small foci within the left posterior superior temporal cortex and the left inferior frontal/orbito-frontal gyri showed significantly greater activity to pragmatically anomalous than to normal sentences (Figure 6, top row, red/yellow, Table 5A). Regions that showed greater activity to the normal sentences than to the morphosyntactically anomalous sentences (Figure 6, middle row, blue, Table 5) included the left superior temporal cortex and the left inferior frontal and orbito-frontal cortices. There was less activity

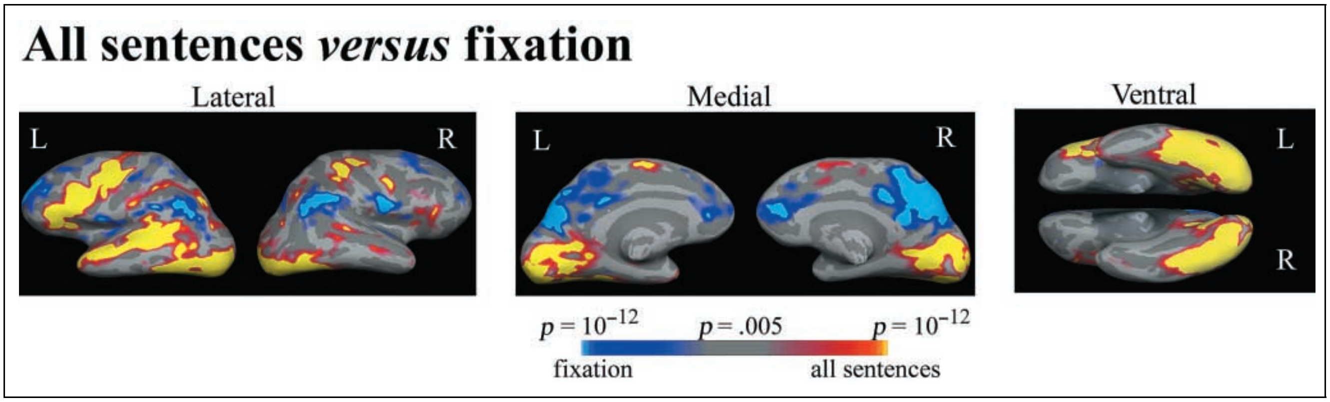


Figure 4. All sentences versus fixation. All sentence types (collapsed together) contrasted with the fixation condition at the third temporal sample/6–9 sec after trial onset. Average functional activity across all subjects was resampled on to a common surface spherical space and displayed upon ''inflated'' brain views with average sulcal and gyral cortical folds shown in dark and light gray, respectively (see Figure 3 for annotations). Yellow/red = greater activity in association with sentences versus fixation; blue = less activity in association with sentences versus fixation (''deactivation'').

