NeuroImage **15,** 1003–1014 (2002)
doi:10.1006/nimg.2001.1026, available online at http://www.idealibrary.com on IDEAL®

Brain Activation Modulated by the Comprehension of Normal and Pseudo-word Sentences of Different Processing Demands: A Functional Magnetic Resonance Imaging Study

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Received May 7, 2001; published online February 7, 2002

Recent data from lesion and brain imaging studies have questioned the well-established assumption of a close functional–anatomic link between syntax and Broca's area and semantics and Wernicke's area. In the present study we used functional magnetic resonance imaging (fMRI) to investigate the neuroanatomical correlates of semantic and syntactic functions and possible interdependencies between the related brain systems. In a completely crossed design we varied syntactic processing demands (easy vs difficult to process word order sequences) and the meaningfulness of sentences (real- vs pseudo-word sentences). In comparison to a backward speech condition we found an activation of the left perisylvian region, including the left inferior frontal cortex and the left superior and middle temporal gyri. Semantic in contrast to pseudo-word sentences elicited a stronger activation in both the anterior and the posterior perisylvian cortex. Syntactic difficulty had its strongest effect within the left inferior frontal region and this effect was more pronounced for semantic than nonsemantic speech. These results suggest that semantic and syntactic language functions are mediated by partly specialized brain systems but that there nevertheless exists a substantial functional overlap of the involved brain structures. © 2002 Elsevier Science (USA)

Key Words: **functional magnetic resonance imaging; semantics; syntax; language comprehension; speech; Broca's area; Wernicke's area.**

INTRODUCTION

Traditionally, Broca's area, Wernicke's area, and the arcuate fasciculus have been considered the most relevant brain structures for language processing and have been functionally related to language production, language comprehension, and the information transfer between the two cortical areas, respectively (Alexander, 2000; Dronkers, 2000b). This model has originally been postulated on the basis of specific impairments of patients with focal brain damage and has in the following been modified and extended as a result of both more precise neuroanatomical data and results from functional imaging studies (reviews: Friederici, 1998; Brown *et al.*, 2000). Nevertheless, the functional role of and mutual dependence between anterior and posterior perisylvian language areas are still a matter of debate (e.g., Caplan, 2000; Dronkers *et al.*, 2000; Grodzinsky, 2000).

Broca's area has been associated with an online computation of syntactical structure (Friederici and Kilborn, 1989) or only with the transformational component of syntax (Grodzinsky, 2000). It has also been noted that the inferior frontal cortex may support other functions as well, most prominently working memory functions (Just and Carpenter, 1992; Caplan and Waters, 1999) which may, however, be specifically related to or support syntactic processes. Finally, brain imaging techniques, which allow a more precise analysis of the location and the extend of brain lesions, have indicated that there is not a perfect correlation between Broca's aphasia and lesions in Broca's area (including the pars triangularis and pars opercularis of the third frontal convolution of the left hemisphere). Similarly, recent data imply that large brain areas of the lateral temporal lobe (including the superior and middle temporal gyrus back to the end of the Sylvian fissure, including the supramarginal gyrus) must be damaged to cause permanent Wernicke's aphasia, i.e., serious impairments in language comprehension (Alexander, 2000; Dronkers *et al.*, 2000). Thus, the exact functional roles of both the anterior and the posterior "language" areas still remain unclear.

In order to separate brain areas concerned with syntactic processes from those mainly supporting seman-

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tic processes, the syntactic complexity of written and spoken sentences was manipulated (Stromswold *et al.*, 1996; Caplan *et al.*, 1999). Larger regional blood flow changes to syntactically more complex than to simpler sentence constructions were observed for left frontal brain regions. Moreover, the number of activated voxels increased as a function of syntactical difficulty not only in anterior (Broca's area) but also in posterior perisylvian cortex (Wernicke's area) (Just *et al.*, 1996). Similar results have been obtained with a violation detection task (Embick *et al.*, 2000). While these studies held semantic processing demands constant, in order to reveal the neuroanatomical correlates of syntactic processing, other investigators employed syntactic and semantic violation detection tasks and compared brain activation patterns elicited by syntactic and semantic task requirements (partly in the same participants): While Kuperberg *et al.* (2000) did not obtain different brain activations in the two tasks, Ni *et al.* (2000) found a more substantiated blood flow change within the inferior frontal region in the syntactic anomaly detection task and an increased activity within the posterior portions of the perisylvian region (and superior frontal lobe) in the semantic anomaly detection task. The latter findings have recently been replicated with a similar violation detection paradigm (Newman *et al.*, 2001). To further isolate semantic and syntactic language aspects Friederici *et al.* (2000) introduced conditions with pseudo-words. They compared the processing of normal prose, syntactic prose (sentences with pseudo-words), and word lists that contained either real words or pseudo-words. While the superior temporal sulcus was more active in both sentence conditions, the inferior frontal sulci of both hemispheres were most active during pseudo-word speech but only weakly activated in the remaining conditions including normal speech. The authors speculated that the latter finding might be due to an automatic processing of normal speech. This hypothesis is supported by another experiment of the same authors (Meyer *et al.*, 2000): One group of participants had to judge the auditorily presented sentences as grammatically correct or incorrect while the other group had, in addition, to correct the errors silently. While an increased blood flow was found for the temporal language areas in both groups, this activation was enhanced in the second group. Moreover, the "repair group" showed an additional right inferior frontal cortex activity.

In sum, neuroimaging studies have confirmed the importance of the left perisylvian cortex for the processing of both written and spoken language in healthy humans (for recent review: Indefrey and Levelt, 2000). The main difference between the brain imaging and patient data is the repeatedly reported right hemispheric activation obtained in the imaging studies while right hemispherical brain damage does usually not result in aphasia (Alexander, 2000). The brain imaging studies, on the other hand, differ with respect to the degree of obtained right hemispheric activity and the degree of specialization observed for anterior and posterior parts of the perisylvian cortex for syntactic and semantic processing, respectively.

