# Common and Distinct Neural Substrates for Pragmatic, Semantic, and Syntactic Processing of Spoken Sentences: An fMRI Study

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## Abstract

■ Extracting meaning from speech requires the use of pragmatic, semantic, and syntactic information. A central question is: Does the processing of these different types of linguistic information have common or distinct neuroanatomical substrates? We addressed this issue using functional magnetic resonance imaging (fMRI) to measure neural activity when subjects listened to spoken normal sentences contrasted with sentences that had either (A) pragmatical, (B) semantic (selection restriction), or (C) syntactic (subcategorical) violations sentences. All three contrasts revealed robust activation of the left-inferior-temporal/fusiform gyrus. Activity in this area was also observed in a combined analysis of all three experiments, suggesting that it was modulated by all three types of linguistic violation. Planned statistical comparisons between the three experiments revealed (1) a greater

difference between conditions in activation of the left-superior-temporal gyrus for the pragmatic experiment than the semantic/syntactic experiments; (2) a greater difference between conditions in activation of the right-superior and middle-temporal gyrus in the semantic experiment than in the syntactic experiment; and (3) no regions activated to a greater degree in the syntactic experiment than in the semantic experiment. These data show that, while left- and right-superior-temporal regions may be differentially involved in processing pragmatic and lexico-semantic information within sentences, the left-inferior-temporal/fusiform gyrus is involved in processing all three types of linguistic information. We suggest that this region may play a key role in using pragmatic, semantic (selection restriction), and subcategorical information to construct a higher representation of meaning of sentences. ■

## INTRODUCTION

As we listen to speech, we continually use different forms of linguistic information—semantic (the meaning of words), syntactic (grammatical) and pragmatic (our understanding of the world)—to build up an overall representation of meaning (Kintsch, 1988; Johnson-Laird, 1987). As these different forms of linguistic information have different rules and representations, they are generally acknowledged to be independent of one another. However, a fundamental question is whether this linguistic autonomy is paralleled by a processing autonomy. This question relates both to the stage at which these linguistic processes influence each other, as well as to their localization in the brain. In this study, we address the issue of localization. We ask the question:

Does the processing of pragmatic, semantic, and syntactic information have distinct neuroanatomical correlates, or do they share a common neural substrate? The evidence for autonomy at the neuroanatomical level is conflicting. A number of neuropsychological and electrophysiological dissociations between semantic, pragmatic, and syntactic processing have been described, yet, there is also evidence that some of the same brain regions may support processing of these different forms of linguistic information.

### Semantic vs. Syntactic Processing

Converging evidence from neuropsychological (Rapcsak & Rubens, 1994; Hodges, Patterson, Oxbury, & Funnell,

1992; Graff-Radford et al., 1990; Kempler et al., 1990; Alexander, Hiltbrunner, & Fischer, 1989; Pietrini et al., 1988; Poeck & Luzzatti, 1988; Sartori & Job, 1988; De Renzi, Zambolin, & Crisi, 1987; Warrington & Shallice, 1984), event-related potential (ERP) (Nobre & McCarthy, 1995), and functional imaging (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Demonet et al., 1992b; Goldenberg, Podreka, Steiner, & Willmes, 1987) studies suggests that left-sided inferior-temporal-cortical regions play a crucial role in lexico-semantic processing. On the other hand, the study of agrammatic aphasic patients has implicated left-anterior-inferior-frontal regions in building up the syntactic structure of sentences (Frazier & Friederici, 1991; Caplan, Baker, & Dehaut, 1985; Caramazza & Zurif, 1976). This is supported by recent functional imaging investigations (Caplan, Alpert, & Waters, 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996).

However, most of the studies exploring syntactic processing have focused on the parsing of complex sentences; the question of whether the same brain regions mediate semantic and syntactic processing within simple sentences has been relatively unexplored. This question is critical, as a central theory of language processing holds that sentence parsing is guided by lexical information held within the verb (reviewed by Garrett, 1992; Levelt, 1989). Verbs contain both semantic and syntactic information. The syntactic informa-

tion—the argument structure or subcategorization frame—places additional constraints on the object noun. Thus, in a semantically violated sentence such as ''the man drank the guitar'' (see Table 1), the semantic selection restriction properties of the verb ''drank'' are incongruous with the object noun ''guitar'' despite the two words being syntactically compatible. In contrast, the sentence ''the young man slept the guitar'' is violated both semantically and syntactically (subcategorically), because the verb ''slept'' cannot take a direct object (which should be preceded by a preposition).

Whether subcategorical syntactic processing can be dissociated from semantic processing within sentences is controversial. From a linguistic perspective, the syntactic aspect of a verb (specified on the subcategorization frame) can be seen as a projection of some of its semantic features (Chomsky, 1981; Bresnan, 1979; Jackendoff, 1978). By this account, the meaning of a verb and its syntactic aspects are tightly intertwined, and might, therefore, be subserved by the same brain networks. On the other hand, Ostrin and Tyler (1995) have described a patient (JG) who cannot process subcategorization information, but who processes lexical–semantic information normally. Moreover, ERP waveforms elicited by subcategorization violations show a more anterior scalp-distribution than those elicited by purely semantic violations (Friederici, 1995; Rosler, Friederici, Putz, & Hahne, 1993), suggesting that the two processes can be spatially dissociated.

**Table 1.** Types of Linguistic Violations

| Linguistic violation | Explanation | Example illustrating how the relationship between verb and object noun can be varied to change meaning of whole sentence[a] | Example used in current study |
|---|---|---|---|
| None | Baseline condition against which the other conditions are evaluated | ''The young man *grabbed* the guitar'' | ''The boy counted the ducks'' |
| Pragmatic (Experiment A) | Sentence is pragmatically implausible with respect to our knowledge of real world events. | ''The young man *buried* the guitar'' | ''The woman painted the insect'' |
| Semantic (selection restriction) (Experiment B) | Semantic properties of verbs are incompatible with the semantic properties of object nouns. | ''The young man *drank* the guitar'' | ''My mother ironed a kiss'' |
| Syntactic (subcategorical violation) (Experiment C) | Intransitive verbs are chosen so that a noun in the direct object position cannot follow them. | ''The young man *slept* the guitar'' | ''His father chattered the umbrella'' |
| Word-strings | Word-strings with no syntactic or semantic structure | ''young the the slept man guitar'' | ''money the the client washed'' |

[a]This example is adapted from that given in *Spoken Language Comprehension* (p. 107) by L.K. Tyler, 1992, London: MIT Press.

## Pragmatic vs. Lexico-Semantic and Subcategorization Processing

"Pragmatic processing" is a rather loosely defined term, and has been used to refer to a wide range of cognitive processes, many operating upon narrative and discourse-level material such as nonliteral language, stories, jokes, and conversations. The study of right-brain-damaged patients suggests that some of these operations are subserved by the right hemisphere (Joanette & Brownell, 1990). In the current study, we use the term "pragmatic processing" in a narrow and specific sense to refer to the use of "real-world knowledge" within simple sentences that do not violate selection restriction or subcategorization (lexically encoded) constraints (see Tyler, 1992, p. 108).[1] Thus, the sentence "the young man buried the guitar" (see Table 1) appears odd only because of what we know about guitars and the likelihood of their being buried. The role of the right hemisphere in processing single sentences of this nature is relatively uninvestigated. On the other hand, there is evidence, both from divided visual fields studies (Faust, Babkoff, & Kravetz, 1995) and neuroimaging studies (Mazoyer et al., 1993; Demonet et al., 1992a), that the right hemisphere may play a role in processing sentences that are semantically violated, although, whether this is a result of violated semantic constraints between individual words within the sentence, or as a result of violations of real-world knowledge, is unknown. In the ERP literature, a bilateral, posteriorly distributed ERP at 400 msec is well known to be elicited by unpredictable (low cloze-probability) sentences (Kutas & Hillyard, 1980; Kutas & Hillyard, 1984). Examination of materials that elicit an N400 suggests that it is evoked to both pragmatic and semantic selection restriction (SR) violations, but the precise relationship between the scalp-distribution and waveform of the N400 and the linguistic constraints of sentences eliciting it, have not been systematically investigated. Therefore, the question of whether there are areas of the brain, particularly the right hemisphere, subserving pragmatic, as opposed to lexico-semantic and subcategorization processing within simple sentences, remains unanswered.

## The Current Study: Design

To date, most functional imaging studies of semantic processing have explored brain regions associated with processing single words. There have been relatively few studies of sentence-level processing, and most of these have contrasted normal sentences with relatively low-level "baseline" conditions such as random strings of words (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). Such designs sometimes assume a hierarchical model of language processing in which different brain areas are thought to be specifically dedicated to processing at the sentential vs. lexical level. This assumption may, to some extent, be justified. For example, some studies suggest that anterior-inferior-temporal regions are specifically engaged in higher-level sentential processing (Mazoyer et al., 1993). However, the investigation of neural correlates of specific levels of sentence processing (i.e., pragmatic, semantic, syntactic) demands alternative approaches.

One approach is to vary the complexity of a particular level of representation within normal sentences. This has a long tradition in the behavioral investigation of syntactic processing and its recent application to functional imaging techniques has implicated perisylvian regions in processing more syntactically complex sentences (Caplan et al., 1998; Just et al., 1996) and inferior-temporal regions in processing more semantically complex sentences (Caplan et al., 1998).