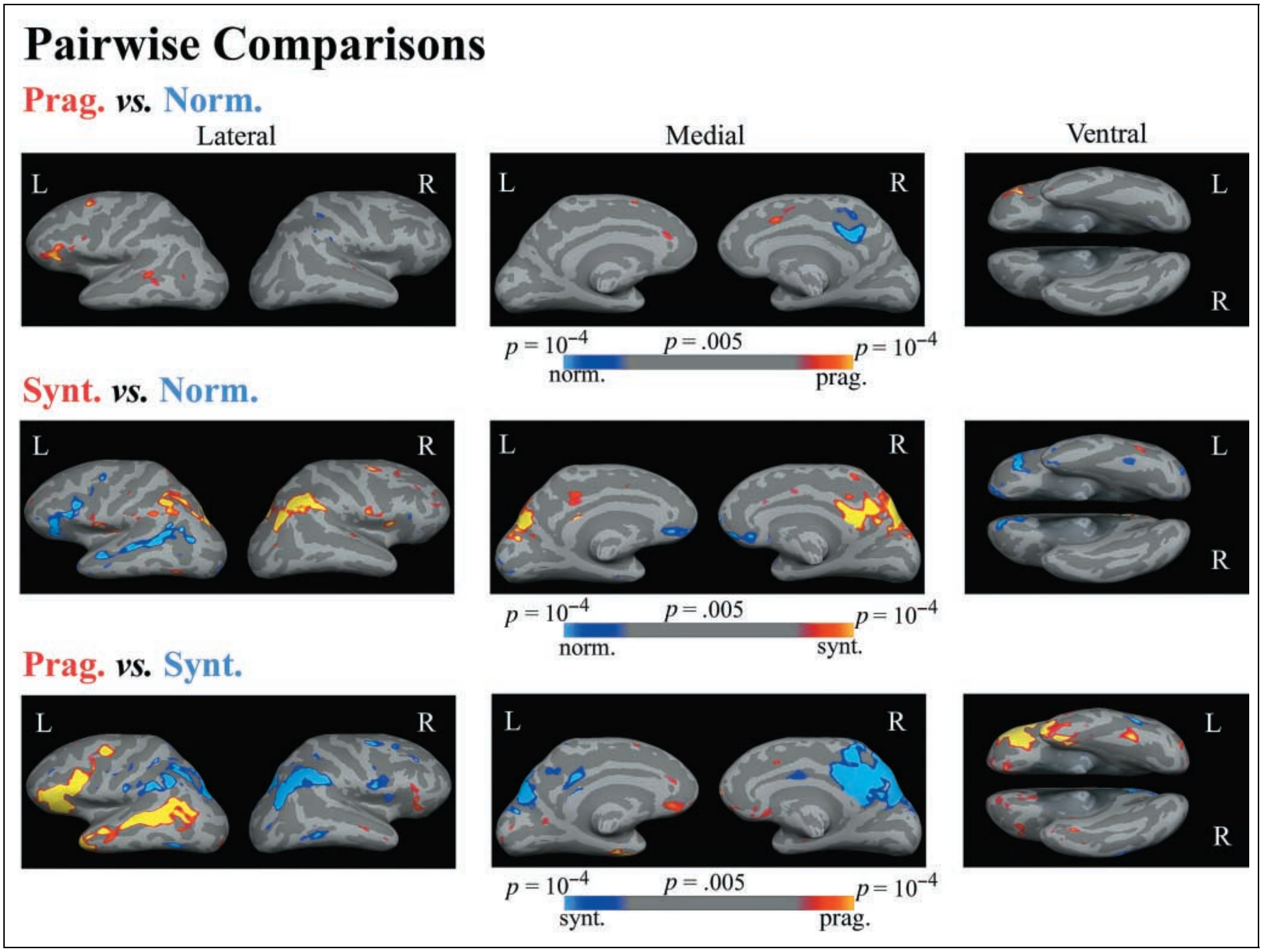


Figure 6. Pairwise comparisons. Contrasts are at the fourth temporal sample: 9–12 sec after trial onset. Average functional activity across all subjects was resampled and displayed as described in the legend to Figure 4. Top row: Prag. vs. Norm. = pragmatically anomalous versus normal sentences; yellow/red = greater activity to pragmatically anomalous than normal sentences; blue = less activity to the pragmatically anomalous than to the normal sentences. Middle row: Synt. vs. Norm. = syntactically anomalous versus normal sentences; yellow/red = greater activity to the syntactically anomalous sentences than to the normal sentence; blue = greater activity to normal than to the syntactically anomalous sentences. Bottom row: Prag. vs. Synt. = pragmatically versus syntactically anomalous sentences; yellow/red = greater activity to pragmatically anomalous than to syntactically anomalous sentences; blue = greater activity to syntactically anomalous sentences than to pragmatically anomalous sentences.