In a recent study Keller *et al.* (2001) independently manipulated syntactic and lexical processing aspects by using conjoined active vs object-relative sentences and nouns with high vs low lexical frequency, respectively. They found an interaction between the two factors for both left frontal and left temporoparietal brain regions, i.e., the hemodynamic response increased as a function of syntactic complexity mainly for sentences with nouns of low lexical frequency. Therefore, Keller *et al.* (2001) proposed that language comprehension is supported by a mutual communication between anterior and posterior language areas. This suggestion is pertinent to reports, showing that semantic features (as lexical frequency) influence the resolution of syntactic ambiguities (Trueswell, 1996). However, the latter findings also suggest that it is not possible to exclude an interaction of syntactic and semantic processing aspects, if real content words are used, even when the same words occur in a syntactic easy and difficult condition (Just *et al.*, 1996; Stromswold *et al.*, 1996; Caplan *et al.*, 1999). Genuine syntactic processes and their neural correlates can only be investigated by manipulating syntactic processing difficulty of sentences with semantically empty words, i.e., pronounceable pseudo-words (see also Hagoort and Brown, 1999). Moreover, a comparison between sentences with real and pseudo-words reveals brain systems essential for semantic processing aspects. This approach was taken in the present investigation.

Syntactic processing demand was operationalized by presenting spoken German sentences with different word orders. Languages differ in the number of permissible word orders, which is a function of the richness of their inflectional morphology. German has case markers for nouns and is therefore relatively flexible with respect to the order of the subject, the direct object, and the indirect object within a sentence. In everyday life different word orders are used to stress particular noun phrases. If sentences are presented in isolation, people show preferences for particular word orders and there is evidence (Pechmann *et al.*, 1996; Röder *et al.*, 2000) that these are guided by the following linear precedence (LP) rules (Uszkoreit, 1986): (1) A sentence is judged more acceptable if the subject precedes the objects; (2) a sentence is rated more acceptable if the indirect object precedes the direct object (see Table 1 for four legal word orders of verb final sentences ranked according to (the proposed) acceptability (high to low)). Moreover, Röder *et al.* (2000) showed that processing times and grammatical acceptability ratings vary as a function of word order not only

TABLE 1a

Examples of the Five Sentence Types with Normal Words (Semantic Sentences)

(1) S-IO-DO	Jetzt wird	der Astronaut	dem Forscher	den Mond	beschreiben.
	Now will	*the astronaut*	*to the scientist*	*the moon*	*describe.*
(2) S-DO-IO	Jetzt wird	der Astronaut	den Mond	dem Forscher	beschreiben.
	Now will	*the astronaut*	*the moon*	*to the scientist*	*describe.*
(3) IO-DO-S	Jetzt wird	dem Forscher	den Mond	der Astronaut	beschreiben.
	Now will	*to the scientist*	*the moon*	*the astronaut*	*describe.*
(4) DO-IO-S	Jetzt wird	den Mond	dem Forscher	der Astronaut	beschreiben.
	Now will	*the moon*	*to the scientist*	*the astronaut*	*describe.*
(5) DO-V-IO-S	Jetzt wird	den Mond	beschreiben	dem Forscher	der Astronaut.
	Now will	*describe*	*the moon*	*to the scientist*	*the astronaut.*

Note. English translations are word by word. (1) to (4) are grammatically correct but vary in syntactical difficulty: (1) and (2) are easy, (3) and (4) are difficult to process, and (5) is grammatically incorrect (Pechmann *et al.*, 1996; Röder *et al.*, 2000).

for sentences with real words but for sentences with pseudo-words as well.

The goal of the present study was to identify brain areas supporting semantic and syntactic processing aspects of language and to substantiate a possible interaction between these two processing streams.

First, the validity of the LP rules for auditorily presented sentences with legal and pseudo-words was tested in a behavioral study. In the consecutive fMRI study, semantic (with real words) and nonsemantic sentences (with pseudo-words) of two levels of syntactical difficulty were presented (factorial design).

Based on the results from both patient and brain imaging studies, we expected a left-lateralized activation of the perisylvian cortex during language processing. Moreover, we predicted that the amplitude of the hemodynamic response should vary as a function of syntactical processing demands particularly in left frontal cortex.

MATERIAL AND METHODS

Participants

In total, 19 students and staff members of the University of Marburg were recruited. Eight (5 female, mean age 22.6 years, range 21–24 years) participated in the behavioral study and the remaining eleven (6 female, mean age 26.3 years, range 21–37 years) took part in the fMRI study. All participants reported to be right-handed, which was confirmed with the Edinburgh handedness inventory (Oldfield, 1971) for the participants of the fMRI study. All participants were native speakers of German, had normal hearing, and had no history of neurological illness. Informed written consent was obtained and participants either earned course credits or were monetarily compensated.

Material and Procedure

Each sentence comprised nine words and was constructed according to the following schema: adverbial-phrase, auxiliary, noun-phrase-1, noun-phrase-2, noun-phrase-3, and verb (Table 1). The words had one to three syllables. The sentences were taken from the material of Rösler *et al.* (1998). A corresponding set of pseudo-word sentences was constructed by keeping all functional words (adverbs, auxiliary verbs, and articles) while all content words were transformed into pronounceable pseudo-words. This was achieved by moving or replacing (up to two) letters in each content word. The resulting pseudo-words had the same number of syllables as the original words and for verbs suffix morphology was kept (pseudo-verbs derived from irregular verbs were inflected regularly). All sentences were read by a professional female speaker. Sentences were initially recorded on a dat-tape and were transferred via the digital input of a TERRATEC (DMX) soundcard onto a hard disk of a computer. Each sentence was trimmed so that the beginning and end of the

TABLE 1b

Examples of the Five Sentence Types with Pseudo-words (Nonsemantic Sentences)

(1) S-IO-DO	Jetzt wird	der Tronasaut	dem Schorfer	den Rond	bebreuschen.
(2) S-DO-IO	Jetzt wird	der Tronasaut	den Rond	dem Schorfer	bebreuschen.
(3) IO-DO-S	Jetzt wird	dem Schorfer	den Rond	der Tronasaut	bebreuschen.
(4) DO-IO-S	Jetzt wird	den Rond	dem Schorfer	der Tronasaut	bebreuschen.
(5) DO-V-IO-S	Jetzt wird	den Rond	bebreuschen	dem Schorfer	der Tronasaut.