A second approach is to contrast normal sentences with sentences that have been violated in different ways. This has been used in both behavioral (Tyler, 1985; Marslen-Wilson & Tyler, 1975) and electrophysiological studies (e.g., Ainsworth-Darnell, Shulman, & Boland, 1998; Hagoort et al., 1993; Osterhout & Holcomb, 1992; Kutas & Hillyard, 1980, Kutas & Hillyard, 1984). In the current investigation, we adapt this approach to the demands of functional magnetic resonance imaging (fMRI) to study the neural correlates of pragmatic, semantic (SR), and syntactic (subcategorization) processing within spoken sentences.

Nine subjects completed three experiments in which blocks of normal sentences were contrasted, in an alternating periodic design, with blocks of (A) pragmatically, (B) semantically (SR), and (C) syntactically (subcategorically) violated sentences. Four subjects completed a further experiment in which normal sentences were contrasted with random strings of words. Throughout each experiment, subjects made judgements on the "sense" of spoken sentences—a task that has been used extensively in ERP studies of sentence processing. In the context of a periodic design in which stimuli are blocked by condition, and there are intrinsic confounds such as expectancy and changes in attentional state, this task is not a demanding one. It was employed to ensure that subjects attended to stimuli during scanning and were able to hear the sentences above the scanner noise. Forcing subjects to process sentences as a whole for meaning may be preferable to more "artificial" lexico-semantic tasks (e.g., lexical decision), which could encourage the adoption of strategies (e.g., a word-by-word analysis of whole sentences) unrelated to everyday speech processing. The data were analyzed by fitting a sinusoidal waveform to the frequency of presentation of contrasting sentence types, thus, revealing brain activity modulated[2] by each type of linguistic violation.

We sought to answer two main questions. First, does the processing of pragmatic, semantic (SR), and subca-

tegorization information within simple sentences have a common neural substrate? We addressed this question both by a qualitative comparison of the brain maps generated in each experiment, and by carrying out a quantitative analysis in which images from all three experiments were combined to construct an overall median image. On the basis of the literature implicating it in lexico-semantic processing (above), and in processing the meaning of whole sentences (Caplan et al., 1998; McCarthy, Nobre, Bentin, & Spencer, 1995), we predicted that the left-inferior-temporal cortex would participate in the processing of all three types of linguistic information.

Our second question was whether distinct brain regions are engaged in processing different types of linguistic information. We therefore carried out planned statistical comparisons, comparing differences in activity between conditions, between the three experiments. For the reasons outlined above, we were particularly interested in which brain regions were engaged in processing (a) pragmatic information as opposed to semantic (SR) or subcategorical (both lexically encoded) information, (b) semantic (SR) vs. subcategorization information, and (c) subcategorization vs. semantic (SR) information.

## RESULTS

### Behavioral (Accuracy) Data

As shown in Table 2, subjects were highly accurate in their judgements of whether or not the sentences made sense. A repeated-measures analysis of variance (ANOVA), 3 (experiment: A, B, C)×2 (sentence-type: normal vs. anomalous), with proportion of errors as the dependent variable, showed no significant main effect of experiment ($F(2, 12)=1.30$, $p=.31$), sentence-type ($F(1, 6)=.27$, $p=.625$), or experiment by sentence-type interaction ($F(2, 12)=.31$, $p=.89$), indicating that there were no differences in the participants' ability to judge whether or not the sentences made sense in the three experiments, or in the proportion of false negative and false positive errors. $A'$, a nonparametric signal detec-

tion measure (e.g., see Linebarger, Schwartz & Saffran, 1983), also did not differ significantly between experiments 1, 2, and 3 ($F(2, 12)=1.34$, $p=.3$). The four subjects who participated in experiment D also performed extremely accurately with proportions of false positives and false negatives ranging from .8 to 3 percent. $A'$ scores in each subject across all four experiments, ranged from .92 to 1.0.

### Functional Imaging Data

#### Overview: Presentation of Data

The data were analyzed by fitting a sinusoidal waveform to the frequency of presentation of contrasting sentence types. This fulfilled our primary aim of revealing brain activity modulated by each type of linguistic violation. As opposed to other methodologies, such as ERPs, neuro-imaging techniques permit examination of the directionality of the response to the stimulus input. In Tables 3, 4, 5, and 6, we therefore report the phase of response in relation to input, i.e., which regions showed greater responses during listening to normal sentences and which showed greater responses when subjects listened to anomalous sentences/word-strings. In the corresponding figures (Figures 1, 2B, and 3), regions that show greater responses during listening to normal sentences are shown in red and regions showing greater responses during listening to anomalous sentences/word-strings are shown in blue.

As we considered any regions that were modulated by the contrasting stimulus conditions as indexing a particular level of linguistic processing (see first paragraph of Discussion for further elaboration), we included both phases of activity in the analyses that compared and combined the three experiments, i.e., in the overall median analysis, and the pair-wise planned statistical comparisons between experiments.

#### Normal Sentences vs. Random Strings of Words

As shown in Table 3, this contrast activated a network distributed bilaterally throughout the temporal lobes.

**Table 2.** Sense Judgements of Anomalous Sentences by Participants During Scanning

| Type of anomaly | Experiment A Pragmatic | Experiment B Semantic (SR) | Experiment C Subcategorization | Random word-strings |
|---|---|---|---|---|
| Percentage of false positives | 4.76 (.04) | 1.66 (.01) | 3.33 (.05) | .83 (.01) |
| Percentage of false negatives | 4.76 (.05) | 2.5 (.03) | 2.5 (.03) | .83 (.01) |
| $A'$ | .97 | .98 | .98 | .99 |

Means are shown with standard deviations in brackets. Probabilities of hits and false alarms were used to calculate a nonparametric measure of sensitivity for each patient. This was $A'$, a signal-detection index which is a measure of sensitivity (signal:noise discrimination level), and is a better reflection of overall sensitivity to sentential incongruity than percentage of correct judgements (discussed in Linebarger, 1983). In determining the $A'$ values, we used the formula developed by Grier (1971): $A'=.5+(y-x)(1+y-x)/4y(1-x)$, where $x$=proportion of false positives and $y=1-$proportion of false negatives.

**Table 3.** Brain Regions Modulated when Normal Sentences are Contrasted with Random Strings of Words

| Region | BA | x | y | z | No. | Prob(max FPQ) |
|---|---|---|---|---|---|---|
| *In phase with normal sentences* | | | | | | |
| L inf. temp./fusiform g. | 37 | −40 | −42 | −7 | 9 | .001 |
| L mid. temp. g. | 21/37 | −32 | −44 | 9 | 48 | .0004 |
| R sup. temp. g | 22 | 46 | −25 | 4 | 30 | .0005 |
| L sup. temp. g. | 22 | −43 | −53 | 20 | 9 | .0009 |
| R insula | – | 35 | 11 | −2 | 9 | .0008 |
| L lingual gyrus | 18 | −20 | −78 | −7 | 6 | .0008 |
| L retrosplen. cortex | 30 | −12 | −53 | 20 | 8 | .001 |
| R orb.-front. cortex | 11 | 20 | 17 | −13 | 8 | .0007 |
| Cerebellar vermis | – | −3 | −67 | −7 | 51 | .0001 |
| L cerebellar cortex | – | −12 | −69 | −13 | 7 | .002 |
| L caud. nucl. | – | −6 | 17 | −2 | 7 | .002 |
| | | | | | | |
| *In phase with random word-strings* | | | | | | |
| med./ant. temp. cortex (uncus) | 34 | −12 | 3 | −18 | 11 | .0008 |
| R temp. pole | 38 | 46 | 6 | −13 | 4 | .002 |
| L parahipp. g. | 35 | −17 | −28 | −13 | 10 | .0009 |
| R and L parahipp. g. | 30 | 6 | −36 | −2 | 40 | .00004 |
| L fusiform g. | 37 | −38 | −53 | −18 | 8 | .0007 |
| R fusiform g. | 37 | 40 | −50 | −13 | 7 | .002 |
| R inf. temp. g. | 37 | 52 | −44 | −7 | 4 | .005 |
| L mid. temp. g. | 21 | −46 | −25 | −2 | 16 | .0002 |
| L sup. temp. g. | 22 | −40 | −47 | 15 | 13 | .0002 |
| L sup. temp./Heschl's g. | 42/41 | −52 | −22 | 15 | 6 | .0006 |
| L insula[a] | – | −40 | −6 | −7 | 58 | .0001 |
| Lingual gyrus | 18 | 3 | −69 | −2 | 70 | .00004 |
| Cerebellum | – | 0 | −50 | −18 | 65 | .0001 |
| R caud. nucl. | – | 6 | 17 | −2 | 9 | .0009 |
| Brain stem | – | −6 | −14 | −7 | 9 | .001 |

BA = Brodmann's areas (designation is approximate). x, y, and z refer to the stereotactic coordinates (Talairach & Tournoux, 1988) of the voxel within each cluster with the largest FPQ (which reflects the significance of periodic change) and Prob(max FPQ) indicates the probability of its false activation. No. = the number of contiguous pixels within a cluster; for simplification, activation foci of three or fewer voxels are not listed. Where there is more than one focus of activation within the same Brodmann's area at the same level above/below the AC–PC plane, that with the greatest number of activated voxels is reported.

[a]Focus of activation extends medially into the striatum.

*Abbreviations*: med/ant temp. cortex = medial/anterior-temporal cortex; temp. pole = temporal pole; parahipp g. = parahippocampal gyrus; inf. temp. g. = inferior-temporal gyrus; mid. temp. g. = middle-temporal gyrus; sup. temp. g. = superior-temporal gyrus; retrosplen. cortex = retrosplenial cortex; orb.-front. cortex = orbitofrontal cortex; caud. nucl. = caudate nucleus.