Table 5. Pairwise Comparisons: Modulation of Activity within the Left Temporal–Frontal Cortex and Bilateral Parietal Cortex to Normal, Pragmatically Anomalous, and Syntactically Anomalous Sentences

(A) Region	*Brodmann's Area*	*Prag. > Synt.*	*Prag. > Norm.*	*Norm. > Synt.*
L inferior frontal gyrus	44/45	×	×	×
L fronto-orbital gyrus	47	×	×	×
L middle frontal gyrus	9/46	×	×	
L superior temporal gyrus (posterior)	22	×		
L superior temporal sulcus (posterior)	22	×	×	×
L anterior occipital sulcus	21/37	×		×
L superior temporal gyrus (anterior)	22	×		
L superior temporal sulcus (anterior)	22	×		
L temporal pole	38	×		
L fusiform gyrus	20	×		

(B) Region	*Brodmann's Area*	*Synt. > Prag.*	*Synt. > Norm.*	*Norm. > Prag.*
L and R inferior parietal lobule (superior)	40	×	×	
L and R intraparietal sulcus	40	×	×	
L and R precuneus	7	×	×	
L and R parieto-occipital sulcus	7/19	×	×	
R posterior cingulate cortex	23/31	×	×	×
R paracingulate cortex	7/31	×		
R subparietal sulcus	7/31	×		
R middle frontal gyrus (posterior)	9/46	×		
R precentral gyrus	6	×		
L and R occipito-temporal sulcus	37	×		

Summary of anatomical localizations of regions that were activated at $p < 10^{-4}$ (uncorrected for multiple comparisons) for the following contrasts: prag. > synt. = pragmatically anomalous minus syntactically anomalous sentences; prag. > norm. = pragmatically anomalous minus normal sentences; norm. > synt. = normal sentences minus pragmatically anomalous sentences; synt. > prag. = syntactically anomalous minus pragmatically anomalous sentences; synt. > norm. = syntactically anomalous minus normal sentences; norm. > prag. = normal sentences minus pragmatically anomalous sentences. Brodmann's regions are approximate. L = left; R = right.

in association with the pragmatically anomalous than the normal sentences in the right posterior cingulate gyrus (Figure 6, top row, blue, Table 5B). Regions that showed greater activity to the morphosyntactically anomalous sentences than to the normal sentences (yellow/red) included the superior parietal cortex (superior parietal lobule, intraparietal sulcus, and the superior part of the inferior parietal lobule) and the precuneus and posterior cingulate on the medial surface (Figure 6, middle row, Table 5B). As shown in Figure 6 (bottom row) and Table 5 (A and B), a direct contrast between the two types of anomalous sentences (omitting the normal sentences) confirmed the overall patterns depicted in the top and middle rows: The left temporal and frontal cortices showed greater activation to pragmatically anomalous sentences (Figure 6, bottom row, yellow/red, Table 5A) while lateral and medial parietal cortices showed greater activity to morphosyntactically anomalous sentences (Figure 6, bottom row, blue, Table 5B).

Discussion

We demonstrated progressive activation (with respect to fixation) of left temporal and left inferior frontal regions and progressive deactivation (with respect to fixation) of bilateral medial and lateral parietal regions to morphosyntactically anomalous sentences, normal sentences, and pragmatically anomalous sentences, respectively. In the left temporal–frontal network, RTs correlated with the degree of activation of the BOLD response across the three conditions. In the parietal network, RTs across the three conditions correlated with the degree of deactivation of the BOLD response across the three conditions.

Previous neuroimaging studies that have compared the effects of syntactic and conceptual anomalies in sentences have shown that largely overlapping widespread networks are involved in processing both of these types of anomalies. These studies have claimed that different parts of these networks play differential roles in processing these two types of anomaly. As discussed in the General Introduction, however, several aspects of the methodologies used in these studies make their interpretation difficult. In the current study, we demonstrate differences in the degree to which both left inferior frontal and left temporal regions are recruited depending on whether a morphosyntactic or a pragmatic anomaly is encountered.

