

Form and Content: Dissociating Syntax and Semantics in Sentence Comprehension

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Summary

The distinction between syntax (sentence form) and semantics (sentence meaning) is fundamental to our thinking about language. Whether and where this distinction is represented at the neural level is still a matter of considerable debate. In the present fMRI study, we examined the neural correlates of syntactic and semantic functions using an innovative activation paradigm specifically designed to unequivocally disentangle syntactic from lexicosemantic aspects of sentence processing. Our findings strongly indicate that a part of Broca's area (BA 44, pars opercularis) is critically implicated in processing syntactic information, whereas the lower portion of the left inferior frontal gyrus (BA 47, pars orbitalis) is selectively involved in processing the semantic aspects of a sentence.

Introduction

Grammar is perhaps the most distinctive feature of human languages; typically, we convey meaning in sentences, where comprehension requires understanding not only individual words but also the syntactic frame in which the words are embedded. Neuropsychological (Zurif et al., 1990; Goodglass, 1993) and event related potential (ERP) studies (Neville et al., 1992; Münte et al., 1993; Rösler et al., 1993) measuring brain activity associated with language processing have long suggested that syntax and semantics may be subserved by distinct cortical areas, but unequivocal evidence of such a dissociation has thus far been elusive. Functional neuroimaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) in particular, offer the spatial resolution needed to make finer inferences about brain-behavior relations. Yet, most functional neuroimaging studies of language published in the last decade have focused on single word processing and have thus been unable to address the neural substrate of syntactic functions, which involve the computation of the grammatical rules encoding relations among words.

Relatively few PET and fMRI studies have investigated language at the sentence level (Mazoyer et al., 1993; Bottini et al., 1994; Just et al., 1996; Stomswold et al., 1996; Bavelier et al., 1997; Müller et al., 1997), and even fewer neuroimaging studies (Just et al., 1996; Stomswold et al., 1996; Caplan et al., 1998) have utilized designs that examined the processing of syntactic information (i.e., sentence form) independently from the

processing of lexicosemantic information (i.e., sentence meaning). These studies have typically varied the syntactic complexity of the stimuli across experimental conditions. For instance, using PET, Stomswold et al. (1996) and Caplan et al. (1998) reported selective activation of the left pars opercularis when subjects made plausibility judgments about complex center-embedded (e.g., "the juice that the child spilled stained the rug") compared to less complex right-branching (e.g., "the child spilled the juice that stained the rug") relative clauses. This type of experimental design, however, does not allow one to unequivocally attribute to this brain region a selective role in syntactic processing, as it is possible that this same area would also become increasingly active in a task where difficulty level (as indexed by significantly longer response times) is varied along a different linguistic aspect. Indeed, while the left inferior frontal gyrus (IFG) is known to play a crucial role in speech production, a number of investigations have reported significant activation in Broca's area using a variety of language tasks involving semantic and phonological processing, word reading, and word generation (Hinke et al., 1993; Rueckert et al., 1994; Bookheimer et al., 1995; Buckner and Tulving, 1995; Zatorre et al., 1996; Rumsey et al., 1997; Fiez and Petersen, 1998). Furthermore, using fMRI and a similar paradigm, Just et al. (1996) found larger volumes of activation in both Broca's and Wernicke's areas as a function of syntactic complexity (i.e., processing complex object relative clauses versus simpler subject relative clauses versus even simpler active conjoint clauses), thus challenging the notion of a unique grammar module located in Broca's area.

In light of the limited, and somewhat conflicting, data on the neural basis of syntactic processing available to date, we conducted an fMRI study to further investigate the neural substrate of sentence comprehension using a task where the syntactic complexity of the stimuli did *not* vary across experimental conditions. Rather, an innovative selective attention paradigm was used where, unbeknownst to the subjects, we manipulated the type of linguistic information (semantic versus syntactic) the subjects had to rely on to decide whether or not the meaning of two sentences differed. The activation paradigm involved two experimental conditions—presented in a blocked design and interleaved with rest periods—where the subjects listened to pairs of sentences. In the "semantic" condition, each pair of sentences was identical in all respects except for one word that was replaced with either a synonym or a different word. In the "syntactic" condition, the sentences in each pair were either cast in a different form (i.e., in the active versus the passive voice) or used a different word order (i.e., preposed versus postposed prepositional phrases). Importantly, the number of sentences in the active and passive forms, as well as the number of preposed and postposed prepositional phrases, was the same in the two conditions.