The left-inferior-temporal/fusiform gyrus was activated in phase with the normal sentences. Other regions activated in phase with the normal sentences included the right insula (Figure 1i), left caudate nucleus (Figure 1i), right-superior-temporal (BA 22, Figure 1ii), and left-middle-temporal gyrus (BA 21/37, Figure 1iii). The right-temporal pole and right-inferior-temporal/fusiform cortex was activated in phase with the word-strings. Other regions activated in phase with the random word-strings included the right caudate nucleus (Figure

**Table 4**. Brain Regions Modulated as Normal Sentences are Contrasted with Pragmatically Anomalous Sentences

| Region | BA | x | y | z | No. | Prob(max FPQ) |
|---|---|---|---|---|---|---|
| *In phase with pragmatically anomalous sentences* | | | | | | |
| L sup. temp. g.[a] | 22/42 | −49 | −31 | 9 | 47 | .0001 |
| Cuneus[a] | 31 | 0 | −69 | 9 | 31 | .00001 |
| Cuneus[a] | 18/19 | 9 | −83 | 15 | 8 | .00009 |
| L retrosplen. cortex[a] | 29/30 | −12 | −39 | 9 | 29 | .00001 |
| L parahipp./fusiform g. | 35/36 | −29 | −36 | −13 | 5 | .001 |
| L insula (ant.) | – | −32 | 14 | −2 | 5 | .0006 |
| R insula (mid.) | – | 43 | 6 | 4 | 6 | .002 |
| L cerebellar vermis | – | −6 | −67 | −7 | 11 | .0001 |
| *In phase with normal sentences* | | | | | | |
| R temp. pole (uncus) | 34/38 | 29 | 3 | −18 | 29 | .00001 |
| L temp. pole | 38 | −38 | 8 | −13 | 14 | .0005 |
| R hippocamp. | – | 26 | −22 | −7 | 5 | .001 |
| L hippocamp. | – | −35 | −31 | −2 | 5 | .001 |
| **L inf. temp./fusiform g.**[b] | **20/36** | **−40** | **−33** | **−7** | **29** | **.0008** |
| L inf. temp./fusiform g. | 37 | −35 | −53 | −2 | 8 | .001 |
| L mid. temp. g. | 21 | −40 | −56 | 9 | 6 | .0001 |
| lingual g. | 18 | 0 | −78 | −2 | 36 | .0001 |
| L orb.-front. cortex | 47/11 | −23 | 25 | −2 | 22 | .0003 |
| R striatum (glob. pall.) | – | 14 | 3 | −7 | 8 | .001 |

Regions indicated in bold are those within the left-inferior-temporal/fusiform cortex.

BA, $x$, $y$, $z$, No., and Prob(max FPQ): as in Table 3.

[a]Indicates whether more than one voxel within this cluster was activated to a significantly greater degree in this experiment than in the other two experiments.

[b]Some voxels within this cluster were activated in phase with the anomalous sentences.

*Abbreviations*: temp. pole = temporal pole; parahipp. g. = parahippocampal gyrus; hippocamp. = hippocampus; inf. temp. g. = inferior-temporal gyrus; mid. temp. g. = middle-temporal gyrus; sup. temp. g. = superior-temporal gyrus; orb.-front. cortex = orbitofrontal cortex; retrosplen. cortex = retrosplenial cortex; glob. pall. = globus pallidus.

1i), bilateral parahippocampal gyri (BA 35, Figure 1i), bilateral lingual gyri (BA 18, Figure 1i), left-middle (BA 21, Figure 1iv), and superior-temporal gyrus (BA 42/41 and BA 22, Figure 1iv).

*Question 1: Which Regions Are Commonly Activated By Contrasting Normal Sentences with (A) Pragmatic, (B) Semantic (SR), and (C) Syntactic (Subcategorization) Violations?*

*(a) Qualitative comparisons between the three experiments.* Figure 3 (top row, $z=−7$) showed that activity in the left-inferior-temporal/fusiform region was modulated by all three types of linguistic violation. This is most clearly seen in Figure 2C, which shows an overlay map of the activation during the three experiments, with areas of coincident activation shown in yellow. In the pragmatic experiment (Table 4; Figure 3A, top), some voxels within this left-inferior-temporal/fusiform cluster were activated in phase with the normal sentences, while others were activated in phase with the anomalous sentences. In the semantic (SR) comparison, this cluster was activated primarily in phase with the normal sentences (Table 5; Figure 3B, top), and in the syntactic subcategorization comparison, this cluster was activated primarily in phase with the anomalous sentences (Table 6; Figure 3C, top). In Tables 4, 5, and 6, regions are named, and Brodmann's areas are given by the position of the voxel with the greatest significance of periodic change. However, for clarity, all activated voxels within the inferior-temporal/fusiform region at 7 mm below the intercommissural plane are shown in bold.

**Table 5.** Brain Regions Modulated as Normal Sentences are Contrasted with Semantically Anomalous Sentences

| Region | BA | x | y | z | No. | Prob(max FPQ) |
|---|---|---|---|---|---|---|
| *In phase with semantically anomalous sentences* | | | | | | |
| R mid. temp. g.[a] | 21 | 43 | −11 | −7 | 14 | .0006 |
| R sup. temp. g.[a] | 22 | 49 | −17 | 4 | 19 | .0006 |
| | | | | | | |
| *In phase with normal sentences* | | | | | | |
| **L inf. temp. g.** | **37** | **−49** | **−44** | **−7** | **6** | **.0004** |
| L lingual g. | 18 | −32 | −72 | −7 | 11 | .0004 |
| L lingual g.[a] | 18 | −9 | −72 | 4 | 13 | .0005 |
| R lingual g. | 18/19 | 20 | −64 | −2 | 12 | .001 |
| R lingual g. | | 12 | −61 | −2 | 9 | .003 |
| | | 12 | −81 | 4 | 8 | .001 |
| R cuneus | 31 | 12 | −67 | 9 | 13 | .0004 |
| L insula (mid.)[a] | – | −43 | −8 | 4 | 17 | .0005 |
| R cerebellum | – | 26 | −69 | −13 | 18 | .0001 |
| R cerebellar vermis | | 12 | −64 | −7 | 65 | .00001 |
| L cerebellum | – | −29 | −69 | −13 | 14 | .0006 |
| R striatum (lent. nucl.) | – | 26 | −6 | 4 | 12 | .0001 |
| Brain stem | – | 0 | −56 | −2 | 10 | .0006 |

Region indicated in bold falls within the left-inferior-temporal/fusiform cortex; BA, *x*, *y*, *z*, No., and Prob(max FPQ): as in Table 3.

[a]Indicates whether more than one voxel within cluster is activated to a significantly greater degree in this experiment than the subcategorization experiment.

*Abbreviations*: inf. temp. g. = inferior-temporal gyrus; mid. temp. g. = middle-temporal gyrus; lent. nucl. = lentiform nucleus.

The other region that appeared to be commonly activated in each of the three experiments was the lingual gyrus, which was activated in phase with the presentation of normal sentences in all three comparisons (Tables 4, 5, and 6, respectively). Of note, however, in contrasting normal with pragmatically anomalous sentences, activation of the cuneus is seen in phase with the anomalous sentences (Figure 3A; Table 4).

(b) *Quantitative analysis of the three experiments: Construction of an overall median image*. To identify brain regions involved in processing normal vs. violated sentences, irrespective of the type of linguistic anomaly, we constructed an overall median image by combining the data from all subjects participating in experiments A, B, and C. This analysis, which comprised 27 comparisons in total, maximized our power to detect a response. By definition, voxels displayed on this median image were activated (in phase with either normal or violated sentences) in at least half of its constituent activation maps. This analysis confirmed that the largest and most significant ($p < .00002$) response was at the base of the left-posterior-temporal lobe, in a cluster of voxels spanning the adjacent parts

of the left fusiform and inferior-temporal gyri (illustrated in Figure 2A). The point of maximal response was in the left fusiform gyrus (BA 20, $x = −40$, $y = −33$, $z = −7$). As shown in Figure 2B, some voxels within this cluster were activated in phase with the normal sentences, while others were activated in phase with the anomalous sentences.

