

Syntactic Processing in Left Prefrontal Cortex Is Independent of Lexical Meaning

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In language comprehension a syntactic representation is built up even when the input is semantically uninterpretable. We report data on brain activation during syntactic processing, from an experiment on the detection of grammatical errors in meaningless sentences. The experimental paradigm was such that the syntactic processing was distinguished from other cognitive and linguistic functions. The data reveal that in syntactic error detection an area of the left dorsolateral prefrontal cortex, adjacent to Broca's area, is specifically involved in the syntactic processing aspects, whereas other prefrontal areas subserve general error detection processes. © 2001 Academic Press

INTRODUCTION

Language is normally used to convey information to the listener. Nonetheless, when reading or listening to meaningless sentences such as “All mimsy were the borogoves, . . .” (from “Jabberwocky” by Lewis Carroll) we do not have to know what “borogoves” are to be able to tell that this noun is the subject of the sentence and that the verb “were” correctly agrees with it in number. This capability suggests the existence of a grammatical processing component (a syntactic parser) that operates independent of lexical semantics. Syntactic parsing, but not the comprehension of the meaning of content words, is usually impaired in a neurological disorder called “agrammatic aphasia.” Patients with this condition typically experience difficulties in the comprehension of sentences like reversible passives (“The boy is kissed by the girl.” vs “The boy kisses the girl.”), for which syntactic parsing is indispensable for understanding (Caplan, 1992). Syntax-specific parsing is also suggested by reaction-time data showing that

the syntactic representation built up by the parser facilitates the detection of prespecified words in “syntactic prose” sentences that have grammatical structure but contain random content words (Marslen-Wilson and Tyler, 1980). Electrophysiological data have provided indirect evidence for the existence of neuronal populations involved in syntactic parsing. Grammatical violations in Jabberwocky-type pseudoword sentences and syntactic prose sentences result in event-related potential (ERP) effects that are clearly different from the so-called N400 effect observed for semantic violations (Kutas and Hillyard, 1980; Osterhout and Holcomb, 1992; Hagoort and Brown, 1994; Münte *et al.*, 1997).

While these findings point to the existence of a dedicated neural substrate for syntactic processing, there is to date no clear evidence as to its anatomical location. While agrammatic aphasia does not seem to be linked to one specific lesion site (Caplan *et al.*, 1996), most PET and fMRI studies on syntactic processing have reported activations in the left posterior-inferior frontal cortex, i.e., Broca's area. In order to identify the neural correlates of syntactic parsing, the authors manipulated either the syntactic complexity of sentences (Stromswold *et al.*, 1996; Just *et al.*, 1996; Inui *et al.*, 1998; Stowe *et al.*, 1998; Caplan *et al.*, 1998, 1999, 2000) or the amount of attention directed to the syntactic structure. The latter was in most studies achieved by grammatical error detection tasks (Nichelli *et al.*, 1995; Kang *et al.*, 1999; Embick *et al.*, 2000; Kuperberg *et al.*, 2000; Meyer *et al.*, 2000a; Ni *et al.*, 2000). In a different approach, Dapretto and Bookheimer (1999) used a sentence-matching task in which subjects were required to detect semantically equivalent sentence pairs that differed either syntactically or lexically. With few exceptions (Nichelli *et al.*, 1995; Stowe *et al.*, 1998; Kuperberg *et al.*, 2000; Meyer *et al.*, 2000a), left posterior-inferior frontal lobe activation was found irrespective of the design chosen to create conditions with a higher syntactic load. Although this is strong

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evidence for an involvement of Broca's area in syntactic processing, it is not fully conclusive. All of the above-mentioned studies used meaningful sentences that required the construction of not only a syntactic representation but also a semantic representation. There is, however, electrophysiological evidence showing that with increasing syntactic complexity or in the presence of syntactic errors there is also an increasing demand on semantic integration at the sentence level, manifested in sentence-final N400 effects (Hagoort *et al.*, 1993). The observed increases in regional cerebral blood flow (rCBF), which were obtained with semantically interpretable stimulus material, may therefore at least in part have reflected semantic rather than syntactic processing. This problem arises even if syntactic complexity is kept constant, as in the study of Dapretto and Bookheimer (1999). To decide, for example, whether "East of the city is the lake" and "East of the city is the river" mean the same things, it is sufficient to retrieve the lexical semantic information of the words "lake" and "river." In the case of the sentences "West of the bridge is the airport" and "The bridge is west of the airport," this decision requires not only syntactic parsing, but also the construction of a semantic representation (mental map) based on the syntactic roles.