As can be seen from the examples listed in Table 1, in the semantic condition the judgment ultimately rested on the comparison between single word meanings, the

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Table 1. Examples of Stimuli Used in the Syntactic and Semantic Conditions

Syntactic Condition	Semantic Condition	
"The policeman arrested the thief" "The thief was arrested by the policeman"	"The lawyer questioned the witness" "The attorney questioned the witness"	same
"The teacher was outsmarted by the student" "The teacher outsmarted the student"	"The man was attacked by the doberman" "The man was attacked by the pitbull"	different
"The pool is behind the gate" "Behind the gate is the pool"	"The car is in the garage" "The auto is in the garage"	same
"West of the bridge is the airport" "The bridge is west of the airport"	"East of the city is the lake" "East of the city is the river"	different

syntactic structure of the sentences within each pair being the same. In contrast, in the syntactic condition, computing and comparing the syntactic structure of the sentences within each pair was essential to determine whether or not their meaning differed, the individual word meanings used in each pair of sentences being identical. As processing language at the higher level of structure—sentences and discourse—is mandatory when one attends to linguistic stimuli, we expected the subjects to process the sentences in all conditions at both the syntactic and semantic levels; however, we also expected the data to reflect that the relative weight each type of processing had in performing the judgment task varied orthogonally between the two conditions. Subjects were not informed about the nature of the experimental manipulation. They were instructed to listen to each pair of sentences and decide whether the two sentences had the same literal meaning. The subjects were debriefed at the end of the scan and did not report noticing any difference between the two experimental blocks.

Results

Behavioral measures were collected outside the scanner environment in a separate testing session, performed at least 6 months after the imaging session. To rule out any effect of previous exposure to the experimental stimuli, behavioral data were also collected on a second group of eight normal volunteers that were exposed to the stimuli only once. No reliable differences were found between experimental conditions on either reaction times or accuracy level (Table 2).

The imaging results from the grouped data showed significant foci of activation for both activation condition

versus rest comparisons in regions typically associated with language processing (Figure 1). Specifically, activation was detected in the IFG (Brodmann's areas 44, 45, and 47), superior and middle temporal gyri (BA 42, 22, and 21), as well as in the supramarginal and angular gyri (BA 40 and 39), with the left hemisphere showing overall greater activation in terms of magnitude and spatial extent. The results of these initial comparisons suggested that within the IFG, BA 45 was activated in both conditions, whereas BA 44 was most strongly activated in the syntactic condition, and BA 47 (bilaterally) was selectively activated in the semantic condition. Furthermore, while activation of canonical language areas in the temporo-parietal cortex was observed in both conditions versus rest, the extent of these activations was greater in the syntactic condition, with portions of BA 22, 38, 39, and 40 found active only in this condition.

To further assess the extent to which the observed pattern of activation was modulated by the specific linguistic aspect maximally taxed in a given condition, we also performed direct statistical comparisons between the two experimental conditions. These analyses identified two condition-specific areas of activation, both located in the left IFG, though in spatially segregated regions (see Figure 2). Specifically, for the syntactic versus semantic comparison, the cluster of cortical activity was centered in the lower section of the pars opercularis (BA 44), whereas for the semantic versus syntactic comparison, the activation was more inferior, with center of maxima found in the pars orbitalis (BA 47).

The location (in Talaraich's coordinates) and peak height of all clusters of activation exceeding a corrected significance level of $p < .05$ (for both magnitude and spatial extent) for each statistical comparison are shown in Table 3.

Table 2. Behavioral Performance

	Mean Response Time (SD)		Mean Accuracy (SD)	
	Group A	Group B	Group A	Group B
Syntactic Condition	5.09 (.32)	5.18 (.28)	98.4 (4.4)	96.8 (5.8)
Semantic Condition	5.06 (.28)	5.13 (.24)	95.8 (6.5)	97.9 (5.8)

Group A refers to the subjects who participated in the fMRI experiment. Behavioral data were collected following the imaging session. Group B refers to the subjects for whom only behavioral data were collected. Mean accuracy is expressed as the percentage of correct responses.