How should these quantitative differences in recruitment of temporal and frontal regions in association with the different sentence types be interpreted? As discussed in the Introduction of this experiment, in functional neuroimaging studies, quantitative differences in the hemodynamic signal within a particular region are generally attributed to differences in processing load (Keller et al., 2001; Stromswold et al., 1996) or ease of access to memory representations (Buckner et al., 2000) that are, in turn, reflected by RT measures. In the current study, the pattern of response within the left temporal–frontal network across the three sentence types mirrored the pattern of RTs, with most activity and the longest RTs in association with the pragmatically anomalous sentences, and least activity and the shortest RTs in association with the morphosyntactically anomalous sentences. To determine whether a sentence is normal or pragmatically anomalous, subjects are required to map words onto information within semantic memory. We suggest that this search and the conceptual integration of words with information in semantic memory takes place in the left temporal–frontal language network and that the degree of recruitment within this network is reflected by subjects' RTs. Longer RTs and more activity within left temporal–frontal regions are seen in association with pragmatically anomalous relative to normal sentences because it requires a longer search through semantic memory to determine that a sentence is implausible rather than plausible. The shortest RTs and least activity within left temporal–frontal regions are observed in association with morphosyntactically anomalous sentences because subjects can make plausibility decisions about these sentences on the basis of a finite set of syntactic rules. As discussed in the Introduction of this experiment, these quantitative distinctions are consistent with the idea that pragmatic and morphosyntactic information are processed in parallel but with different time courses.

Parietal Network and Differential Deactivation

There are two ways of looking at the patterns of response within the bilateral medial and lateral parietal cortex. The first is to ignore the fixation condition and to interpret the differential response in these regions to each type of sentence only in relation to each other. The pairwise difference maps depicted in Figure 6 show greater parietal activity in association with syntactically anomalous than in association with normal sentences (Figure 6, middle row, yellow) and in association with pragmatically anomalous sentences (Figure 6, bottom row, blue), suggesting some function of these regions during the processing of morphosyntactic information.

However, unlike activity within the left temporal–frontal cortex, the pattern of response within the parietal cortex did not mirror the pattern of RTs across the three sentence types: Although most activity in this region was seen in association with the morphosyntactically anomalous sentences, RTs to these sentences were shortest. This suggests that we should consider mechanisms other than a direct role of the parietal cortex in detecting or computing either morphosyntactic structure or semantic/pragmatic meaning as the source of these BOLD signal effects.

A second way of looking at these data takes into account the polarity of BOLD response in association with each type of sentence in relation to the fixation trials. We know from Figures 4 and 5 that the parietal cortex was "deactivated" in relation to the low-level fixation condition (i.e., it showed less activity to all sentences than to the fixation condition) and that most deactivation was observed in association with the pragmatically anomalous sentences and least deactivation was observed in association with the morphosyntactically anomalous sentences. This differential "deactivation" (in comparison with fixation) is what gave rise to the differences in relative activity in these parietal regions in the pairwise comparisons that contrasted activity of each sentence type to one another. The pairwise difference maps depicted in Figure 6 show greater parietal activity in association with morphosyntactically anomalous than in association with normal sentences (Figure 6, middle row, yellow). This arose because there was less deactivation in association with morphosyntactically anomalous sentences than in association with normal sentences. Similarly, greater parietal activity in association with normal sentences relative to pragmatically anomalous sentences arose because there was less deactivation in association with normal sentences than in association with pragmatically anomalous sentences.

Some of these parietal regions (particularly, the precuneus and adjacent posterior cingulate cortex on the medial surface) have a high resting baseline activity (Raichle et al., 2001) and have been reported as "deactivated" in a variety of cognitive tasks (Raichle, 1998; Shulman et al., 1997). It has been hypothesized that these medial regions mediate the continuous gathering of incoming sensory information at rest, and that differential deactivation of this region in association with various tasks reflects differential focused attention to such tasks (Raichle, 1998). Thus, the degree of activation of these regions may result from the extent to which attentional resources are allocated in the sentence task. This of course raises the question of how specific such processes are to syntactic processing. We think that it is unlikely that the increased BOLD parietal response in association with morphosyntactically anomalous sentences relative to normal sentences or pragmatically anomalous sentences is a specific marker of linguistic syntax. However, the differential deactivation in these regions still gives important information about the neurocognitive processes involved in parsing syntactic information and how these are different from those employed during conceptual processing. What we believe to be most relevant is the fact the brain responds differently to processing the morphosyntactic and pragmatic anomalies presented in the current study. The fact that two different neural systems are modulated in opposite directions to these two types of anomalies provides new evidence for how the brain makes this distinction.