In order to exclude the contribution of semantic factors, we modified the two most frequent experimental designs, syntactic error detection and complexity variation, by using meaningless pseudoword sentences. Our results provide evidence for posterior-frontal neuronal populations that are sensitive to the grammatical structure of sentences, independent of their meaning.

MATERIALS AND METHODS

Subjects

All participants (five female and five male) were consistent right-handers according to their scores on two handedness tests (Oldfield, 1971; Steingrüber, 1971). Subjects were in the age range of 23 to 38 years, with a mean age of 26.8 years. They were all native speakers of German, in good health, and gave written informed consent in accordance with the declaration of Helsinki. The study was approved by the Ethics Committee of the Heinrich-Heine-University Düsseldorf and by the District Government Cologne.

Experimental Design

The PET experiment involved a cognitive conjunction design (Price and Friston, 1997) with three syntactic and two nonsyntactic conditions (see Fig. 1). In the syntactic conditions, subjects were visually pre-

sented with syntactically complex German sentences containing errors of case and number marking. All content words had been replaced by meaningless, phonotactically legal German pseudowords. In two of the syntactic conditions the task was to utter the sentences in their correct form. These two conditions differed in the degree of syntactic variability of the complex sentences. All stimulus sentences in the less variable correction condition contained embedded subject-relative clauses. In the more variable correction condition half of the sentences contained embedded object-relative clauses. In the example sentences below, grammatical markers are printed in bold and grammatical violations are marked by * for clarification. Parts of speech were indicated by parentheses. The participants were instructed which parts of speech were to remain unchanged when rendering the sentences grammatical.

Stimulus example of less variable syntactic correction condition (SC1):

(**der** Donk) (*der*) (*die Feumern*) (*lomt*)

(***telchen**) (*das Grumel*)

(the^{singular} donk) (who) (lomes) (the feumers)

*(**telch**_{plural}) (the grumel)

Correct response:

"Der Donk, der die Feumern lomt, telcht das Grumel."

"The donk, who lomes the feumers, telches the grumel."

Stimulus example of more variable syntactic correction condition (SC2):

(**der** Donk) (**der**) (*die Feumern*) (*lomen*)

(**telchen**) (*das Grumel*)

(the^{singular} donk) *(who_{nominative}) (the feumers)

(lome) *(**telch**_{plural}) (the grumel)

Correct response:

"Der Donke, **den** die Feumern lomen, telcht das Grumel."

"The donk, whom the feumers lome, telches the grumel."

Object-relative clause sentences were recognizable by number disagreement of the subject of the main clause and the verb of the relative clause. Note that in German, unlike English, there is no word order difference between subject and object relative clauses.

In the third syntactic condition (syntactic judgment, SJ) subjects repeated sentences of the syntactically more variable type without correction and performed an overt grammaticality judgment. In all syntactic tasks, grammatical errors could be detected only by determining the grammatical roles of each of the pseudowords. Therefore, subjects had to assign a grammatical structure by using the available syntactic information provided by pseudoword endings and by articles. Correction required the marking of main verbs and relative pronouns with appropriate grammatical features for overt sentence production. Syntactic judg-

	Syntactic tasks			Non-syntactic tasks	
	SC1	SC2	SJ	PJ	PP
Syntactic processing					
Judgement-related processes					
Error-detection related processes					
Phonetic encoding and articulation					
Input-related processes					

FIG. 1. Hypothesized cognitive components (left column) of the five experimental tasks. All tasks involved input-related processes, such as visual/graphemic processing, lexical search processes, and grapheme-to-phoneme conversion of the written stimuli (brown). All tasks except silent phonotactic judgment (PJ) involved processes related to overt language production (phonetic encoding and articulation, red). All tasks except pseudoword pronunciation (PP) involved processes related to the detection of (syntactic or phonotactic) errors (blue). The syntactic (SJ) and phonotactic (PJ) judgment tasks shared processes related to an explicit yes/no judgment (yellow). Only the syntactic tasks (SC1, SC2, SJ) involved syntactic processing (green). (SC1, correction of syntactically less variable complex sentences; SC2, correction of syntactically more variable complex sentences; SJ, syntactic judgment of syntactically more variable complex sentences; PJ, phonotactic judgment; PP, pseudoword pronunciation.)

ment required decision-related response preparation and execution processes.