Discussion

The present findings indicate that, within the extensive neural network underlying sentence comprehension, distinct cortical regions can be identified that underlie two fundamental aspects of language processing—namely, syntax and semantics. While canonical language areas in both frontal and temporo-parietal cortices were activated during sentence processing, activity within this functionally distributed system was modulated by the particular linguistic function maximally engaged in a given condition. Using an activation paradigm

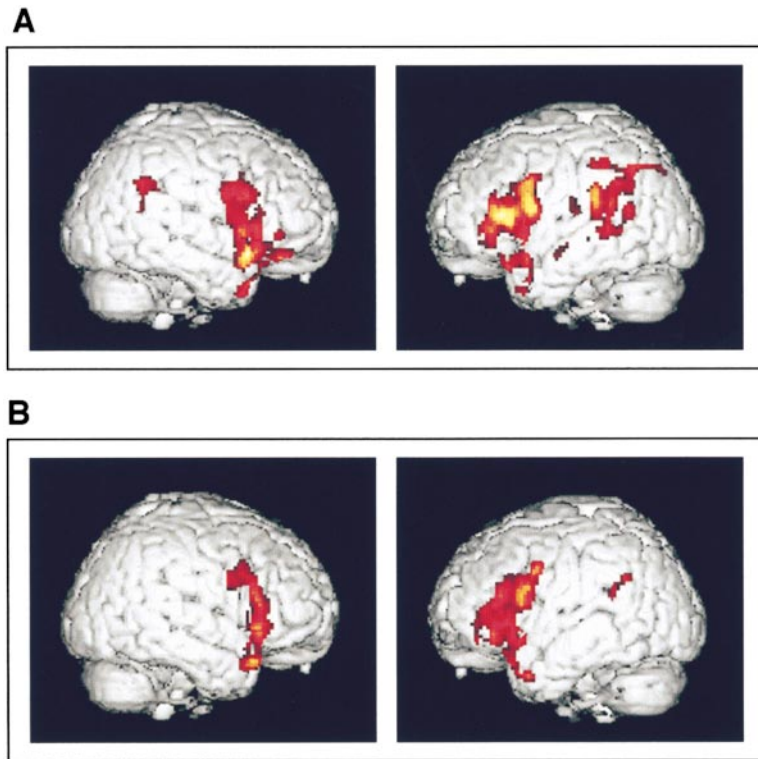


Figure 1. Brain Activity Observed during a Sentence Judgement Task Posing Differential Demands on Syntactic and Semantic Processing

Statistical parametric maps of the t statistics (transformed to the unit normal distribution) for the syntactic condition versus rest (A) and semantic condition versus rest (B) comparisons rendered onto a standard brain, thresholded at $Z = 3.72$, $p = 0.0001$ (uncorrected), with a spatial extent threshold set at $p < .05$ (corrected).

specifically designed to implicitly and selectively engage syntactic aspects of sentence processing in one condition and lexicosemantic processing in the other, we show that a part of Broca's area, centered in the pars opercularis (BA 44), is particularly involved in computing the syntactic structure of sentences, whereas the lower portion of the left IFG (BA 47) is selectively implicated in processing the lexicosemantic information. This double dissociation observed in the left inferior frontal gyrus for syntactic and semantic processing represents unequivocal evidence that these linguistic functions are indeed subserved by distinct cortical areas.

From a methodological perspective, it is important to note that reliable differences were detected between conditions, despite constant task demands (as indexed by identical performance in the two conditions in two groups of subjects) and virtually identical stimuli used in the two activation conditions. The present findings then indicate that an activation paradigm where the subjects' attention is implicitly directed toward different aspects of the same linguistic stimuli across experimental conditions represents a viable tool to study the neural basis of different linguistic functions. This approach offers a considerable advantage over other experimental designs in that it provides a means to unambiguously attribute differences in the pattern of cortical activity observed between activation conditions to the targeted linguistic component, unconfounded by differences in levels of task difficulty or in the nature of the stimuli used across conditions.