Summary

We have demonstrated quantitative differences in activity within the same regions in association with morphosyntactic and pragmatic anomalies in sentences. Note that, as discussed in the Introduction of this experiment, these findings do not rule out regional specialization of morphosyntactic and pragmatic parsing. However, they give new insights into how the brain distinguishes between these two types of information during sentence processing. It will be interesting to explore the generalizability of these fMRI findings to processing other types of linguistic anomalies.

GENERAL DISCUSSION

ERP and fMRI techniques offer trade-offs between temporal and spatial resolution and can therefore give complementary information. There is therefore much interest and some progress (Dale et al., 2000) towards linking these two techniques. There are, of course, caveats in making such links. Although it is known that alterations in neuronal activity induce local changes in the electric fields (Mitzdorf, 1985), cerebral metabolism, and cerebral perfusion (Belliveau et al., 1991; Fox, Raichle, Mintun, & Dence, 1988), the precise relationships between hemodynamic and electrical signals measured using fMRI and EEG respectively are unclear. The current study did not attempt to quantitatively link ERP and fMRI measures.† Its main focus was the fMRI experiment and the primary aim of the ERP study was simply to illustrate a distinction in the ERP responses elicited by these particular stimuli as these subjects performed the same task as in the fMRI experiment. Nonetheless, the use of the same paradigm with these complementary techniques allows us to begin to conceptually link our ERP and fMRI findings.

Pragmatic anomalies were associated with increases in activity (relative to normal sentences) within the left frontal–temporal network, while morphosyntactic anomalies were associated with increases in activity within the parietal network (relative to normal sentences). These findings are consistent with the qualitative distinction in the N400 and the P600 effects that were elicited by the same anomalies in the ERP experiment. However, as we have emphasized, differences in the electrophysiological response between conditions tell us about cognitive processes occurring within several hundred milliseconds following the presentation of the critical verb. On the other hand, differences in the BOLD responses between conditions tell us about cognitive processes that occur seconds after the presentation of the critical verb, including those processes that are related to the decision component of the task itself. We have suggested that the fMRI findings can be linked with the behavioral findings and that the neural distinction in processing these two types of information was not purely qualitative but, in addition, quantitative. In this way, we have illustrated how an ERP and fMRI study using the identical paradigm and task can give complementary information, giving us a depth of understanding that each technique cannot give in isolation.

It is tempting to link the increased recruitment of left temporal–frontal regions in association with pragmatic anomalies in the event-related fMRI experiment to the increased N400 amplitude in association with the same pragmatically anomalous verbs in the ERP experiment. This would be consistent with the results of MEG and intracranial electrode studies that have implicated the posterior temporal (Dale et al., 2000; Helenius, Salmelin, Service, & Connolly, 1998; Halgren et al., 2002), anterior inferior temporal cortex (McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995; Halgren et al., 2002), and left inferior frontal cortices (Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994, Halgren et al., 2002; Guillem, Rougier, & Claverie, 1999) as generators of the N400. It is also possible that increased fMRI activity (or BOLD signal) in the parietal cortex in association with syntactic anomalies contributes to the P600 effect elicited by the same anomalies in the ERP experiment. This potential link can be made regardless of whether the polarity of activity of the parietal cortex in relation to the fixation condition is interpretable in its own right (i.e., regardless of the two ways of looking at the fMRI data discussed above). These links are speculative. Nonetheless, they provide the basis of hypotheses that will be tested in future experiments in which these two sources of data will be linked quantitatively.

Conclusions

There remain many unanswered questions and we have raised important theoretical questions regarding how the BOLD response to each type of anomalous sentence should be interpreted in relation to one another, to a resting fixation condition, and to subjects' decision RTs and ERP responses. Nonetheless, our main fMRI results are clear: First, the same regions were modulated to different degrees by both pragmatically and morphosyntactically anomalous sentences. Second, two different networks—a left temporal frontal network and a bilateral parietal network—were modulated in opposite directions to these types of anomalies. This provides new information about the neural basis for processing the form and meaning of sentences.