*Question 2: Are Distinct Brain Regions Involved in Processing Different Types of Linguistic Information?*

It is clear from Tables 4, 5, and 6, and Figures 2C and 3 that there were marked differences in patterns of activation between the three experiments. We went on to test whether these qualitative differences were significant by carrying out planned statistical comparisons between experiments. We first explored which areas were engaged in processing pragmatic as opposed to lexically encoded (i.e., selection restriction or subcategorization) information. The null hypothesis was tested at the 682 voxels that were significantly activated in one or both of the brain activation maps, with a probability of Type I error for each test $\alpha = .01$. For this size of test, we expected no more than six false positive voxels over

**Table 6.** Brain Regions Modulated as Normal Sentences are Contrasted with Syntactically (Subcategorically) Violated Sentences

| Region | BA | x | y | z | No. | Prob(max FPQ) |
|---|---|---|---|---|---|---|
| *In phase with subcategorically violated sentences* | | | | | | |
| **L inf. temp./fusiform g.** | **20** | **−43** | **−31** | **−7** | **16** | **.0004** |
| | | | | | | |
| *In phase with normal sentences* | | | | | | |
| L hippocamp. | – | −26 | −14 | −13 | 12 | .001 |
| R parahipp. g. | 27 | 12 | −31 | −2 | 9 | .0009 |
| L parahipp. g. | 30/35 | −17 | −33 | −2 | 12 | .0007 |
| L fusiform g. | 37 | −38 | −42 | −2 | 11 | .002 |
| L inf. temp/mid. temp. g. | 37/39 | −35 | −69 | 9 | 12 | .0008 |
| L mid. temp. g. | 21 | −49 | −53 | 9 | 9 | .001 |
| R sup. temp./mid. temp. g. | 22/21 | 49 | −14 | −2 | 7 | .002 |
| L sup. temp. g. | 22 | −46 | −47 | 15 | 10 | .0003 |
| R orb.-front. cortex | 47 | 46 | 22 | −2 | 5 | .003 |
| R lingual g. | 18 | 20 | −53 | 4 | 32 | .0002 |
| R lingual g. | 19 | 20 | −53 | −2 | 9 | .0004 |
| L lingual g. | 18 | −3 | −78 | −2 | 6 | .0004 |
| L lingual g. | 18 | −9 | −53 | 4 | 5 | .002 |
| L retrosplen. cortex | 30 | −14 | −50 | 9 | 54 | .0002 |
| R post. cing. g. | 30 | 14 | −50 | 15 | 4 | .001 |
| R cerebellum | – | 9 | −56 | −7 | 9 | .0005 |
| L thalamus | – | −12 | −22 | 9 | 8 | .002 |

BA, *x*, *y*, *z*, No., and Prob(max FPQ): as in Table 3.

Region indicated in bold falls within the left-inferior-temporal/fusiform cortex.

*Abbreviations*: inf. temp. g. = inferior-temporal gyrus; hippocamp. = hippocampus; parahipp. g. = parahippocampal gyrus; mid. temp. g. = middle-temporal gyrus; sup. temp. g. = superior-temporal gyrus; orb.-front. cortex = orbitofrontal cortex; retrosplen. cortex = retrosplenial cortex; post. cing. g. = posterior cingulate gyrus.

the search volume under the null hypothesis. In total, 46 voxels demonstrated significant difference in mean fundamental power quotient (FPQ). These regions included the left-superior-temporal gyrus, retrosplenial cortex, and cuneus (Figure 4, left column marked with a superscript in Table 4; Table 7A). As can be seen by referring to Figure 3A(bottom), these areas were activated primarily in phase with pragmatically anomalous as opposed to normal sentences. We also carried out comparisons between the semantic (SR) and the subcategorization experiments. Here, the null hypothesis was tested at the 422 voxels that were significantly activated in one or both of the brain activation maps, again with probability of Type I error for each test $\alpha=.01$. For this size of test, we expected no more than four false positive voxels over the search volume under the null hypothesis. In total, 32 voxels demonstrated significant difference in mean FPQ. Regions activated to a significantly greater degree in the semantic (SR) vs. the syntactic (subcategorization) experiment included the

right-superior and middle-temporal gyri and the left insula (Table 7B; indicated with a superscript a on Table 5; Figure 4, middle column). Both right temporal regions were activated primarily in phase with semantic (SR) anomalous as opposed to normal sentences (see Figure 3B, top and middle). The final contrast revealed no voxels in the syntactic (subcategorization) experiment that were activated to a significantly greater degree than in the semantic (SR) experiment (Figure 4, right column).

*Summary of Results*

In summary, contrasting normal sentences with random strings of words revealed activity in a widespread network distributed bilaterally throughout the temporal lobes. Our key finding was a highly significant modulation of activity in the left-inferior-temporal/fusiform region in three separate experiments contrasting normal sentences with (A) pragmatically, (B) semanti-

cally (SR), and (C) subcategorically violated sentences. Activity in this area was also observed in an overall median analysis combining the three experiments. Taken together, these findings suggests that activity in this area was modulated by all three types of linguistic violation. Planned comparisons between experiments revealed (1) a greater difference between conditions in activation of the left-superior-temporal gyrus for the pragmatic experiment than the two other experiments, (2) a greater difference between conditions in activation of the right superior and middle-temporal gyrus in the semantic (SR) experiment than the syntactic (subcategorization) experiment, and (3) no regions activated to a greater degree in the syntactic (subcategorization) experiment than the semantic experiment.

## DISCUSSION

### Assumptions in Design and Interpretation

In this study, we contrasted normal sentences with sentences that were linguistically violated in three different ways. Following both behavioral (Tyler, 1985; Marslen-Wilson & Tyler, 1975) and electrophysiological studies (e.g., Ainsworth-Darnell et al., 1998; Hagoort et al., 1993; Osterhout & Holcomb, 1992; Kutas & Hillyard, 1980, Kutas & Hillyard, 1984), we interpret responses associated with each of these contrasts as indexing a specific level of linguistic processing. Underlying this interpretation, however, are two important assumptions.

#### Phase of Activity

The first assumption is that, within each experiment, brain activity in phase with both normal sentences and each particular type of linguistic violation, reflects that specific level of linguistic processing. These experiments, thus, do not follow a traditional "cognitive subtraction" design, which focuses on activity associated with an "active" experimental condition over and above a "baseline" control condition. Rather, by fitting a sinusoidal waveform to the frequency of presentation of two active conditions (normal sentences and anomalous sentences), we reveal all brain activity modulated by each contrast, and, by inference, associated with each level of linguistic processing. Because we cannot make precise inferences as to the meaning (at a psycholinguistic level) of activity in phase with normal as opposed to anomalous sentences (see below), we included both phases of activity in analyses comparing and combining the separate three experiments.

Nonetheless, our methods did enable us to examine the directionality (phase) of response in relation to stimulus input, i.e., which regions showed greater responses in listening to normal sentences, and which

showed greater responses in listening to anomalous sentences/word-strings, within each experiment. This phase information is open to several different interpretations to which we refer throughout this section.

First, at a cognitive level, responses in phase with anomalous sentences/word-strings could reflect relatively greater "energy" required to *access* a word that has not been "preactivated" by its preceding context (Elman & McClelland, 1984; Marslen-Wilson & Welsh, 1978; Marslen-Wilson & Tyler, 1980), an attempt to *integrate* contextually inappropriate words into a coherent whole (Holcomb, 1993; Rugg, 1990) or an error-signal indicating that a violation in context has occurred. Responses in phase with normal sentences could reflect relatively greater "energy" required to successfully *utilize* pragmatic, semantic (SR), and subcategorization information to interpret normal sentences. Distinguishing between these possibilities is further complicated because, at a neural level, we cannot distinguish Blood Oxygenation Level Dependent (BOLD) activation resulting from local increases in synaptic activity during one phase, from a net reduction in local synaptic activity during the opposing phase (for discussion, see Bullmore et al., 1996a). Nor is it possible to distinguish the effects of facilitatory or inhibitory synaptic activity.

#### Blocked Design

The second assumption we have made in attributing activity associated with each experimental contrast with a specific level of linguistic processing is that subjects are processing the normal sentences in the same way for each experiment, i.e., that they are not adopting different cognitive strategies dependent upon the contrasting experimental condition. The potential generation of such "functional contexts" unique to each experiment, is an intrinsic confound of blocked-design binary comparisons. To disentangle this issue, we are currently carrying out event-related fMRI studies (see Rosen, Buckner, & Dale, 1998; Buckner et al., 1996) in which we can determine the hemodynamic response to each different type of sentence in comparison with a low-level condition, randomly presented within a single experiment.

### Normal Sentences vs. Random Word-strings

The comparison of normal (unviolated) sentences with unrelated strings of words indicates which brain regions were involved in normal sentence processing: Areas activated in phase with normal sentences as opposed to word-strings included superior-temporal gyrus (bilaterally), as well as the left middle and inferior-temporal gyri. Similar regions (particularly, BA 21/37) have been activated in listening to normal speech (Fink et al., 1996; Mazoyer et al., 1993) and in contrasting visually presented sentences with random strings of words (Bottini

et al., 1994), suggesting that they play an important role in normal sentence processing.