Note. (1) to (4) are grammatically correct but vary in syntactical difficulty: (1) and (2) are easy, (3) and (4) are difficult to process, and (5) is grammatically incorrect (Röder *et al.*, 2000).

resulting wav files (resolution 44 kHz, 16 bit) corresponded to the onset and offset of the sentence, respectively. The mean duration of the sentences was 2.8 s (range 2.5–3.4 s). They were either grammatically "easy" or grammatically "difficult." Easy sentences were those in which the word order of the noun phrases was either canonical (subject (S)–indirect object (IO)–direct object (DO)) or in which only the order of the indirect and direct object was changed (S-DO-IO). Difficult sentences deviated substantially from the canonical form in that the subject was moved behind the objects (IO-DO-S, DO-IO-S). Thus, there were four conditions, syntactically easy sentences with real content words (condition easy semantic, ES), syntactically difficult sentences with real content words (difficult semantic, DS), syntactically easy sentences with pseudo-words (easy nonsemantic, EN), and syntactically difficult sentences with pseudo-words (difficult nonsemantic, DN). In addition, a "backward speech" (B) condition was created by playing sentences of these four conditions backward. The latter condition was used in the fMRI study only.

In the behavioral study, eight blocks of 80 sentences each (four blocks for condition ES and DS and four blocks for condition EN and DN) were presented. Blocks of semantic and nonsemantic sentences alternated while easy and difficult sentences were randomly intermixed. The order of the eight blocks was balanced across participants. Across blocks, the same sentence scenarios were used for all four word order conditions but each sentence occurred only once within a block. Sentences were presented with headphones (Okano KH133 digital, 50–60 dB(A)) using the software package ERTS (Experimental Run Time System, Berisoft). Participants had to press one of five keys (the one, two, three, four, or five key of the number board of a PC keyboard) to indicate if they thought the sentence was grammatically very acceptable (=5) or grammatically not acceptable (=1). The next sentence of a block was presented 1500 ms after the response. The whole session lasted about 2 h.

For the fMRI study, four different protocols were composed which comprised the five conditions B, ES, DS, EN, and DN. Each block contained seven different sentences which were separated on average by 1.5 s of silence (range 1.2–1.8 s); periods of silence were adjusted so that the first sentence of the next block started exactly 30 s after the onset of the first sentence of the previous block. A run comprised 22 blocks, two blocks of semantic speech (one ES and one DS block) always altered with two blocks of nonsemantic speech (one EN and one DN block) and these double blocks were separated by one block of backward speech. The order of the easy and the difficult condition in these double blocks was altered within and across runs, and the order of semantic and nonsemantic blocks was balanced across the four protocols used. Two protocols had four blocks of ES (28 sentences), four blocks of DS (28 sentences), three blocks of EN (21 sentences), three blocks of DN (21 sentences), and eight blocks of backward speech (54 sentences; the last backward speech block comprised 5 sentences only) and two protocols comprised three blocks of ES and DS, four blocks of EN and DN, and eight blocks of backward speech. The total duration of a run was 10:50 min (the last backward speech block lasted only 20 s). Due to time limitations each participant received only three of the four protocols (the first participant had received all four runs); across participants each protocol was used about equally often. Across the four runs, nearly each sentence scenario was used both in the easy and in the difficult condition. For the backward speech condition four randomly selected blocks of semantic and four blocks of nonsemantic speech of a run were played backward. In each run either two or three sentences were substituted by an ungrammatical word order (the verb was moved after the direct object in word order DO-IO-S, see Table 1; this word order is judged less acceptable than the least preferred legal word order by native German speakers (Röder *et al.*, 2000)). This corresponds to 2 and 3% illegal word orders, if related to the four sentence conditions (ES, DS, EN, DN), and to 1.3 and 2% illegal word orders, if related to all five conditions. Across runs, illegal word orders occurred equally often in semantic and nonsemantic speech conditions.

Stimuli were presented via a home-made tubing system connected to a noise-protecting headphone (75–85 dB(A)). Participants were asked to attentively listen to the sentences. They were instructed to count the number of genuine syntactic violations and had to report their count at the end of each run.

Participants of both studies were informed that German allows many different word orders although some of them may sound awkward. In the fMRI study they were in addition told that despite this flexibility of the German language, there are illegal word orders as well. An example of each word order was given but for the illegal construction another ungrammatical word order was used than the later employed one. Two to four randomly selected semantic, nonsemantic, and backward sentences were played to the participants before the experiment proper started in order to familiarize them with the different conditions.

fMRI Data Acquisition

The functional MR images were acquired with a 1.5-T General Electric (Signa Horizon) scanner with an echo planar imaging (EPI) upgrade using the standard quadrature head coil. In total 130 EPI volumes were acquired in each run; each volume comprised 22 axial slices (thickness 5 mm, gap 0) with an in-plane resolution of 3.75 × 3.75 mm (FOV 240 × 240 mm, matrix 64 × 64; TR 5000 ms, TE 60 ms, flip angle = 90°).

A whole-head 3D volume (124 continuous axial slices; thickness 1.4 mm) was acquired (duration 11 min) from each participant in the same session by using a fast-spin gradient echo sequence (FSPGR; FOV 240 × 180 mm, matrix 256 × 192, resulting in an in-plane resolution of 0.9375 × 0.9375 mm; TR 11.1; TE 4.2, Nex 3).

Two functional runs were followed by the acquisition of the structural 3D volume and the session terminated with a third functional run. Participants were blindfolded and their heads were immobilized both with a vacuum cushion and with the tightly fitting headphones.

Data Analysis

Behavioral Study (Grammaticality Judgments)

Mean rating scores were calculated for each of the eight conditions: four word orders (S-IO-DO, S-DO-IO, IO-DO-S, DO-IO-S) with either semantic or nonsemantic words. These scores were submitted to an analysis of variance (ANOVA) with Semantics (semantic vs nonsemantic) and Syntax (S-IO-DO, S-DO-IO, IO-DO-S, DO-IO-S) as repeated measurement factors.

fMRI Study

Behavioral data (error detection). The mean signed deviation of a participant's count from the actual number of illegal word orders in a run was calculated.

fMRI data. Analyses and visualization were performed with the BrainVoyager 3.9 software (BrainInnovation; www.brainvoyager.de). It comprised (1) a preprocessing and normalization (Talairach and Tournoux, 1988) of the data; (2) single participant analyses; and (3) across participants analyses.