In the two nonsyntactic tasks (pseudoword pronunciation and phonotactic judgment) all the stimulus material of the syntactic tasks was reordered to length-matched lines. Each line contained only articles/pronouns, pseudoverbs, or pseudonouns so that no syntactic relations were present. During pseudoword pronunciation the subjects simply read out the lines. This task controlled for input-related language processing below the syntactic level and for processes related to the overt pronunciation of pseudowords.

Stimulus examples of pseudoword pronunciation condition (PP):

- (*Feumern*) (*Grumel*) (*Plutt*) (*Donk*) (*Lintern*)
- (*der*) (*die*) (*das*) (*die*) (*der*) (*das*) (*der*) (*die*) (*der*)
- (*fütten*) (*brasen*) (*wülzt*) (*hürten*) (*lopppt*) (*lätscht*)

During phonotactic judgment, subjects spotted violations of the phonotactic constraints of possible German words caused by substitution of a letter in a pseudoword. In the resulting written nonwords, violations of phonotactic constraints corresponded to violations of orthographic constraints. Therefore, the task could also be performed as an orthographic judgment. The task controlled for possible general error detection processes that were not syntax-specific, as well as for response selection and execution processes involved in explicit judgment tasks.

Stimulus examples of phonotactic judgment condition (PJ):

- (*Feumern*) (*Grumel*) (*Plutt*) *(*Djnk*) (*Lintern*)
- (*der*) (*die*) (*das*) (*die*) (*der*) (*das*) (*der*) *(*dpr*) (*das*)
- (*fütten*) (*brasen*) (*wülzt*) (*hürten*) (*lopppt*) (*lätscht*)

Since the resulting nonwords, such as *Djnk*, were unpronounceable, this task was performed silently.

Using different stimuli, the subjects were trained on all tasks 1 week before PET scanning. During the PET scanning session they underwent five sequential rCBF measurements. The sequence of conditions (pseudoword pronunciation, less variable syntactic correction, more variable syntactic correction, phonotactic judgment, and syntactic judgment) was reversed for half of the subjects.

Experimental Procedures

The stimuli were presented in whole-sentence format in the center of a digital VT340 monitor screen, subtending a visual angle of 20–30°, depending on sentence length. Stimulus presentation began approximately 30 s prior to PET scanning and lasted for 2 min. Differences in task complexity, manifest as faster response times in pilot testing for the relatively easier tasks, were compensated for by varying the stimulus durations (6 s for pseudoword pronunciation and phonotactic judgment, 8 s for syntactic judgment, and 10 s for the syntactic correction tasks) such that continuous task-related processing throughout the PET scanning period was achieved in all tasks. The interstimulus interval was 200 ms in all conditions.

Stimulus presentation onset markers and subject responses were recorded on DAT tape and analyzed for voice onset time, response sentence duration, and errors. Grammaticality and phonotactic judgments were given as go–no go responses by a small movement of the left foot for stimulus items containing no violations. The responses were scored by an observer. During the