Thus, our results showing selective activation of the pars opercularis in the condition requiring deeper level of syntactic analysis provide strong evidence for the notion that this region is intimately involved in the processing of syntactic information. While no reliably

greater activity was observed in posterior temporal and parietal regions for the syntactic versus semantic condition, a qualitative analysis of the pattern of cortical activity observed for each condition compared to rest suggests that the syntactic condition was associated with an overall larger volume of activation (as indexed by the number of clusters of significant activation, as well as the number of voxels within these clusters), despite identical difficulty level across conditions. These findings are then in agreement with a previous report by Just et al. (1996) indicating that the amount of neural activity observed during language processing varies as a function of the computational demands imposed by a cognitive task, even when the qualitative differences in the type of computations required do not involve quantitative differences in processing time.

The present research findings are also relevant to the role of the IFG in the processing of semantic information. Consistent with a large number of neuroimaging studies linking activity in the inferior prefrontal cortex to semantic processing (Demb et al., 1995; Shaywitz et al., 1995; Martin et al., 1996; Binder et al., 1997), we found extensive prefrontal activation in both activation conditions, which ultimately required subjects to make semantic judgments about the meaning of pairs of sentences, as well as selective activation of the more inferior portion of the IFG (i.e., BA 47) in the activation condition requiring a higher degree of semantic processing. While others have supported the notion of semantic processing in the more anterior portions of the IFG (Fiez, 1997), Thompson-Schill et al. (1997) have recently challenged the role of the left inferior prefrontal cortex in the retrieval of semantic information, arguing instead that the prefrontal activity observed in many neuroimaging studies may in fact be attributed to the "selection" demands

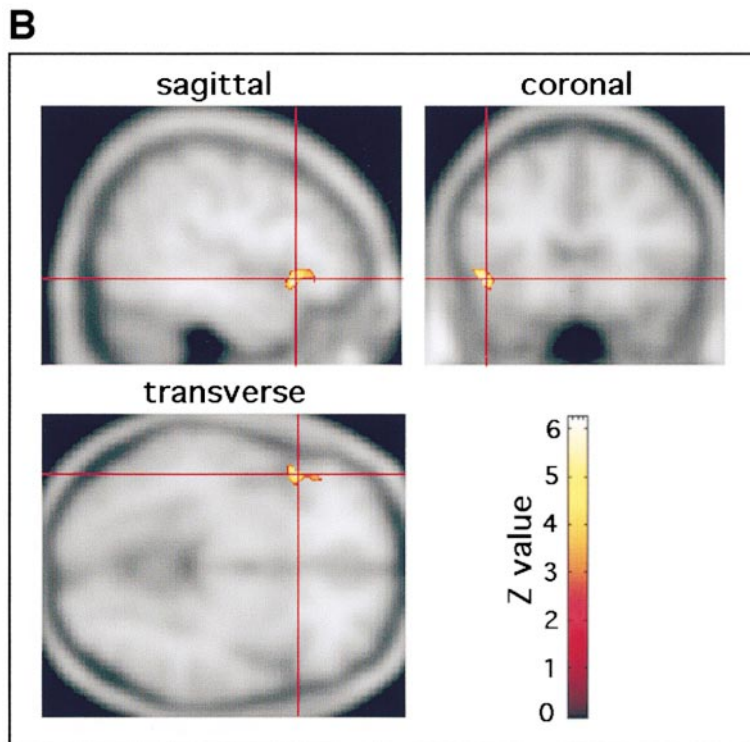
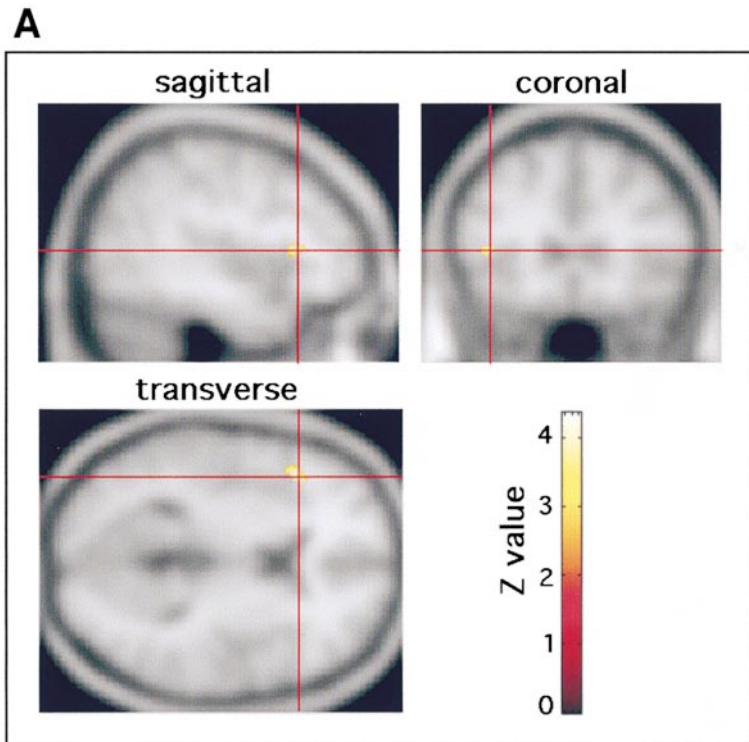