1. Preprocessing and normalization. The 3D structural data set of each participant was first interpolated into a volume with a voxel size of 1 × 1 × 1 mm. This volume was then transformed into the standard brain of the Talairach and Tournoux atlas (1988).

The first two acquisitions (i.e., 22-slice EPI volumes) of each functional run were disregarded. The linear drift of each pixel time course was removed. The 22 functional slices were coregistered with the structural data set, separately for each run. A 3D volume of the functional data was created that comprised the time-course information as well. In the next step, a 3D motion correction was applied.

2. Single participant analyses. A General Linear Model (GLM) with four predictors (ES, DS, EN, DN) was calculated for each participant taking into account all three runs. The (sinusoidal) predictor functions were shifted by one volume (5 s) in order to compensate for the delay of the hemodynamic response. Voxels were defined as "active" if the multiple correlation coefficient R was lager than 0.5 and if more than 100 adjacent voxels had an R larger than 0.5. Active voxels were assigned with respect to the Talairach and Tournoux atlas to regions of interest (ROIs, see below).

3. Across participants analyses. (a) Percentage of signal change: The voxel time courses for significantly activated voxels within each ROI were averaged across volume three, four, and five of all blocks of the three runs, separately for each participant and condition. These values were entered as dependent variable into an ANOVA with the repeated measurements factors Semantics (semantic vs nonsemantic), Syntax (easy vs difficult), and ROI. (b) Across participants GLM analyses: All three runs of each of the eleven participants were submitted to a GLM analysis. Since the variance of voxel time courses may vary between runs and participants, a z-normalization of each signal time course was performed. In addition, the functional 3D maps were spatially smoothened using a Gaussian kernel of 6-mm FWHM in order to compensate for interindividual differences. First, corresponding to the single-participant analysis, a GLM with predictors ES, DS, EN, and DN was calculated; the threshold was set to $R > 0.4$; $F(4/4347) = 207$, $P < 0.0001$, corrected). Second, the Syntax effect was assessed by comparing ES and EN with DS and DN (threshold, $R > 0.2$; $F(4/4347) = 90.56$, $P < 0.0001$, corrected). Third, effects due to semantic content were estimated by the contrast ES, DS vs EN, DN (threshold, $R > 0.2$; $F(4/4347) = 90.56$, $P < 0.0001$, corrected).

The main focus of the present study was on two ROIs: (I) the inferior frontal region comprising the pars triangularis (BA 45) and pars opercularis (BA 44) and (II) the posterior superior and middle temporal gyri including the superior temporal sulcus (including posterior BA 21, 22). It turned out (see Results) that the remaining activations could be assigned to the following three regions: (III) central and posterior part of the middle frontal gyrus (BA 6); (IV) anterior and central parts of the cingulate gyrus (BA 24, 32); and (V) anterior convolution of the inferior parietal lobe (supramarginal gyrus, BA 40).

RESULTS

Behavioral Data

Behavioral Study: Grammaticality Ratings

The mean rating scores averaged across the eight participants are shown in Fig. 1. While sentences with different word orders differed in their acceptability ($F(3,21) = 52.52$, $P < 0.0001$), the ratings were comparable for semantic and nonsemantic sentences (there was neither a main effect of Semantics ($P > 0.98$) nor

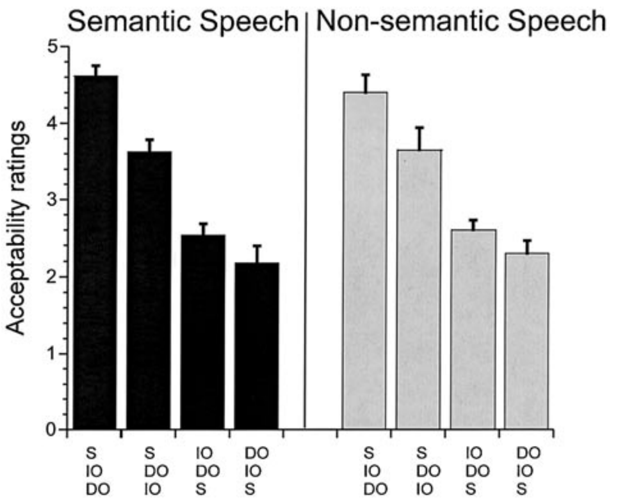

FIG. 1. Grammaticality acceptability ratings for four different word orders in German verb final sentences with semantic (left, black bars) and nonsemantic words (right, gray bars). 1, "not acceptable"; 5, "very acceptable"; S, subject; IO, indirect object; DO, direct object.

a Semantic × Syntax interaction ($P > 0.40$)). Pairwise comparisons showed that all four word orders differed in their acceptability (all $P < 0.007$); that is, the more the word order of a sentence deviated from the canonical form, the lower was the acceptability judgment.

fMRI Study: Error Detection

On average, the count of the participants deviated from the correct number of illegal word orders in a run by 1.29 (range 0–3).

fMRI Data

Single Participant Analysis

Active areas (with the Talairach and Tournoux coordinates of the center of gravity of the activated voxel clusters) of each participant are shown in Table 2: All 11 participants showed significantly activated voxels in the left inferior frontal cortex (ROI I) and in brain areas surrounding the posterior superior temporal sulcus (ROI II).

In addition, 10 participants had significant activations in the left middle frontal gyrus (ROI III), 9 had significantly activated voxels in the left anterior and central cingulate gyrus (ROI IV), and 7 participants showed an activation of the left inferior parietal lobe (ROI V). In 5 participants significant activations could be detected in the right hemisphere: 2 participants showed active voxels in the right inferior frontal cortex, 2 in the right superior temporal sulcus, and 1 in the right middle frontal gyrus.