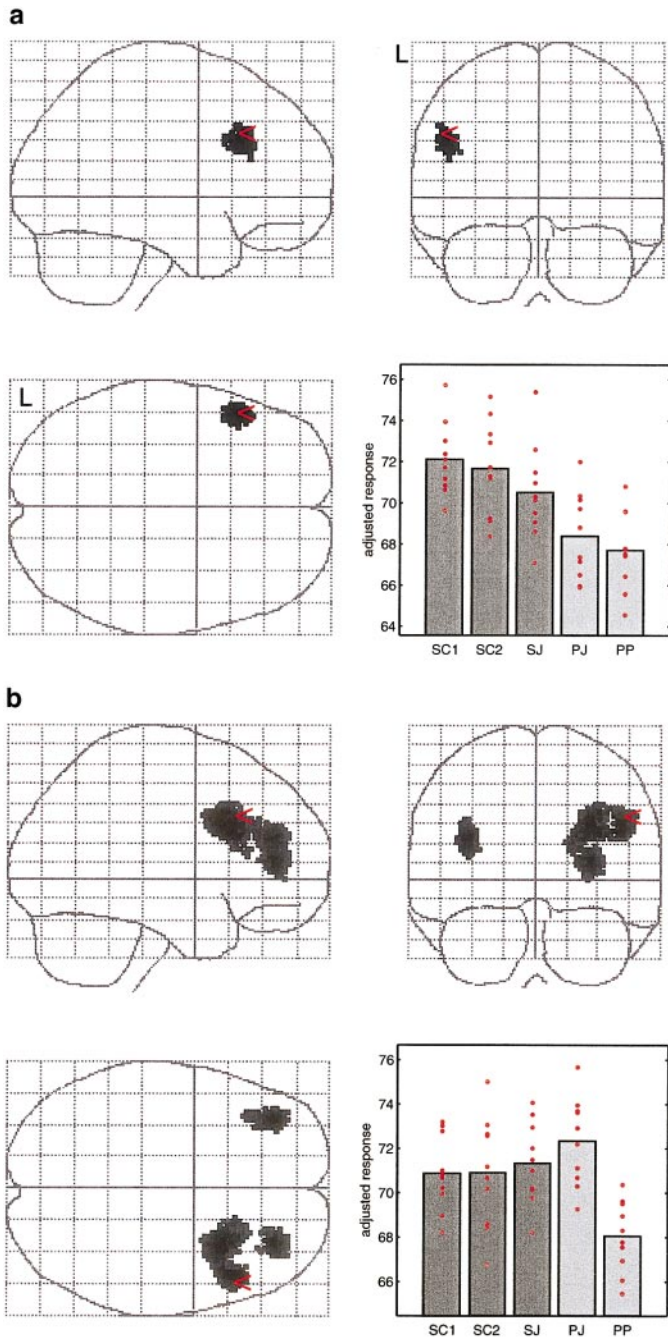


FIG. 2. Statistical parametrical maps of conjunctions masked with the corresponding single contrasts. The plots in the lower right quadrants show the responses (adjusted to a mean global CBF of 50 ml/100 g/min) in all conditions at the locations indicated by arrowheads. (BA, Brodmann area, x, y, z coordinates as given by SPM96). (a) Common activations of the three syntactic tasks vs both control tasks (conjunction SC1-PP and SC2-PP and SJ-PP and SC1-PJ and SC2-PJ and SJ-PJ). The voxel of highest Z score (indicated by an arrowhead) was located in the left middle frontal gyrus ($Z = 4.45$, BA 9, $x, y, z = -50, 24, 34$). (b) Common activations of the three syntactic tasks and the phonotactic judgment task vs pseudoword pronunciation (conjunction SC1-PP and SC2-PP and SJ-PP and PJ-PP). Local maxima were located in the depth of the right inferior frontal sulcus ($Z = 5.24$, BA 44/9, $x, y, z = 28, 16, 30$; $Z = 4.85$, BA 10, $x, y, z = 30, 42, 12$) and in the left middle frontal gyrus ($Z = 4.67$, BA 46,