METHODS

Subjects

Five male and nine female right-handed, native English subjects (mean age 23) gave informed consent to participate. Three of the 14 subjects did not take part in the ERP experiment. Between the ERP and fMRI experiments, at least 2 weeks elapsed, the order of participation was counterbalanced, and subjects viewed different stimulus lists.

Stimuli Construction

Ten-word sentences providing a fairly highly constraining context were constructed for 240 verbs. Each sentence contained an animate subject noun (or noun phrase) that was separated from the critical verb by at least one other intermediate word. In half the sentences, the critical verb was the final word of the sentence and in the other half, the sentence continued with from one to five additional words. Syntactically anomalous sentences were constructed by introducing a morphosyntactic violation between the subject, an auxiliary when one was present, and the main verb (either by violating subject–verb agreement or by using a finite in place of an infinitival verb). Sentences were divided into three lists (each with 240 sentences, 80 of each experimental condition), allowing for counterbalancing of experimental conditions between subjects. Pragmatically anomalous sentences were constructed by replacing the critical verbs with verbs selected from sentences of another list. Preratings on 12 volunteers who did not participate either in the fMRI or ERP experiments confirmed that normal sentences were indeed interpreted as more "normal" than the pragmatically anomalous or morphosyntactically anomalous sentences.

Stimulus Presentation and Task

In both ERP and fMRI experiments, the subject's task was to decide whether each sentence made sense. In both experiments, each word appeared for 300 msec with an interstimulus interval of 100 msec. In the ERP experiment, the first word of each sentence was preceded by a fixation point "+" at the center of the screen and, at the end of each trial, subjects viewed a 1100-msec blank-screen interval followed by a "?" that remained on the screen until the subject pressed one of two buttons to indicate his/her decision and to start the next trial. Subjects were instructed to wait until the "?" cue before responding. This delayed response was designed to reduce any contamination of the ERP waveform by response sensitive components such as the P300 (Donchin & Coles, 1988). In the event-related fMRI experiment, each sentence was not preceded by a fixation point; rather, 80 visual fixation trials (fixate on a "+" symbol for the duration of a 6-sec trial) were interspersed with the experimental trials. The random interleaving of the sentence "events" with such "fixation events" or "null events" is critical for the efficient estimation of the entire hemodynamic response in rapid event-related fMRI experimental designs, enabling the deconvolution of the recorded fMRI time courses (Burock et al., 1998). In addition, rather than self-pacing through the trials, at the end of each 10-word (4-sec) sentence, subjects had 2 sec to indicate their decisions by pressing one of two buttons (using the index and middle fingers of their left hand).

Event-Related Potential Acquisition and Statistical Analysis

EEG was recorded from 64 tin electrodes, amplified by an Isolated Bioelectric Amplifier System Model H&W-32/BA with a bandpass of 0.01–40 Hz and continuously sampled at 200 Hz. Electrodes were also placed below each eye to monitor for eye movements, as well as on the left and right mastoids. During recording, all active electrodes were referenced to the right mastoid; offline, they were algebraically re-referenced to the mean activity between the two mastoids. ERPs time-locked to the critical word in each sentence were formed off-line from trials free of ocular and muscular artifact. Linearly interpolated voltage maps were produced by the EMSC Data Editor program (Source Signal Imaging).