Across Participants Analyses

Percentage of signal change. ROI I and ROI II of the left hemisphere: More difficult sentences elicited larger blood flow changes than easier sentences (main effect Syntax) (Table 3, Fig. 2) and semantic speech led to higher blood flow changes than nonsemantic speech (main effect Semantics). The Syntax effects were larger for semantic than nonsemantic speech (Semantics × Syntax), in particular within the left inferior frontal cortex (Syntax × Semantics × ROI).

Differently phrased, the ANOVAs calculated separately for the frontal and posterior language areas

TABLE 2

Number of Active Voxels and Talairach Coordinates of the Point of Gravity for Significantly Activated Clusters (Single Participant Analysis, Four Predictor GLM Model) (Parameters: cluster size > 100, R > .5).

	Lateral inferior frontal region (ROI I)		Superior and middle temporal gyri (ROI II)		Middle frontal gyrus (ROI III)		Cingulate gyrus (ROI IV)		Inferior parietal region (ROI V)		Activated regions in the right hemisphere	
Participant No.	No. of voxels	*X/Y/Z*	No. of voxels	*X/Y/Z*	No. of voxels	*X/Y/Z*	No. of voxels	*X/Y/Z*	No. of voxels	*X/Y/Z*	No. of voxels	*X/Y/Z*
1	122	−38/27/2	516	−59/−21/2	390	−44/15/21	198	−4/4/53	121	−44/−24/45		
2	256	−44/7/23	2426	−49/−50/3	403	−48/−3/36	191	0/2/49	—	−/−/−		
3	135	−46/5/6	1300	−49/−27/1	201	−47/0/40	—	−/−/−	2035	−56/−42/28		
4	2963	−45/23/16	3056	−55/−36/7	2234	−44/2/35	956	−3/10/50	195	−55/−38/41	106	43/23/10 (inferior frontal cortex)
5	127	−53/25/2	286	−51/−28/0	196	−51/4/38	282	−6/2/53	—	−/−/−	293	41/8/33 (middle frontal gyrus)
6	1399	−49/30/12	2599	−46/−47/5	2279	−47/0/35	1476	0/−1/54	130	−49/−49/22	325	42/39/3 (superior temporal sulcus)
7	1411	−47/35/12	2653	−47/−37/4	3457	−44/1/32	1470	0/−1/54	126	−49/−49/24	320	43/34/0 (superior temporal sulcus)
8	3394	−40/26/7	4551	−54/−36/3	4454	−42/3/39	2501	0/10/49	764	−27/−50/43	463	40/27/14 (inferior frontal cortex)
9	135	−51/16/1	2170	−52/−47/14	651	−50/4/16	—	−/−/−	1616	−58/−52/21		
10	141	−43/10/17	329	−61/−23/0	—	−/−/−	125	−2/10/53	—	—	—	
11	1063	−44/21/12	1539	−44/−36/10	889	−50/5/36	1810	−4/8/49	—	—	—	

TABLE 3

ANOVA Results with Percentage of Signal Change as Dependent Variable: Semantics (Semantic vs Nonsemantic) × Syntax (Easy vs Difficult) × ROI (ROI I vs ROI II)

Effect	*df*1/*df*2	*F*	*P* (*F*)
Semantics	1/10	10.69	0.0084
Syntax	1/10	55.71	0.0001
ROI	1/10	—	—
Semantics × Syntax	1/10	4.61	0.0673
Semantics × ROI	1/10	5.77	0.0372
Syntax × ROI	1/10	10.27	0.0094
Semantics × Syntax × ROI	1/10	9.24	0.0125

(Table 4) confirmed that, although semantic speech in general elicited higher blood flow changes than nonsemantic speech (main effect Semantics for both areas), the Syntax effect was of similar size for semantic and nonsemantic speech within the posterior temporal lobe but was larger for the semantic than nonsemantic speech within the left inferior frontal cortex (Semantics × Syntax). The Syntax effect was, however, significant for semantic and nonsemantic speech in both ROIs ($P < 0.05$).

ROI III–V of the left hemisphere: Sentences with difficult word orders elicited higher blood flow changes than sentences with easy word orders in middle frontal gyrus (ROI III) and cingulate gyrus (ROI IV) (Table 4). In the cingulate gyrus a larger hemodynamic response was observed for semantic than nonsemantic sentences (main effect Semantics) and the Syntax effect was larger for the semantic than nonsemantic speech (Syntax × Semantics). No significant effects were obtained for the inferior parietal lobe (ROI V).

Across participants GLM analyses. The contrast of all four conditions (ES, DS, EN, DN) vs backward speech (B) confirmed a significant activation of the inferior frontal cortex (ROI I), the superior and middle temporal gyrus (ROI II), the middle frontal gyrus (ROI III), and the cingulate cortex (ROI IV) of the left hemisphere (Table 5a and Fig. 3). Significant activations of the right hemisphere (in the inferior frontal cortex and insula) could only be detected when the threshold was lowered to $R > 0.3$.

The contrast ES/EN vs DS/DN (Syntax effect; Table 5b, Fig. 4) showed that processing difficulty had a significant effect upon the activation level and extend of the inferior frontal region (ROI I), the superior and middle temporal gyrus (ROI II), middle frontal gyrus (ROI III), the cingulate gyrus (ROI IV) of the left hemisphere, and the right insula. Semantic speech elicited a stronger activation than nonsemantic speech within all ROIs (contrast, ES/DS vs EN/DN = Semantic effect; Table 5c, Fig. 5).

DISCUSSION

The present study investigated the neuroanatomical correlates of semantic and syntactic aspects of speech processing by independently manipulating the syntactic difficulty and the meaningfulness of sentences.