Figure 2. Selective Activation Associated with Syntactic and Semantic Processing during Sentence Comprehension

Areas of selective activation for the syntactic versus semantic (A) and semantic versus syntactic (B) conditions overlaid onto a standard brain, thresholded at $Z = 3.72$, $p = 0.0001$ (uncorrected), with a spatial extent threshold set at $p < .05$ (corrected).

(i.e., the selection of information among competing alternatives from semantic memory) present in the activation tasks used in these investigations, rather than to semantic processing per se. Though it is not clear how our task should be rated in terms of selection demands, it should be noted that activity in BA 47, within the IFG, was also found in Müller et al.'s (1997) study during passive listening to sentences, that is, in a condition

likely to involve semantic processing in its most naturalistic context. Together with Müller et al.'s findings, our data then provide converging evidence linking the more inferior section of the IFG to lexical semantic aspects of sentence processing.

Finally, our findings also confirm the involvement of prefrontal regions during a receptive language task, further suggesting that Broca's area plays a significant role

Table 3. Foci of Activation

Comparison			Syntactic Condition versus Rest				Semantic Condition versus Rest			
Region (Brodmann Area)			x	y	z	Z	x	y	z	Z
Inferior frontal gyrus	(BA 44)	L	-52	10	28	7.06				
	(BA 45)	L	-40	30	14	6.89	-56	22	2	7.20
	(BA 45)	R					54	24	18	6.20
	(BA 47)	L					-46	30	-6	7.14
	(BA 47)	R					50	24	-6	6.45
Middle temporal gyrus	(BA 21)	L					-42	-18	-12	5.42
Superior temporal gyrus	(BA 22)	L	-58	-58	14	6.43	-52	-44	22	5.09
Transverse temporal gyrus	(BA 41)	L	-60	-36	16	5.59	-36	-28	8	4.89
Temporal pole	(BA 38)	L	-48	20	-16	7.31				
	(BA 38)	R	56	10	-10	6.20				
Supramarginal gyrus	(BA 40)	L	-42	-56	38	5.03	-54	-54	32	4.57
Inferior parietal lobe	(BA 40)	R	40	-50	42	4.15				

Comparison			Syntactic versus Semantic Condition				Semantic versus Syntactic Condition			
Region (Brodmann Area)			x	y	z	Z	x	y	z	Z
Inferior frontal gyrus	(BA 44)	L	-44	22	10	4.44				
	(BA 47)	L					-48	20	-4	4.15

L and R refer to the left and right cerebral hemispheres, respectively, while x, y, and z reflect positions in Talairach coordinate space corresponding to the left-right, anterior-posterior, and superior-inferior dimensions, respectively. Z refers to the highest Z score within a region.