The averaged ERPs were quantified by calculating the mean amplitude values (relative to a 100-msec prestimulus baseline) for the voltage points in two time epochs (350–550 and 550–850 msec after stimulus onset). The resulting data for each time epoch were analyzed with five ANOVAs for repeated measures at parasagittal columns of scalp electrodes along the anterior–posterior axis of the head. In all analyses, we included a sentence type factor (normal, pragmatic, and morphosyntactic) and, in all but midline analyses, we included a hemisphere factor (left and right). The midline analysis had five levels of electrode site (FPz, Fz, Cz, Pz, Oz). The inner medial analysis had three levels of electrode site (FC1/FC2, C1/C1, CP1/CP2). The outer medial analysis had seven levels of electrode site (AF1/AF2, F1/F2, FC3/FC4, C3/C4, CP3/CP4, P1/P2, PO1/PO2). The inner lateral analysis had seven levels of electrode site (AF3/AF4, F5/F6, FC5/FC6, C5/C6, CP5/CP6, P5/P6, PO3/PO4). The outer lateral analysis had seven levels of electrode site (FP1/FP2, AF7/AF8, F7/F8, FT7/FT8, T3/T4, TP7/TP8, T5/T6, PO7/PO8, O1/O2). The Geisser–Greenhouse correction was applied in all cases. Significant main effects and interactions in these global ANOVAs were followed up by planned simple-effects ANOVAs that allowed comparisons between each sentence type. In the tables, we indicate significance at $p < .05$, $p < .01$, $p < .001$, and $p < .0001$ for each ANOVA. In deciding whether a particular effect was significant, we used a standard significance level of alpha = .05 for overall ANOVAs in which all three sentence types were included. Planned simple effects analyses that were carried out to determine more specifically which sentence types differed from one another were evaluated at the more stringent level of alpha = .01, that is, we employed a simple Bonferroni correction as five separate analyses (one at each electrode column) were carried out. We note, however, that such a correction is conservative as the effects at each electrode column were not independent of one another. We, therefore, also report effects that approached significance, $.01 < p < .05$.

Functional Magnetic Resonance Imaging Acquisition, Preprocessing, and Statistical Analysis

Functional imaging took place on a 3.0-T General Electric scanner with echoplanar imaging upgrade (Advanced NMR Systems). Head motion was minimized using pillows and cushions around the head and a forehead strap. Subjects viewed the three types of sentences over eight functional runs. Each functional run lasted 4 min and 16 sec during which 2040 T2*-weighted echoplanar images were acquired (24 slices covering the whole brain, 85 images per slice, 4 mm thickness, in-plane resolution of 3.125 mm, slices oriented approximately 10/grad axially, 1 mm between slices), using an asymmetric spin echo sequence (TR = 3 sec; TE = 20 msec; flip angle = 90/grad). Functional scans were preceded by a series of T1-weighted inversion recovery echoplanar anatomic images (24 slices, 4 mm thickness, skip 1 mm between slices) acquired in plane with the functional images and an automatic shim procedure to optimize magnetic field homogeneity. Functional images were normalized to correct for signal intensity changes and temporal drift, spatially filtered (1.5-voxel Hanning radius), and selectively averaged for each subject across runs (Burock et al., 1998; Dale & Buckner, 1997) to yield 10 mean and variance values (from 9 sec before the onset of a trial through 18 sec after its onset, at TR = 3 sec) for all sentence types and fixation trials.

Subjects also underwent two conventional structural scans on a 1.5-T General Electric scanner, each lasting 9.53 min and constituting an RF-spoiled GRASS sequence (SPGR; 124 slice, 1.3 mm thickness, sagittal orientation, TR = 24 sec, bandwidth = 10.42, FOV = 25, NEX = 256 × 192; flip angle = 30/grad). These anatomical images were used to construct models of each subject's cortical surface, an automated procedure involving segmentation of the cortical white matter (Dale, Fischl, & Sereno, 1999; Dale & Sereno, 1993), tessellation of the gray/white border, inflation of the folded surface tessellation patterns (Fischl, Sereno, & Dale, 1999; Dale & Sereno, 1993), and automatic correction of topological defects in the resulting manifold (Fischl, Liu, & Dale, 2001). Each subject's reconstructed brain was morphed to an average spherical surface representation that optimally aligned the main sulcal and gyral features across subjects (Fischl, Sereno, & Dale, 1999; Fischl, Sereno, Tootell, et al., 1999). This procedure provides accurate matching of morphologically homologous cortical locations among participants while minimizing metric distortion. This established a spherical-based coordinate system into which the selective averages and variances of each subject's functional data were resampled.