Syntactically easy and difficult sentences were constructed by varying the word order of the nominal phrases (subject, indirect object, and direct object). Such a permutation is legal in German because the role assignments are fully determined by case marking definite articles. Nevertheless, behavior data with visual (Pechmann *et al.*, 1996; Rösler *et al.*, 1998; Röder *et al.*, 2000) and auditory (present study) presentation provided evidence that the more a sentence deviates from its canonical word order (number of LP rules violated), the longer it takes to understand this sentence and the less acceptable is its grammaticality rating. Therefore, it is reasonable to assume that by varying the word order of German verb-final sentences different processing loads are imposed upon the neural systems supporting syntactic functions proper. Sentences without any meaning were created by substituting all content words with pronounceable pseudo-words. These sentences varied in their processing difficulty and grammatical acceptability (present study and Röder *et al.*, 2000) as their meaningful counterparts, suggesting that the syntax manipulation was similar for meaningful and pseudo-word sentences. Compared to backward speech, semantic and nonsemantic speech processing was accompanied by significant blood flow changes in

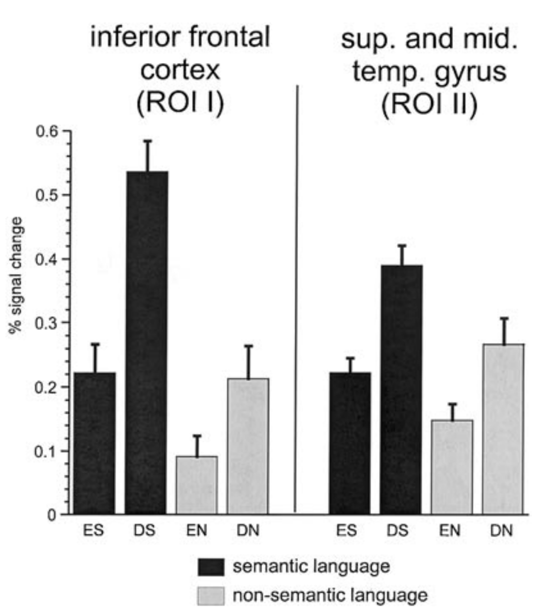

FIG. 2. Percentage of signal change for semantic (black bars) and nonsemantic (gray bars) speech in lateral frontal cortex (ROI I) and superior and middle temporal gyrus (ROI II); E, easy word orders (subject first position sentences); D, difficult word orders (subject last position sentences).

TABLE 4

ANOVA Results with Percentage of Signal Change as Dependent Variable: Semantics (Normal vs Pseudo-word) × Syntax (Easy vs Difficult) Separately for the ROIs

ROI	*df* 1/*df* 2	Semantics		Syntax		Semantics × Syntax	
I (inferior frontal cortex)	1/10	11.17	0.0075	83.88	0.0001	6.90	0.0253
II (sup./mid. temp. gyrus)	1/10	5.51	0.0408	23.38	0.0007	—	—
III (middle frontal gyrus)	1/9	3.50	0.0941	11.26	0.0084	—	—
IV (cingulate gyrus)	1/8	18.08	0.0028	27.69	0.0008	8.81	0.0179
V (inf. par. lob.)	1/6	—	—	—	—	—	—

the left perisylvian cortex. Right hemispheric activity was very small and was only seen in a minority of participants. The strongest effect of syntactic difficulty (word order effect) was observed for the left lateral frontal cortex and this effect was larger for semantic than nonsemantic speech. Meaningful speech elicited a higher brain activation than pseudo-word speech. In addition to the 'classical' perisylvian language areas, significantly activated voxels were detected in the middle frontal gyrus, the anterior cingulate gyrus, and inferior parietal region.

In the following the observed effects of semantic content and syntactic difficulty will be discussed and possible alternative accounts will be considered.

A higher activation for semantic than for nonsemantic speech was seen in the present study for temporal areas, i.e., brain structures which have both, on the basis of data from patients with focal brain lesions (see Introduction, e.g., Alexander, 2000) and imaging studies (Wise *et al.*, 2001), been associated with the processing of lexical/semantic information. Brain imaging studies have provided evidence that (in particular ventral) temporal regions are activated by intelligible speech (Binder *et al.*, 2000; Scott *et al.*, 2000). In the inferior frontal cortex we observed, in contrast to earlier studies (Hagoort *et al.*, 1999; Friederici *et al.*, 2000), a higher activation for semantic than nonsemantic speech as well.

Our results for the syntactical difficulty manipulation are consistent with other brain imaging studies that manipulated the syntactic complexity of written and spoken language: the largest effects of syntactic processing load were found in the left inferior frontal cortex (Stromswold *et al.*, 1996; Caplan *et al.*, 1998, 1999). Since other factors which affect sentence processing were held constant (as in Ben-Shachar *et al.*, 2001) and because we observed a modulation of inferior frontal cortex activity as a function of syntactic difficulty for both semantic and nonsemantic speech, our results are consistent with the proposal that the inferior frontal gyrus is essential for the "computation of grammatical transformations" (Grodzinsky, 2000) or more general, an online computation of the syntactic structure (Friederici and Kilborn, 1989). The latter was originally proposed on the basis of observations in Broca's aphasics showing that they have specific problems to analyze intrasentential dependencies among constituting phrases and did not show syntactic priming effects when short prime-target intervals were used, respectively.

In the present study participants had to analyze the syntactic structure of the sentences in order to decide whether or not a word order was legal. This was not an easy task because word orders that deviate substantially from the canonical form are experienced as somewhat awkward as well. As a consequence we most likely observed an extended activation of the inferior frontal cortex. This assumption is consistent with the suggestion of Friederici *et al.* (2000) according to which the activation of left frontal language areas ". . . is a function of the input's deviance from normal speech."