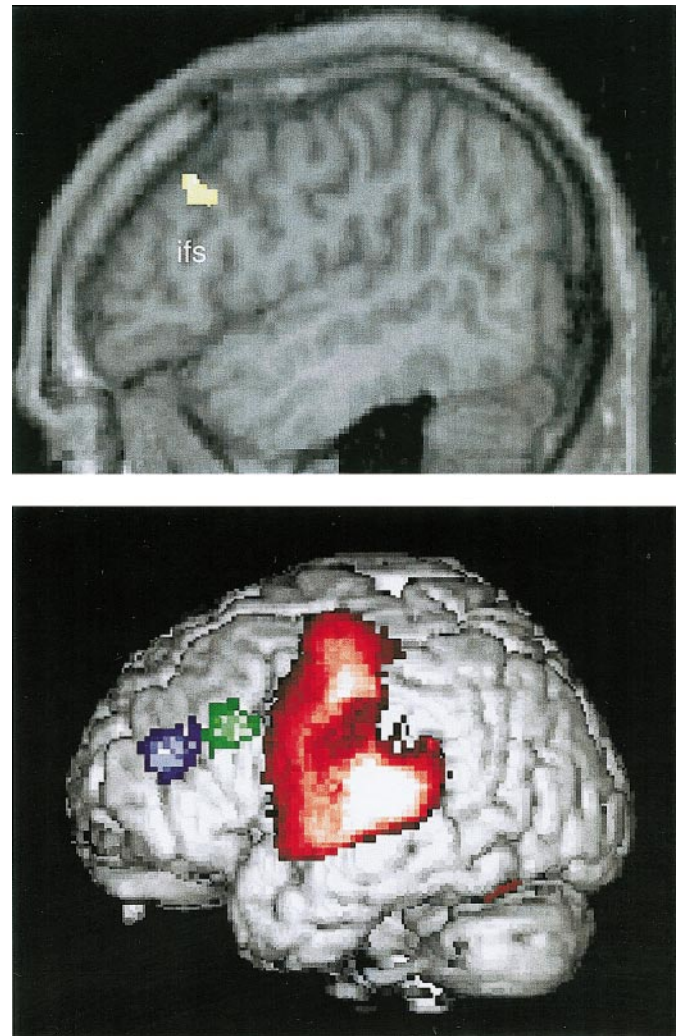


FIG. 3. Top: Color overlay of the syntactic activation focus (see Fig. 2a) on an anatomically standardized (MNI-template, SPM96) sagittal MR section of a typical subject. The greater part of the activation was located dorsally of the inferior frontal sulcus (ifs). Bottom: Relative anatomical location of syntactic activation focus (green) with respect to left-hemispheric activations related to error-detection (blue, see Fig. 2b) and overt language production (conjunction SC1-PJ and SC2-PJ and SJ-PJ and PP-PJ, shown in red). The maximum of the syntactic activation was located at a distance of minimally 2 cm from the maxima of the other activation areas. The left-hemispheric activation areas of the three conjunctions were projected onto a surface rendering of the SPM96 template brain.

sampling period of the PET measurement (40 s) only “no go” items were presented to avoid movement contamination of the PET data.

$x, y, z = -36, 44, 24$). Adjusted responses are plotted against conditions for the right hemispheric homologue ($x, y, z = 50, 24, 34$, indicated by an arrowhead) of the syntactic activation maximum in (a). In contrast to the left-hemispheric responses, the right-hemispheric responses are not syntax-specific.

Data Acquisition

PET data were recorded with a GE/Scanditronix 4096+ scanner. Scanning started at the time of intravenous injection of the tracer into the right brachial vein. Reconstructed activity images comprised a period of 40 s starting with tracer arrival in the brain. For each scan, approximately 40 mCi [^{15}O]butanol was injected as a bolus. The arterial tracer concentration was measured using an intra-arterial cannula in the left brachial artery to enable rCBF quantification. A combined dynamic–autoradiographic approach delivered image volumes of quantitative rCBF (Herzog *et al.*, 1996).

Data Analysis

For data analysis we used the statistical parametric mapping (SPM, version 96) software provided by the Functional Imaging Laboratory, London (Friston *et al.*, 1995). The image volumes were realigned, normalized into standard stereotactic space (using the template of the Montreal Neurological Institute provided by SPM96), smoothed with a 20-mm (full width at half-maximum) Gaussian filter, and corrected for residual within- and between-subject global CBF variation by ANCOVA. Statistical tests were performed on single activation–control contrasts as well as conjunctions of two or more activation–control contrasts. Conjunctions were masked with the set of corresponding single contrasts at $P < 0.05$. We report clusters of activated voxels exceeding a significance threshold of $P < 0.01$ (corrected, uncorrected voxel threshold $P < 0.00005$). These rather conservative thresholds were considered appropriate in the absence of a priori hypotheses about possible locations of rCBF increases observed with a new paradigm.

RESULTS

According to our task analysis (see Fig. 1), the isolation of neuronal populations activated during syntactic processing required the identification of significant activation differences that all syntactic conditions had in common with respect to *both* nonsyntactic conditions. The corresponding conjunction analysis yielded one significant activation focus in the left middle frontal gyrus, BA 9 (dorsolateral prefrontal cortex, see Figs. 2a and 3), dorsally adjacent to BA 45 or Broca's area. There was no significant interaction with gender. Direct comparisons of the syntactically more versus less variable correction conditions as well as syntactic correction versus syntactic judgment conditions yielded no significant differences.

We further analyzed whether the implicit or explicit error detection components present in our tasks would

give rise to rCBF increases that should not be related to the processing of syntax. To this end we searched for common effects of the syntactic tasks and the phonotactic judgment task relative to the pseudoword pronunciation baseline. This conjunction (see Fig. 2b) yielded extensive right prefrontal activations, as well as left anterior-inferior prefrontal activations.

We also conducted reverse comparisons to identify areas of significant rCBF increase in the pseudoword pronunciation baseline relative to the syntactic tasks and the phonotactic judgment task. In all cases there were extensive bilateral foci covering the sensorimotor and superior temporal cortices as well as cerebellar and supplementary motor area (SMA) activation. The same pattern of activations was obtained as the main effect of all tasks with overt spoken responses relative to the silent phonotactic judgment task (see Fig. 3, bottom).

The overall error rate for grammaticality judgments was 22.7%, with 1 of the 10 subjects performing at chance level. The overall error rate for phonotactic judgments was 10.7%, all of the subjects performing above chance level.