Group statistical voxelwise maps were constructed using a t statistic. In Table 4 (all sentences vs. fixation), we list all anatomical regions that reached a significance level of $p < 10^{-12}$ (uncorrected for multiple comparisons). In reporting the pairwise comparisons between the different sentence types, we used a lower threshold of $p < 10^{-4}$ (uncorrected for multiple comparisons at the cortical surface). We display our averaged functional activation on a map of average folding patterns of the cortical surface, derived using the surface-based morphing procedure (Fischl, Sereno, & Dale, 1999; Fischl, Sereno, Tootell, et al., 1999). This allowed us to view functional activity in relation to the anatomy of sulcal and gyral folds. To orient readers, we provide an annotated figure of the unfolded average curvature (Figure 3) and Tables 4 and 5 summarize the anatomical localizations and give approximate Brodmann's areas. In the figures, we use a color scale to display activity not only at the threshold used to determine significance (see above) but also below this threshold to illustrate the extent of activation across the cortical surface.

In addition to constructing voxelwise maps over the whole of the cortical surface, we carried out repeated measures mixed-effect ANOVAs to examine the effects of sentence type and time epoch on the percent signal change relative to the fixation baseline in several anatomic regions-of-interest. These selected anatomic regions-of-interest were first delineated on the Talairach atlas. Each anatomic region was further constrained by using a functional mask that was unbiased with respect to examining the effects of stimulus type (normal, pragmatically, and morphosyntactically anomalous sentences) and time epoch (6–9 and 9–12 sec) in the repeated measures ANOVAs. This functional mask was generated in volumetric Talairach space (Talairach & Tournoux, 1988) and constituted an estimate of "activation" or "deactivation" associated with presenting all sentences in comparison with fixation over two time epochs that, as discussed in the Results section, corresponded approximately to the first and second halves of the 6-sec sentence trial (6–9 and 9–12 sec). In this statistical mask, a voxel was considered activated if it reached a statistical threshold of $p < 10^{-7}$ at either or both of these two time epochs.

APPENDIX

A sample of stimuli is listed. The critical verbs are underlined. For each scenario, the critical verbs (in order) are nonanomalous, pragmatically anomalous, and morphosyntactically anomalous.

We couldn't sleep at night because the baby would cry/remember/cries.
All through the amazing fireworks display the crowd would watch/curtsey/watches.
Churches and synagogues are holy places where people can pray/hurry/prays.
If the post office is closed John cannot mail/shoot/mails the letter.
When the floor was dirty the janitor would mop/eat/mops it.
For good photographs we hoped that the infant would smile/phone/smiles.
To indicate that she agreed the old woman would nod/rent/nods.
I was surprised at what the art students could draw/lick/draws.
When she caught the cold the girl started to sneeze/jump/sneezes.
If you want something badly you should ask/dance/asks for it.
Before she learned to walk our baby began to crawl/dive/crawls.
The detectives realized that any minute the gunman might shoot/swim/shoots.
Even though they were losing the soldiers continued to fight/iron/fights.
During those inspiring art lessons the students would always paint/scream/paints.
If she was ever attacked the girl would definitely scream/smile/screams.
Because the water is so shallow the swimmers cannot dive/write/dives.
Even if the man is innocent the lawyer will prosecute/cry/prosecutes.
Although I tried explaining it the student still didn't understand/yawn/understands.
After the damage to his eyes the man couldn't see/yell/sees.
For breakfast the boys would only eat/bury/eats toast and jam.
During each of the basketball games the cheerleaders would cheer/prosecute/cheers.
To greet the Queen of England the ladies should curtsey/complain/curtseys.

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The data reported in this experiment have been deposited in The fMRI Data Center (http://www.fmridc.org). The accession number is 2-2002-1136X.

Notes

[*] We use the term *conceptual information* in the most general sense to distinguish it from *syntactic information*. *Conceptual information* encompass lexico-semantic information (the semantic representation of single words), higher level semantic information (the semantic representation of whole sentences and discourse), and pragmatic information (our real-world knowledge). We use the above terms more specifically in reference to specific studies that have manipulated these different parameters. We use the terms *morphosyntactic* and *pragmatic* to refer to the specific types of syntactic and conceptual parameters, respectively, that were manipulated in the current study.

[†] This was because we lacked the precise electrode location information required to coregister ERP and fMRI data.

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