Effects of syntactical difficulty were not only observed in anterior parts of the perisylvian language areas but also in the posterior superior and middle

TABLE 5a

GLM across Participants Analysis: Active Regions for the Four Predictor Model (ES, DS, EN, DN vs Backward) ($R > 0.4$)

ROI	BA	Talairach coordinates *X*	*Y*	*Z*	No. of activated voxels
Left hemisphere					
I (inferior frontal cortex)	44, 45	−41	10	21	1690
II (sup. and mid. temp. gyrus)	21, 22	−48	−35	4	914
III (middle frontal gyrus)	6	−47	1	36	1152
IV (cingulate gyrus)	32	−2	4	51	724

TABLE 5b

GLM across Participants Analysis: Syntax Effect—Active Regions for the Contrast: ES, EN vs DS, DN ($R > 0.2$)

ROI	BA	Talairach coordinates X	Y	Z	No. of activated voxels
Left hemisphere					
I (inferior frontal cortex)	44, 45	−45	12	16	2126
II (sup. and mid. temp. gyrus)	21, 22	−47	−45	9	120
III (superior frontal gyrus)	6	−44	3	36	1519
IV (cingulate gyrus)	24, 32	−2	6	50	1778
Right hemisphere					
Insula		31	19	2	177

temporal cortex (as in Just *et al.*, 1996; Ben-Shachar *et al.*, 2001; Keller *et al.*, 2001). The interaction between both factors, however, was reliable only in left lateral frontal cortex. This extends the results of Keller *et al.* (2001) by demonstrating that a functional specialization of language areas, nevertheless, exists to some degree, at least for auditory language comprehension (Keller *et al.*, 2001, had used a visual presentation mode): The inferior frontal cortex might specifically contribute to the use of syntactic structure to compute the meaning of a sentence (e.g., Caplan and Waters, 1999). Moreover, it has been shown that lexical frequency influences the resolution of syntactic ambiguities (Trueswell, 1996), implying an interaction between semantic and syntactic analyses. Inferior frontal cortex may contribute to integrative processes and an interactive use of semantic and syntactic information during language comprehension.

Keller *et al.* (2001) suggest that it might be fruitful to investigate the time points up to which different language aspects are possibly processed independently and to determine which brain areas are activated at different time points. The time resolution of fMRI methodology is, however, not sufficient for this purpose but event-related potential studies, e.g., with the sentence material of the present study could shed some light onto this issue (see Rösler *et al.*, 1998).

In sum, our data are consistent with the suggestion that the straight forward association of Broca's area with syntactic operations and Wernicke's area with lexical/semantic representations may be to simple. Although a specialization for some subfunctions of both language aspects may exist, the two areas seem to interact more closely than originally thought. This interactive network idea for language comprehension, as postulated by Keller *et al.* (2001), is also consistent with the reported more complex impairment patterns of brain-damaged patients (Caplan, 2000; Dronkers, 2000a; Dronkers *et al.*, 2000).

In agreement with the data from aphasic patients is the strong left predominance of the language-related activity observed in the present study, because in most righted-handed people aphasia is associated with a damage of the left hemisphere (e.g., Alexander, 2000). This strong activation asymmetry is most likely due to the demanding syntactic task and the baseline (backward speech) used (Binder *et al.*, 2000; Kanasaku *et al.*, 2000; Scott *et al.*, 2000). Reliable right hemispheric activity was only obtained for lateral frontal cortex in the across participants analysis for semantic vs nonsemantic speech which is in agreement with the proposal that this region may be involved in the processing of semantic meaning as well (Shaywitz *et al.*, 1995).

TABLE 5c

GLM across Participants Analysis: Semantic Effect—Active Regions for the Contrast: ES, DS vs EN, DN ($R > 0.2$)

ROI	BA	Talairach coordinates X	Y	Z	No. of activated voxels
Left hemisphere					
I (inferior frontal cortex)	44, 45	−42	19	17	5713
II (sup. and mid. temp. gyrus)	21, 22	−46	−33	1	565
III (middle frontal gyrus)	6	−41	6	31	4117
IV (cingulate gyrus)	24, 32	−1	11	46	3248
Insula		−39	21	1	2045
Right hemisphere					
I (inferior frontal cortex)	44, 45	40	27	23	1265
Insula		34	20	4	2172

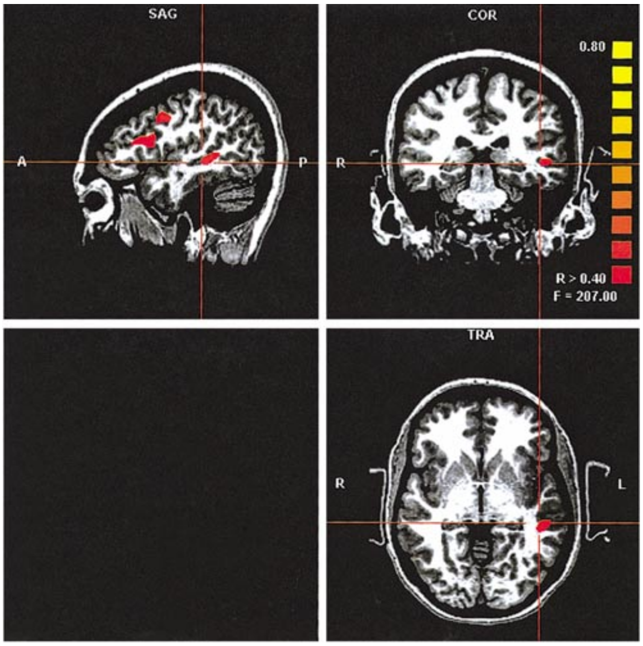

FIG. 3. Activated voxels ($R > 0.4$; not all shown) as revealed by the across participant analysis (GLM) using four predictors (ES, DS, EN, DN). The activations are overlaid onto a single subject's brain. Shown are the sagittal, coronal, and axial view at cursor position $X = -46$, $Y = -31$, $Z = 0$).

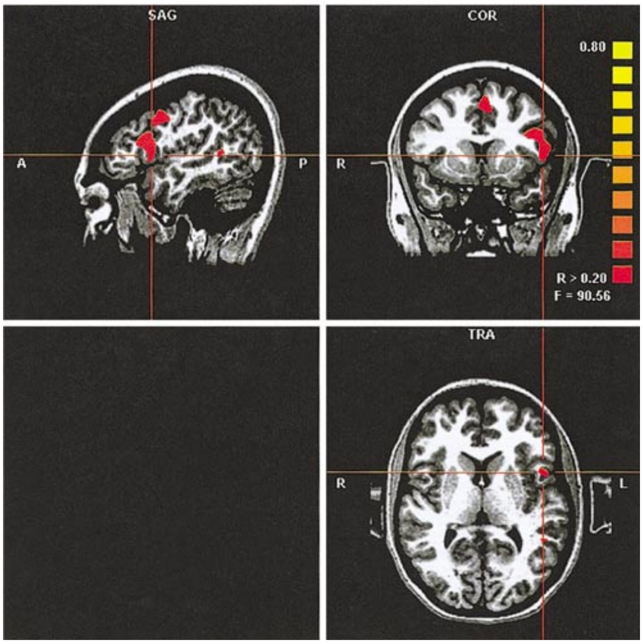

FIG. 4. Activated voxels ($R > 0.2$; not all shown) as revealed by the across participant analysis (GLM) for the syntax effect: contrast ES, EN vs DS, DN. The activations are overlaid onto a single subject's brain. Shown are the sagittal, coronal, and axial view at cursor position $X = -48$, $Y = 7$, $Z = -7$).