However, as discussed in the Introduction, the idea that more regions are activated during listening to whole sentences as opposed to single words rests on the assumption of a serial model of processing, which is probably somewhat simplistic. Indeed, in the current comparison, there were also many foci activated in phase with word-strings rather than with the normal sentences—a comparison that was not reported by
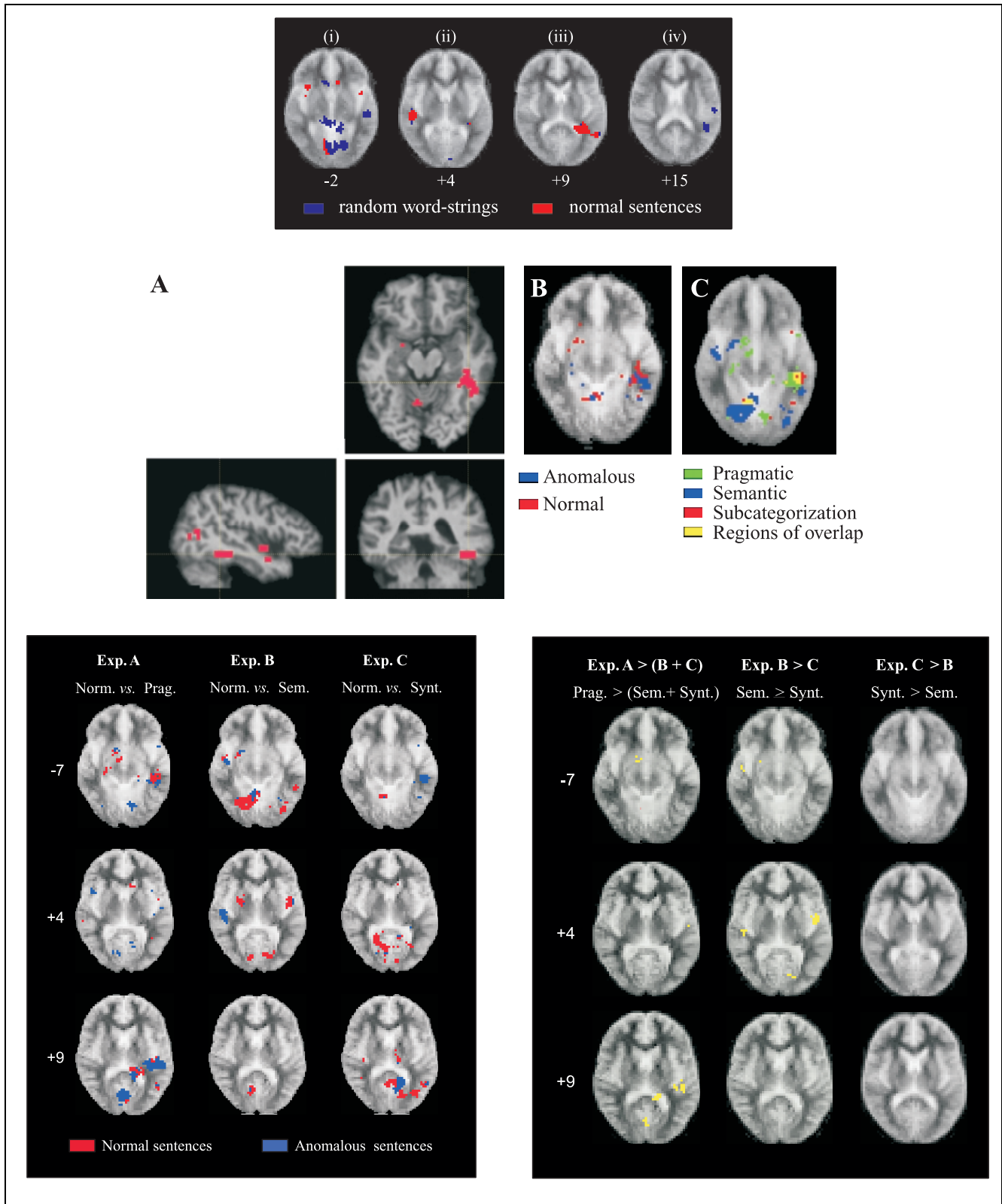
Bottini et al. (1994), and which cannot be deduced from data reported by Mazoyer et al. (1993), who contrasted both sentences and word-strings independently with a resting scan. These foci included bilateral superior-temporal, inferior-temporal, and fusiform gyri, the medial-temporal lobe (bilateral parahippocampal gyri) as well as a small focus in the right-temporal pole, an area previously activated during reading (Fletcher et al., 1995) and listening to (Mazoyer et al., 1993) stories and to anomalous sentences (Mazoyer et al., 1993).

One explanation for the response of temporal regions in phase with the presentation of the word-strings is that it reflects a relatively greater demand on *accessing* (see above) networks subserving a representation of meaning for each individual word (Damasio et al., 1996; Martin et al., 1996; Vandenberghe et al., 1996; Pietrini et al., 1988; Sartori & Job, 1988). By this account, there would be less activation in accessing words in coherent sentences, which, according to a connectionist model (Elman & McClelland, 1984; Marslen-Wilson & Tyler,

1980; Marslen-Wilson, 1987), would be preactivated (or less inhibited) by their preceding context.

The robust activation of the parahippocampal gyri, which are thought to be involved in processing (and, thus, encoding) unfamiliar, novel information (Knight, 1996; Tulving, Markowitsch, Kapur, Habib, & Houle, 1994; Eichenbaum, Otto, & Cohen, 1992) for storage within the neocortex, may reflect an attempt to ''bind'' together (Squire & Zola-Morgan, 1991) or *integrate* (see above) the word-strings, to form a gestalt representation of meaning.

## Areas Modulated by All Three Types of Linguistic Anomaly

The primary goal of this study was to determine whether there were areas in the brain that were modulated by all three types of anomaly. We interpret our qualitative comparisons of the three separate generic brain activation maps constructed for each experiment in conjunction with our findings by constructing an overall median

**Figure 1.** Generic brain activations (at $p<.005$) as normal sentences are contrasted with random strings of words. From left to right, transverse sections through four participants' normalized, averaged brains, at 2 mm below and 4, 9, and 15 mm above the AC–PC line. The left side of each map represents the right side of the brain. The main foci activated in phase with normal sentences (colored red) illustrated here are: (i) The right insula, the left caudate nucleus; (ii) the right-superior-temporal gyrus (BA 22); (iii) the left-middle-temporal gyrus (BA 21/37). Foci activated in phase with random strings of words (colored blue) illustrated here are (i) the right caudate nucleus, bilateral parahippocampal gyri (BA 35), (ii) bilateral lingual gyri (BA 18), (iii) left-middle-temporal gyrus (BA 21), and (iv) the left-superior-temporal gyrus (BA 42/41, BA 22).

**Figure 2.** Modulation of the left-inferior-temporal/fusiform gyrus in all three experiments, i.e., in contrasting normal sentences with pragmatically, semantically, and subcategorically violated sentences. All sections are at 7 mm below the AC–PC line. The left side of each map represents the right side of the brain. (A) This overall median brain activation map is derived from a total of 27 individual images (i.e., experiments A, B, and C); voxels have a probability of false activation, $p<.005$. Activation foci are superimposed on spoiled GRASS MR images (transverse, coronal, and sagittal sections). The main activation focus (illustrated by the dotted yellow lines) is at the base of the left-posterior-temporal lobe, spanning the fusiform and inferior-temporal gyrus. (B) Voxels colored red depict activation in phase with normal sentences; voxels colored blue depict activation in phase with anomalous sentences. Activation foci of the overall median image are superimposed upon a gray-scale template of participants' normalized, averaged high-resolution EPI images. (C) An overlap image of three generic brain activation maps constructed by contrasting normal sentences with pragmatically (green), semantically (blue), and subcategorically (red) violated sentences. Pixels shown in yellow are activated in at least two of the three experiments, and, again, include a cluster at the base of the left-temporal cortex. Again, all activation foci are superimposed upon an averaged gray-scale template.

**Figure 3.** Normal sentences vs. (A) pragmatically violated, (B) semantically (SR) violated, and (C) syntactically (subcategorically) violated sentences. Images shown are 7 mm below (top row), 4 mm above (middle row), and 9 mm above (bottom row) the AC–PC line. Voxels have a probability of false positive activation, $p<.005$. All activation foci are superimposed upon a gray-scale template of participants' normalized, averaged high-resolution EPI images. Voxels colored red depict activation in phase with normal sentences; voxels colored blue depict activation in phase with anomalous sentences. The left side of each map represents the right side of the brain. *Experiment A, Norm. vs. Prag.* Brain areas modulated in contrasting normal sentences with pragmatically anomalous sentences. Note that activation foci in the left-superior-temporal gyrus, retrospenial cortex, and occipital cortex (bottom) are activated primarily in phase with the pragmatically anomalous sentences. *Experiment B, Norm. vs. Sem.* Brain areas modulated in contrasting normal sentences with semantically anomalous sentences (with selection–restriction violations). Note that foci in the right-middle and superior-temporal gyri (top, middle) are activated primarily in phase with the semantically-anomalous sentences. *Experiment C, Norm. vs. Synt.* Brain areas modulated in contrasting normal sentences with syntactically anomalous sentences (with subcategorization violations). Note the absence of activation in the superior-temporal cortex.

**Figure 4.** Planned difference activation maps demonstrating significant differences in activation between the three main experiments. Both phases of activity for each of the individual experiments illustrated in Figure 3 were included in constructing the activation maps illustrated here (see Discussion for further explanation). As for Figure 3, all images shown are 7 mm below (top row), 4 mm above (middle row), and 9 mm above (bottom row) the AC–PC line. The left side of each map represents the right side of the brain. The gray-scale template is as for Figure 3. *Experiment A>(Experiment B+Experiment C).* Areas activated to a significantly greater degree in the pragmatic experiment (Experiment A) than the semantic (SR) (Experiment B) and the syntactic (subcategorizations) (Experiment C) experiments include the left-superior-temporal gyrus (bottom, maximum difference FPQ, $p<.0001$), retrospenial cortex (bottom, maximum difference FPQ, $p<.00001$), and occipital cortex (bottom, maximum difference FPQ, $p<.0001$). *Experiment B>Experiment C.* Areas activated to a significantly greater degree in the semantic (SR) experiment (Experiment B) than the syntactic (subcategorization) experiment (Experiment C) include the right-middle-temporal (bottom, maximum difference FPQ, $p<.001$), right-superior-temporal (middle, maximum difference FPQ, $p<.001$), and left insula (middle, maximum difference FPQ, $p<.0001$). *Experiment C>Experiment B.* Shows that there were no voxels activated to a significantly greater degree in the syntactic (subcategorization) experiment (Experiment C) than the semantic (SR) experiment (Experiment B).