in language processing in the absence of any overt, or covert, language production. However, in light of a recent PET study reporting only modest involvement of inferior frontal regions during passive listening to sentences (Müller et al., 1997), one must entertain the hypothesis that the considerable greater extent of cortical activation in prefrontal regions observed in the present study, as well as in several other investigations (Mazoyer et al., 1993; Bottini et al., 1994; Stomswold et al., 1996) may at least in part be attributed to the particular task demands used in all of these studies (e.g., making plausibility judgment, or semantic decisions about sentence meanings). Nevertheless, our results present a challenge to traditional notions of Broca's area as a single linguistic processing unit with primarily expressive functions. Two aspects of receptive language, semantic and syntactic analysis of sentence meaning, appear to have distinct neural substrates within the IFG. This conforms to the general principle of functional segregation in the human cerebral cortex, according to which local ensembles of strongly interconnected cells share input and/or output properties that differ from the input and/or output properties of other ensembles. These functionally segregated local collectives are then functionally integrated through recursive and parallel processing (Edelman, 1993; Iacoboni et al., 1998). The breadth of deficits observed in patients with Broca's aphasia—including phonological awareness, articulation, naming, syntactic comprehension, strategic semantic priming, and word generation (Luria, 1966; Caramazza and Berndt, 1978; Blumstein et al., 1982; Ojemann, 1992; Hagoort, 1993)—are best explained by damage to distinct functional brain regions with specific linguistic processing affinities, rather than to a single undifferentiated linguistic module.

Experimental Procedures

Eight subjects (four males, four females, mean age 25.4 years; range 20–36 years) participated in the imaging part of this study (group A). Additional behavioral data on the same activation paradigm used

in the fMRI study were collected in a separate group of eight subjects (four males, four females, mean age 24.2 years; range 20–35 years) (group B). All subjects were right-handed monolingual native speakers of English. None of them had a history of neurologic or psychiatric conditions.

Functional MR Images were collected on a GE 3 Tesla scanner equipped with echo-planar imaging (EPI) from Advanced NMR. For each subject, a conventional sagittal scout scan was first obtained from which the functional images were prescribed. Using an EPI gradient echo sequence (TR = 2500 ms; TE = 45 ms; matrix size 64 × 64; FOV = 20 cm), 84 functional images were collected for each subject over 16 or 17 axial slices (4 mm thick/1 mm gap). According to the atlas of Talairach and Tournoux (1988), the most inferior and superior slices approximately corresponded to z = -30/-25 and z = +45/+50, respectively. A set of coplanar high-resolution EPI structural images (TR = 4000 ms; TE = 65 ms; matrix size 128 × 128; FOV = 20 cm) were also collected at the same time to later allow for spatial normalization of each subject's data into a standard coordinate system.

In each activation condition, eight pairs of sentences (recorded by a female native speaker of American English) were presented through stereo headphones at a rate of one pair every 7.5 sec; for half the pairs, the meaning was the same; for the other half, the meaning was different. The order of presentation of sentence pairs with same versus different meanings was randomized in both conditions. The order of presentation of the two conditions was counter-balanced across subjects. The activation conditions alternated with three rest periods of 30 sec each, during which the subjects were simply instructed to rest.

To correct for head motion, the functional images for each subject were realigned with AIR (Woods et al., 1998) using a six parameter rigid body transformation model and a least-square cost function with intensity scaling. Following realignment, the data were analyzed with SPM96 (Wellcome Department of Cognitive Neurology, London, UK). In order to perform intersubject averaging, all images were transformed into a standard space, (Talairach and Tournoux, 1988) by matching each scan (in a least-squares sense) to a template image that already conformed to the standard space. This spatial normalization involved a 12 parameter affine (linear) and quadratic (nonlinear) three-dimensional transformations, followed by a two-dimensional piece-wise nonlinear matching using a set of smooth basis functions that allow for normalization at a finer anatomical scale (Friston et al., 1995). As a final preprocessing step, all images were smoothed using a 6 mm FWHM isotropic Gaussian kernel to increase the signal to noise ratio.

Condition effects were estimated according to the general linear

model, using a box-car reference function with a 6 sec delay to compensate for the lag in the hemodynamic response. Global activity was entered as a confounding covariate. The contrasts between each activation condition versus rest were examined first. The direct contrasts between the two activation conditions were then examined using the respective activation versus rest contrasts as masks. The resulting foci of activation were characterized in terms of spatial extent (k) and peak height (u). The corrected significance of each region was estimated using distributional approximations from the theory of Gaussian Fields, both in terms of the probability that a region of the observed number of voxels could have occurred by chance [$P(n_{\max} > k)$], and that the peak height observed could have occurred by chance [$P(Z_{\max} > u)$], over the entire volume analyzed.

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