Finally, alternative accounts for the activation patterns observed in the present study need to be considered. The modulation of left frontal cortex activity as a function of syntactical processing load as observed here or in other studies (Stromswold *et al.*, 1996; Caplan *et al.*, 1998, 1999; Ben-Shachar *et al.*, 2001) could also been attributed to differences in working memory load (Kutas and Kluender, 1994; Rösler *et al.*, 1998; Caplan *et al.*, 1999). In the reaction time experiment of Röder *et al.* (2000) it took participants longer to process pseudo-word sentences than the corresponding sentences with legal German words (but factors Syntax and Semantics did not interact!). If the differences in inferior frontal cortex activity as a function of word order and semantic content were due to differences in memory load, higher activity for the nonsemantic sentences would have to be predicted from the reaction time data. This was, however, not the case. Röder *et al.* (2000) speculated that the main effect of Semantics in their study was due to the memory component in the task because participants had to answer a question that focused on the thematic roles of the noun phrases which is presumably harder for sentences with pseudowords than sentences with real words.

It could be argued that the frontal activation indicates language-unspecific processes as selection, monitoring, and evaluation. However, given the reaction time data of Röder *et al.* (2000) (see above), such accounts would predict higher blood flow changes for

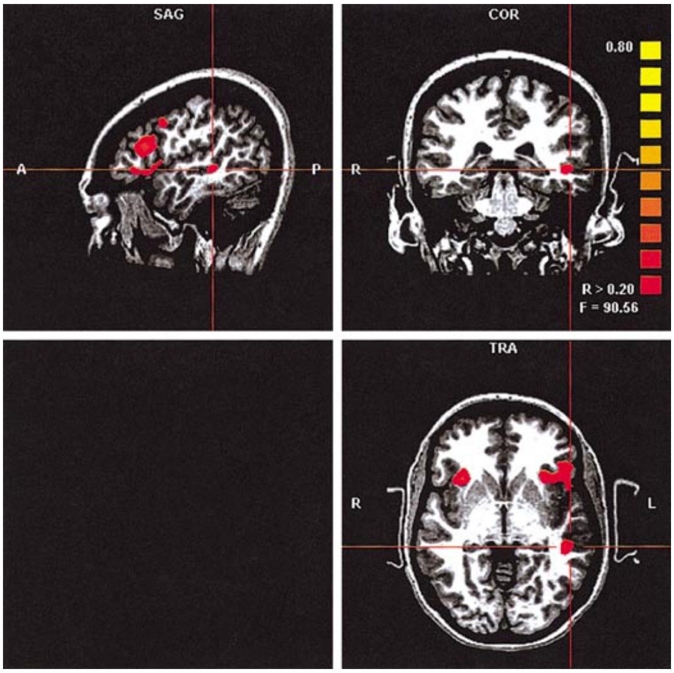

FIG. 5. Activated voxels ($R > 0.2$; not all shown) as revealed by the across participant analysis (GLM) for the semantic effect: contrast ES, DS vs EN, DN. The activations are overlaid onto a single subject's brain. Shown are the sagittal, coronal, and axial view at cursor position $X = -50$, $Y = -32$, $Z = 0$).

nonsemantic language too, since both reaction times and error rates were higher for nonsemantic than semantic sentences. Finally, it could be argued that participants used different strategies to process different word orders of semantic and nonsemantic speech, respectively. This seems unlikely, however, because in the reaction time study of Röder *et al.* (2000), error rates neither varied as a function of word order, nor was there a significant Semantic by Syntax (word order) interaction while these effects were significant for the hemodynamic response in left inferior frontal cortex. Of course behavioral data alone cannot definitively rule out arguments of strategic or other unspecific differences and the behavioral tasks used in the present study and by Röder *et al.* (2000) were not exactly the same. However, as shown by Pechmann *et al.* (1996) the processing load differences between different word order constructions become manifest in behavioral data across a great number of distinct tasks. This suggests a great generality of the syntactic processes which are invoked by this material and, therefore, it seems unlikely that the activations seen in the present study are exclusively caused by unspecific, strategic effects. This conclusion is further substantiated by considering the specific impairment patterns in patients with brain damage in different parts of the left perisylvian region.

CONCLUSION

Here, we found a very reliable activation of the anterior and posterior perisylvian region with a strong preponderance in the left hemisphere both during semantic and nonsemantic speech. The fact that all 11 participants showed significantly activated voxels in these areas makes our paradigm and stimuli a promising tool for the investigation of changes in the cerebral organization of language due to brain damage (Rosen *et al.*, 2000) or altered early input conditions.

Syntactic difficulty and semantic content affected the activity level of both anterior and posterior language areas. Semantic and syntactic manipulations interacted in inferior frontal cortex, a finding which is consistent with the idea that brain areas show some processing specificity although both language aspects seem to be supported by overlapping brain systems.

ACKNOWLEDGMENTS

The study was supported by grants of the German-American Academic Council Foundation (GAAC) to B.R. and H.N. and Ro 254/12-1 of the German Research Foundation (DFG) to F.R. For technical support we are grateful to Dr. J. Fadili, Professor Dr. R. Goebel, Dr. H. Haan, Dipl.-Ing. C. Moderer, Dr. L. Muckli, Rainer Müller, Dipl.-Phys. T. Müller, Dr. M. Obert, and Professor Dr. H. H. Schulze. Dr. J. Streb provided most of the original sentence material and Dipl.-Psych. K. Jost, Dipl.-Psych. M. Rösner, and Cornelia Schönwald helped to prepare the spoken sentence material.

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