**Table 7.**

| Region | BA | x | y | z | No. | Prob(max. diff. FPQ) |
|---|---|---|---|---|---|---|
| (A) Brain regions showing a significantly greater power of response in Experiment A (normal vs. pragmatically anomalous sentences) than Experiments B and C (normal vs. semantically and subcategorically violated sentences, respectively) | | | | | | |
| L sup. temp. g. | 22 | −43 | −31 | 9 | 7 | .0002 |
| L retrosplen. cortex | 29 | −12 | −39 | 9 | 8 | .00001 |
| Cuneus | 31 | 3 | −72 | 9 | 6 | .0005 |
| Cuneus | 18 | 9 | −81 | 15 | 3 | .0001 |
| (B) Brain regions showing a significantly greater power of response in Experiment B (normal vs. semantically violated sentences) than in Experiment C (normal vs. subcategorically violated sentences) | | | | | | |
| R sup. temp. g. | 22 | 43 | −19 | 4 | 5 | .001 |
| R mid. temp. g. | 21 | 49 | −8 | −7 | 4 | .001 |
| L insula (mid.)[a] | 22 | −43 | −8 | 4 | 12 | .0001 |

$x$, $y$, and $z$ show the coordinates of the voxel within each cluster showing the largest difference in FPQ (which reflects the significance of periodic change), and Prob(max. diff. FPQ) indicates the probability of its false activation. For simplification, activation foci of three or fewer voxels are not listed.

[a]In Experiment B, activation of this region was in phase with the normal sentences rather than the semantically anomalous sentences.

*Abbreviations*: sup. temp. g. = superior-temporal gyrus; retrosplen. cortex = retrosplenial cortex; mid. temp. g. = middle-temporal gyrus.

image made up from all three experiments. In the overall median image, the two most robust areas of response were the left-basal-temporal cortex/fusiform gyrus and the lingual gyrus. As both these areas were modulated in contrasting normal sentences with pragmatically, semantically, and subcategorically violated sentences in the three separate experiments, we deduced that they were common to all three experiments, and were involved in processing all three types of linguistic information.

*The Left-Inferior-Temporal/Fusiform Cortex: The Integration of Different Forms of Linguistic Information?*

A general role for the left-inferior-temporal cortex/fusiform gyrus in lexico-semantic processing is supported by evidence from neuropsychological deficits shown by patients with dementia (Hodges et al., 1992; Graff-Radford et al., 1990; Kempler et al., 1990; Poeck & Luzzatti, 1988), herpes simplex encephalitis (Pietrini et al., 1988; Sartori & Job, 1988; Warrington & Shallice, 1984), and posterior cerebral artery infarcts (Rapcsak & Rubens, 1994; Alexander et al., 1989; de Renzi et al., 1987). Lesions of the left-inferior-temporal/fusiform cortex can give rise to a transcortical sensory aphasia (Rapcsak & Rubens, 1994; Alexander et al., 1989; Kertesz, Shappard, & MacKenzie, 1982), characterized by semantically incoherent fluent speech and poor comprehension, and recent neuroimaging work in schizophrenia suggests that this region may play a role in the pathophysiology of ''formal thought-disorder,'' which is also characterized by fluent, incoherent speech (McGuire et al., 1998). The role of the inferior-tempor-

al/fusiform gyrus in lexico-semantic processing is also supported by intracranial ERP recordings (Nobre & McCarthy, 1995) and a number of functional imaging studies (Damasio et al., 1996; Martin et al., 1996; Vandenberghe et al., 1996; Demonet et al., 1992b; Goldenberg et al., 1987). A region with similar Talairach coordinates to the peak activation focus in our overall median image has been implicated in the semantic processing of both auditorily (Demonet et al., 1992b) and visually (Sakurai et al., 1993) presented verbal stimuli, as well as in the generation of single words (Warburton et al., 1996) and whole sentences (Muller et al., 1997).

However, the engagement of the left-inferior-temporal/fusiform gyrus in all three experiments suggests that it participates in processing not only in semantic processing of individual words, but also in processing pragmatic, semantic (SR), and subcategorization information within whole sentences. One possibility is that it acts as a site of integration of the three different forms of linguistic information. This would be consistent with its proximity to the site proposed as a generator of the N400 ERP to visually presented sententially incongruous words (McCarthy et al., 1995), which is also thought to index this integration process (Holcomb, 1993; Rugg, 1990).

Intriguingly, in the overall median analysis, some voxels within this cluster were activated in phase with the normal sentences, while others were activated in phase with the anomalous sentences (Figure 2B). There are several possible interpretations of this observation. First, an intrinsic problem in paradigms, such as this one, in which we are contrasting two ''active'' stimulus

conditions, is that the net power of response is relatively small. As the variance of the $\gamma$ parameter (used to define phase) is inversely proportional to the power of response, the heterogeneity of phase in this cluster may reflect error in estimation of $\gamma$. A second possibility is that this may reflect a "steal" phenomenon (resulting from local shunting of oxygenated blood towards active voxels and away from neighboring inactive voxels (see Binder et al., 1994). Third, the median image is derived from three experiments, and the phase of activation of this basal temporal region varied between experiments. Fourth, as discussed above, one cannot make precise interpretations of events at a neuronal or cognitive level from the phase of BOLD response. Despite these caveats, we should not exclude the possibility that immediately adjacent areas participate in the detection of anomalies in violated sentences and in the use of different types of linguistic information to process normal sentences.

### Inferior-Occipital and Left-Inferior-Temporal/Fusiform Cortex: Mental Imagery and Verbal Representations

A second major focus of activation observed in the overall median image was the lingual gyrus. Activation of "visual" regions in the absence of differential visual sensory input is not a new finding: It has previously been noted during the retrieval of verbal information (e.g., Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996), as well as during the perception of auditory stimuli such as music (Zatorre, Evans, & Meyer, 1994). Both inferior-occipital and temporal cortices constitute part of a hierarchically organized ventral visual stream (Ungerleider & Haxby, 1994) specialized for object recognition/categorization (Sergent, Ohta, & MacDonald, 1992a) and their coactivation during the presentation of auditory verbal stimuli—both single words (D'Esposito et al., 1997; Goldenberg et al., 1987) and whole sentences (Goldenberg et al., 1989)—has usually been interpreted as indexing a process of visual imagery.

Visual imagery is thought to play a key role in sentence comprehension (Eddy & Glass, 1981), and an interaction between coherence (normal vs. semantically violated) and imagery has previously been explored using functional imaging techniques by Demonet et al. (1992a). Although this latter SPECT study did not reveal significant differences in brain areas activated in contrasting coherent with incoherent and imageable with nonimageable sentences, the dataset did not include the inferior-occipital and temporal regions where we found differential responses to normal and anomalous sentences.

In the present study, there was generally more activation of the lingual gyrus when subjects listened to normal as opposed to anomalous sentences. This may reflect greater success in forming (as opposed to trying to form) visual images of normal than anomalous sentences, as indicated by the imagery ratings made by a separate group of normal volunteers (see Methods). The activation of the cuneus in phase with pragmatically violated sentences may reflect the fact that they were rated as more imageable than semantically and syntactically anomalous sentences (see Methods). Pragmatically anomalous sentences are anomalous only with respect to our real-world knowledge, and it is possible to both image and make sense of their content. Perhaps, like metaphorical sentences (Bottini et al., 1994), making sense of some of the pragmatically anomalous sentences necessitated some imagery.

The role of the inferior-temporal cortex in lexico-semantic processing (Damasio et al., 1996; Martin et al., 1996; Vandenberghe et al., 1996; Demonet et al., 1992b; Goldenberg et al., 1987) and visual imagery (Mellet, Tzourio, Denis, & Mazoyer, 1998; D'Esposito et al., 1997; Goldenberg et al., 1987) of individual words may well be functionally related. The left temporo-occipital junction has long been thought to play an important role in linking visual input with semantics: Lesions in this general area lead to a range of syndromes including associative agnosias (Feinberg, Rothi, & Heilman, 1986; McCarthy & Warrington, 1986; Ferro & Santos, 1984), anomias (de Renzi et al., 1987; Rapcsak, Gonzalez-Rothi, & Heilman, 1987; Poeck, 1984), alexia (Damasio & Damasio, 1983), and optic or tactile aphasias (Coslett & Saffran, 1989; Larrabee, Levin, Huff, Kay, & Guinto, 1985; Beauvois, Saillant, Meininger, & L'Hermitte, 1978; L'Hermitte & Beauvois, 1973). The precise function of temporo-occipital association areas as opposed to "earlier" visual areas in imagery is controversial (Roland & Gulyas, 1994). However, one interpretation of our data is that the posterior-inferior-temporal cortex integrates different forms of linguistic information into a higher-order representation of meaning, which is subserved by ventral occipital areas.

## Differences in Activation Between the Three Experiments

### Pragmatic vs. Semantic and Subcategorization Processing: The Role of the Right Hemisphere

Qualitative comparisons of the brain activation maps contrasting normal sentences with pragmatically anomalous sentences revealed left-superior-temporal activation in phase with the pragmatically anomalous sentences. Comparison between the pragmatic experiment and the two other semantic/syntactic experiments confirmed that this activation of the left-superior-temporal gyrus was unique to the pragmatic experiment, suggesting that this region plays a specific role in extralexical pragmatic processing within sentences. Although regions within the left-superior-temporal gyrus are associated with processing speech-specific

acoustic (Binder et al., 1994; Binder, Frost, Hammeke, Rao, & Cox, 1996; Fiez, Raichle, Balota, Tallal, & Petersen, 1996), phonological (Demonet et al., 1992b; Demonet, Celsis, Agniel, & Al, 1994; Sergent, Zuck, Levesque, & MacDonald, 1992b), and syntactic (Just et al., 1996; Mazoyer et al., 1993) information, all of which were matched between the two conditions, this region is also thought to play a role in the lexico-semantic processing of individual words (Howard et al., 1992; Price et al., 1992; Frith, Friston, Liddle, & Frackowiak, 1991; Wise et al., 1991; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Petersen, Fox, Posner, Mintun, & Raichle, 1989). Thus, one possibility is that its activation in this study reflects a greater demand for lexical analysis in interpreting pragmatically anomalous as opposed to normal sentences. Specifically, it may be that when subjects fail to make complete sense of a pragmatically anomalous sentence on first encounter, they engage a "second-pass" processing mechanism, reevaluating the meaning of particular words within it, leading to "reactivation" (Damasio, 1989) of perisylvian regions.

The fact that the left, rather than the right temporal cortex was activated in phase with the pragmatically anomalous sentences seems to go against the idea that the right hemisphere plays a specific role in processing pragmatic information (Joanette & Brownell, 1990). However, as stated in the Introduction, the deficits shown by right-brain-damaged patients tend to be in processing narrative and discourse-level material, such as nonliteral language, stories, jokes, and conversations, and the ability of such patients to process pragmatically violated sentences of the nature used in the current study has not been investigated. One possibility is that the right hemisphere is recruited in processing language that is more severely violated in meaning than the purely pragmatically violated sentences used in the current study. This would be consistent with our observation that the right-superior and middle-temporal gyri were engaged in contrasting the normal with the semantically (SR) anomalous sentences. The semantically (SR) anomalous sentences were rated as quantitatively more implausible (and, by definition, more pragmatically unlikely) than the purely pragmatically violated sentences.

The involvement of the right hemisphere processing the semantically (SR) anomalous sentences accords with several previous imaging studies that have reported reduced left/right asymmetry in contrasting semantically anomalous (as opposed to normal) sentences with a rest condition (Mazoyer et al., 1993; Demonet et al., 1992a). As stated above, one explanation is that the semantic (SR) violated sentences used in these studies and the current investigation demanded a second-pass pragmatic analysis mediated by right-temporal regions. An alternative explanation is that the right hemisphere is plays a specific role in processing lexico-semantic fea-

tures of verbs and object nouns, which, by definition, were violated in the semantic (selection-restriction) anomalous sentences. This explanation would be consistent with divided visual field studies that have demonstrated a reduced left hemisphere advantage in processing words that are primed by weakly related words (Chiarello, 1991) and semantically incongruent sentence stems (Faust et al., 1995), and with the idea that the right hemisphere plays a role in bringing together relatively "coarse" associations at a lexico-semantic level. Further work manipulating the plausibility of sentences independently of their semantic selection-restriction constraints is required to distinguish between these two explanations.

## Syntactic vs. Semantic Processing

Neither left- nor right-superior-temporal regions were engaged in comparing normal with subcategorically violated sentences, and statistical comparison of the subcategorization and the semantic experiments confirmed that right-superior-temporal activation was restricted to the semantic contrast. This was particularly surprising, as the subcategorization violations used in the present study (where the meaning of the intransitive verb was usually incompatible with the overall meaning of the sentence) would be expected to engage a semantic analysis. We suggest that when processing subcategorically violated sentences, subjects failed to engage the second-pass analysis (mediated by right- and left-superior-temporal regions as proposed above) to the same degree as when processing semantically violated sentences. In other words, when the listener fails to construct the appropriate syntactic object, the semantic or pragmatic implications of the verb-argument structure are not evaluated (see Tyler, 1992, p. 110). This is consistent with the findings of Hagoort et al. (1993) of a relative absence of scalp-recorded electrophysiological activity in response to subcategorical violations.

Another intriguing observation was the absence of regions activated in the syntactic as opposed to the semantic experiment. Specifically, Broca's area was not activated. This finding is inconsistent with studies of agrammatic aphasic patients (Frazier & Friederici, 1991; Caplan et al., 1985; Caramazza & Zurif, 1976) and functional imaging investigations (Caplan et al., 1998; Stromswold et al., 1996) that have implicated left-inferior-frontal regions in building up the syntactic structure of sentences. One explanation is that subcategorical information, which is lexically bound, is processed differently from other types of syntactic information. Indeed, Tyler et al. (1992) and Tyler et al. (Tyler, Ostrim, Cooke, & Moss, 1995) has showed that, in processing speech online, agrammatic aphasics are generally able to access subcategorization information. Moreover, electrophysiological studies suggest that the processing of

lexically bound syntactic information can be dissociated from processes of structural analysis and reanalysis (reviewed by Friederici, 1995). Thus, it may be that that the processing of subcategorical information is not subserved by the same regions as those supporting more complex syntactic analyses.

## Conclusions and Future Directions

In summary, we have shown similarities and differences in the neuroanatomical correlates of using pragmatic, semantic selection restriction, and subcategorization information to process simple sentences. As hypothesized, contrasting normal sentences with all three types of violated sentences engaged the left-inferior-temporal/fusiform gyrus, suggesting that these three levels of processing share a common neural substrate. We propose that the inferior-temporal/fusiform cortex mediates the integration of different forms of linguistic information. This extends the idea that basal temporal regions interface between semantic processing of verbal material and a general amodal semantic system at the level of single words (Damasio et al., 1996), and proposes that it also bridges online linguistic analysis and an emerging higher-order possibly visual representation of spoken highly imageable sentences.

We also showed that left- and right-superior-temporal regions were activated in association with pragmatically and semantically (SR) violated sentences, respectively, but that there were no brain regions uniquely associated with processing subcategorically violated sentences.

In this study, because we were not measuring brain activity time-locked to each linguistic anomaly, we cannot make precise inferences about the temporal sequence of cortical activity engaged in putatively intermediary processing stages and later stages in accessing a ''final representation'' of each sentences' meaning. This distinction between process (or function) and representation (end-product or structure) has been repeatedly highlighted within general models of cognition (Paivio, 1986), and has been discussed explicitly within normal models of speech processing (Tyler, 1992, p. 110). We hope to address some of these issues in future studies examining activation time-locked to single trials (Rosen, Buckner, & Dale, 1998; Buckner et al., 1996).

## METHODS

### Subjects

Nine male, right-handed (Annett, 1970) volunteers were recruited. Informed written consent for participation in the study was obtained in accordance with the Declaration of Helsinki. Ethical permission for the study was obtained from the local research Ethical Committee. All participants were native speakers of English. All were healthy, on no medication, and had no history of neurological or psychiatric illness.

Subjects took part in three separate experiments, in which normal sentences were contrasted with (A) pragmatically, (B) semantically, and (C) syntactically (subcategorically) violated sentences. The order of the experiments was counterbalanced. Four of the subjects also completed an additional experiment in which normal sentences were contrasted with random strings of words. Two subjects performed this experiment first, and two subjects performed it last.

### Construction of Stimulus Materials

For all experiments, normal and anomalous sentences were constructed from familiar (high frequency) nouns, verbs, and function words. Some sentences were adapted from Tyler (1992). All sentences took the same form: a subject noun followed by a verb, followed by an object noun. The sentences varied in content so that subjects did not encounter the same words four times during the scanning session (which might have led to repetition priming effects). Because judgements of whether or not a sentence is anomalous can be subjective, we asked 20 normal volunteers who did not undergo scanning to judge whether or not a battery of sentences made sense. Only those sentences for which there was a one hundred-percent consensus were selected. The random word strings used in the last experiment were constructed by randomly mixing words of 60 normal sentences, and, then, grouping sequentially these scrambled words into strings of fives and sixes. The resulting word-strings had neither semantic nor syntactic structure.

Median values of the frequency, imageability, and concreteness of nouns, verbs, and function words in each experiment are shown in the Appendix. In each of the four experiments, we used Mann–Whitney $U$-tests to test for significant differences in each of these parameters between words comprising normal and anomalous sentences/word-strings. We used Kruskall–Wallis ANOVAs to test for significant differences (at $p < .05$) in these parameters between the words comprising experiments A through D.

There were no significant differences in the frequency of words constituting normal and anomalous sentences/word-strings in any four experiments, and there were no significant differences between the four experiments in the frequency of words comprising the sentences (normal and anomalous, taken together). There were also no significant differences between normal and anomalous sentences/word-strings in the imageability and concreteness of their component nouns and verbs (taken together), in any of the four experiments. Finally, there were no significant differences between the four experiments in the imageabil-

ity of nouns and verbs (taken together). However, because the imageability of a sentence may not correspond to that of its component words, we asked a separate group of 18 healthy volunteers to rate all sentences (presented auditorily and in random order) on a seven-point analogue scale, according to how easily and vividly each sentence evoked a visual image. The imagery scores of each volunteer were collapsed across sentences to give average scores for each condition (normal vs. anomalous) in each of the three experiments. These average scores were entered into a repeated-measures ANOVA, which showed a significant main effect of condition ($F(1, 17)=74.0$, $p<.0001$), reflecting higher imageability ratings given to normal than anomalous sentences. There was also a highly significant experiment by condition interaction ($F(2, 34)=76.0$, $p<.0001$), arising because volunteers gave higher imageability ratings to pragmatically anomalous sentences than semantically ($t(17)=8.7$, $p<.0001$) and syntactically anomalous sentences ($t(17)=8.2$, $p<.0001$).

For each functional imaging experiment, the normal and anomalous sentences (or word-strings) were grouped in sixes and tape-recorded with a naive male reader at a rate such that each sentence lasted 3 sec, with 2-sec silence before the next sentence.

## Experimental Task and Procedure

Prior to scanning, subjects were told that they would hear a series of sentences, and that, after each sentence, they should decide whether or not it "made sense." The four subjects who performed the normal vs. word-strings experiment were warned that during one of the experiments, they would hear random strings of words. After being given a few examples of normal sentences and each type of anomalous sentence/random word-string, subjects were then asked if they understood the criteria for acceptability, and additional examples were provided as required. Sentences were presented in 10 alternating (normal vs. anomalous) blocks of six (30 sec per block) through headphones designed to reduce scanner noise. After hearing each sentence, subjects pressed one of two buttons with the index finger of their right hand, depending on whether or not it made sense. Their response temporarily (for .5 sec) terminated a display of the words "sense" and "nonsense" on the left and right sides of a computer screen, which was viewed throughout the scanning period to remind subjects which button to press, and to provide a uniform visual input. The sides of the screen on which these words were displayed and, hence, the buttons used to indicate "sense" or "nonsense," were counterbalanced across subjects. Subjects had approximately 2 sec to respond to each sentence and their accuracy was recorded.

## Image Acquisition

Gradient–echo echoplanar MR images were acquired on a 1.5T GE system (General Electric, Milwaukee WI, USA) retrofitted with Advanced NMR hardware (ANMR, Woburn MA, USA) at the Maudsley Hospital, London. A quadrature birdcage headcoil was used for radiofrequency (RF) transmission and reception. Head movement was limited by foam padding within the head coil and a restraining band across the forehead. For each 5-min experiment, $100 T_2$*-weighted images depicting BOLD contrast (Ogawa, Lee, Kay, & Tank, 1990) were acquired at each of the 10 noncontiguous planes parallel to the intercommissural (AC–PC) plane: TE=40 msec, TR=3000 msec, in-plane resolution=3.1 mm, slice thickness=5.5 mm, interslice gap=.5 mm. The dataset covered the inferior and middle parts of the brain, but did not include the superior parts of the frontal and parietal cortex. Data were thus acquired from the entire temporal and occipital cortex and the inferior portions of the frontal and parietal cortex. In the same scanning session, a 43-slice, higher-resolution inversion recovery echoplanar image of the whole brain was acquired in the AC–PC line: TE=73 msec, TI=180 msec, TR=16,000 msec, in-plane resolution=1.5 mm, slice thickness=3mm.

## Image Analysis

### Sinusoidal Regression Modeling and Construction of Group Median Images

Movement of the head during image acquisition was estimated individually for each fMRI dataset, and the effects of motion were corrected by realignment and regression (Brammer et al., 1997). The power of periodic signal change at the (fundamental) frequency of alternation between the two stimulus conditions ($\omega=1/60$ Hz in all four experiments) was estimated by fitting a sinusoidal regression model to the motion-corrected time series at each voxel. The model included a pair of sine and cosine waves at fundamental frequency, parameterized by coefficients $\gamma$ and $\delta$, respectively. The power of periodic response to the input function was estimated by ($\gamma^2+\delta^2$); and this fundamental power divided by its standard error yielded a standardized test statistic, the FPQ, at each voxel (Bullmore et al., 1996a). The timing of signal maximum at fundamental frequency with respect to the periodic input function was defined by the sign of $\gamma$. If $\gamma>0$, signal maximum occurred during the first (normal sentences) condition; if $\gamma<0$, signal maximum occurred during the second (anomalous sentences/word-strings) condition (Bullmore et al., 1996b). Each observed fMRI time series was randomly permuted 10 times and FPQ estimated after each permutation. This resulted in 10 parametric maps (for each subject at each plane) of FPQ estimated under the null hypothesis that FPQ is not determined by periodic experimental design (Bullmore et al., 1996a).

All parametric maps of FPQ were then registered in standard stereotactic space (Talairach & Tournoux, 1988) and smoothed by a 2-D Gaussian filter with full width at half maximum, FWHM=10.8 mm (Brammer et al., 1997). Voxels demonstrating a significant power of response over all subjects under each experimental condition were identified by computing the median value of FPQ at each voxel of the observed FPQ maps and comparing it to a null distribution of median FPQ ascertained from the permuted FPQ maps. For a one-tailed test of size $\alpha=.005$, the critical value was the $100(1-\alpha)$th percentile value of the randomization distribution. Generically, activated voxels were color coded according to the median value of $\gamma$ at each voxel, to identify the timing of generic activation with respect to the input function, and superimposed on a gray-scale template to form a generic brain activation map or GBAM (Brammer et al., 1997).

### Planned Comparisons Between the Three Experiments

Differences between the three experiments were tested using two planned comparisons (or contrasts), which each required construction of two FPQ maps per subject in standard space. Because within the individual experiments we interpret all regions that were modulated by the experimental contrast, irrespective of phase (the sign of $\gamma$), as indexing a specific level of linguistic processing (see first paragraph of the Discussion), we included both phases of response within individual experiments (i.e., both signs of $\gamma$) in these statistical comparisons between experiments. For the first contrast, the comparison was between experiment A and the average of experiments B and C; the required maps were the observed map for experiment A and the mean map of experiments B and C. This contrast aimed to identify voxels activated in the pragmatic experiment to a significantly greater degree than the other two experiments. For the second

contrast, the comparison between experiments B and C, the observed maps for conditions B and C were used. Here, we aimed to identify voxels activated to a greater degree in the semantic experiment than the syntactic experiment and voxels activated to a greater degree in the syntactic experiment than the semantic experiment.

To estimate the differences between experiments in mean FPQ, we fitted the following repeated-measures ANOVA model at each voxel of the observed FPQ maps in standard space: $FPQ_{i,j}=\beta_0+\beta_1 E_{i,j}+e_{i,j}$. Here, $FPQ_{i,j}$ denotes standardized power in the $i$th individual under the $j$th experimental design, $\beta_0$ is the overall mean FPQ, $\beta_0+\beta_1$ is the mean FPQ under one of the contrasted pair of experimental designs, and $\beta_0-\beta_1$ is the mean FPQ under the other experimental design, $E$ is a dummy variable coding experimental design, and $e_{i,j}$ is a residual quantity unique to the $i$th individual. The null hypothesis of zero difference in mean FPQ between experiments was tested by comparing the coefficient $\beta_1$ to the critical values of its nonparametrically ascertained null distribution (Bullmore et al., 1999a, Bullmore et al., 1999b). To do this, the elements of $E$ were randomly permuted 10 times at each voxel, $\beta_1$ was estimated at each voxel after each permutation, and these estimates were pooled over all intracerebral voxels to sample the permutation distribution of $\beta_1$. Because of the repeated-measures nature of the data, the permutation procedure was constrained so that if FPQ observed in the $i$th individual in one experiment was randomly assigned a code of one in the permuted variable $E$, then FPQ observed in the same individual under the other experimental condition was automatically assigned a code of $-1$ (Edgington, 1980). Differences in mean FPQ between experiments were tested for significance only at those voxels which were generically activated by one or both of the experiments considered independently, thereby, substantially reducing the search volume or number of tests conducted.

## APPENDIX

Median frequency, concreteness, and imageability ratings of component words of normal sentences and anomalous sentences/word-strings in experiments A through D.

| | | Experiment A | | Experiment B | | Experiment C | | Experiment D | |
|---|---|---|---|---|---|---|---|---|---|
| | | Normal | Anomalous | Normal | Anomalous | Normal | Anomalous | Normal | Anomalous |
| All words | frequency | 274 | 224 | 206 | 220 | 242 | 188 | 228 | 186 |
| | concreteness | 381 | 398 | 399 | 436 | 387 | 388 | 420 | 392 |
| | imageability | 398 | 469 | 443 | 478 | 389 | 453 | 507 | 465 |
| Verbs and nouns | frequency | 70 | 38 | 57 | 54 | 54 | 28 | 53 | 52 |
| | concreteness | 552 | 580 | 564 | 580 | 547 | 569 | 579 | 550 |
| | imageability | 567 | 570 | 567 | 567 | 560 | 575 | 592 | 562 |

Values of the frequency, imageability, and concreteness of nouns, verbs, and function words in each experiment were derived from the Oxford Psycholinguistic Database (Quinlan, 1992) and other sources (Gilhooly & Logie, 1980; Kucera & Francis, 1967).

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## Notes

1. We follow Tyler (1992) and Marslen-Wilson et al. (Marslen-Wilson, Brown, & Tyler, 1988) in making the distinction between pragmatic violations, which can only be inferred with respect to our real-world knowledge, on the one hand, and selection-restrictions and subcategorization violations, which are considered to be lexically encoded (Jackendoff, 1978; Chomsky, 1965), on the other hand. However, we do not imply that real-world knowledge is not used in processing the other types of anomalous sentences: the semantic selection-restriction anomaly is also, by definition, a pragmatic anomaly. The key difference between the selection-restrictions violations and the pragmatic violations is that featural semantic relations between verb and object noun are not violated in the latter. Similarly, the subcategorisation anomaly could also be considered semantically/pragmatically anomalous, although this is more controversial.

2. Throughout the text, we have used the term "modulate" to refer to brain activity irrespective of its directionality in relation to stimulus input. As explained in the first paragraph of the Discussion, this is because we consider both phases of response (i.e., regions activated in phase with normal sentences, as well as regions activated in phase with anomalous sentences/word-strings) as indexing a particular level of linguistic processing.

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