Due to technical problems, the voice recordings of four participants could not be analyzed. The remaining six subjects made no syntactic errors in the 72 sentences of the syntactically less variable correction condition (SC1) and 10 (13.9%) syntactic errors in the 72 sentences of the syntactically more variable correction condition (SC2). Considering only correct responses, both voice onset times (SC2 1.64 s; SC1 1.14 s; $t = 5.71$, $df = 22$, $P = 0.000$, two-tailed) and response durations (SC2 5.37 s; SC1 4.96 s; t test with correction for inequality of variances, $t = 2.67$, $df = 17.52$, $P = 0.016$, two-tailed) were significantly longer for items in the more variable correction condition.

DISCUSSION

Activations Related to Overt Speech Production

Comparing all tasks involving overt language production with silent phonotactic judgment, we found bilateral sensorimotor, superior temporal, cerebellar, and SMA activation. This activation pattern corresponds exactly to the results of a recent meta-analysis of 25 overt and 33 silent word production experiments (Indefrey and Levelt, 2000) relating activation of these areas to phonetic encoding, articulation, and self-monitoring processes. The same activation pattern resulted from the comparison of pseudoword pronunciation with the syntactic tasks. Given the higher overt language production rate in pseudoword pronunciation, this result confirms findings reported by Price *et al.* (1996) on the effect of increased rates of oral responses.

Activations Related to Error Detection and Response Processes

The design of the present study was such that brain activations related to general cognitive processes related to error detection could be distinguished from processes related to syntactic processing proper. This was achieved by calculating conjunction analyses involving a nonsyntactic error-detection task, namely phonotactic judgment. Considering this as a control condition with respect to the syntactic tasks, we isolated syntax-specific activations (see below), i.e., common activations of the syntactic tasks that were not shared by nonsyntactic error detection. In addition, the phonotactic judgment task enabled us not merely to control for nonspecific components related to error-detection and judgement processes, but to make their neural correlates visible by looking at cerebral areas responding to the syntactic tasks *and* nonsyntactic error detection. Since not only our syntactic tasks, but also most previous imaging work on syntactic processing (Nichelli *et al.*, 1995; Stromswold *et al.*, 1996; Just *et al.*, 1996; Caplan *et al.*, 1998, 1999, 2000; Kang *et al.*, 1999; Embick *et al.*, 2000; Kuperberg *et al.*, 2000; Meyer *et al.*, 2000a, Ni *et al.*, 2000), comprised syntactic or semantic error detection components, it was of particular interest to isolate neural correlates of these components, in order to determine which of the reported activations were due to task components that were not related to syntactic processing *per se*. We found that all tasks involving error detection activated the prefrontal cortex bilaterally, but more strongly on the right. Although, generally spoken, the nature of our tasks seems compatible with a characterization of the prefrontal cortex as being involved in supervisory attention (Shallice, 1988), the present study was not designed to specify the functional role of these prefrontal activations beyond the conclusion that they are not specifically related to syntactic processing.

Activations Related to Syntactic Processing

The three syntactic conditions, although different in task requirements and degree of syntactic variability, shared an area of significant rCBF increase with respect to the two nonsyntactic conditions, of which one controlled for general error detection processes (phonotactic judgment), the other for processes related to overt articulation (pseudoword pronunciation). The observed activation focus was located at the caudal and ventral end of the extension of Brodmann area 9 in Talairach space. This is a region of considerable variation with respect to cytoarchitectonic areas. The activation maximum fell (caudally) 2 mm outside of the conservative coordinates for BA 9 as reported by Rajkowska and Goldman-Rakic (1995). In terms of coordinates, therefore, Brodmann areas 46, 45, and 44 were possible candidates, too. Projection of the activation

maximum onto individual standardized anatomical MR scans of the 10 participants (see Fig. 3, top, for an example), however, showed the maximum to be dorsal from the inferior frontal sulcus in all cases. Recent data on the intersubject variability of Broca's area (Amunts *et al.*, 1999) show that the dorsal bank of the inferior frontal sulcus may be part of Brodmann area 45 in some cases. However, this does not hold for the free surface of the middle frontal gyrus. It seemed, therefore, more appropriate to describe the area as adjacent to, rather than in, Broca's area. This does not necessarily point to a functional difference with respect to other studies observing syntax-related activations in Broca's area. Note, for example, that our activation focus ($-50, 24, 34$) was closer to that of Caplan *et al.* (1998, $-42, 18, 24$) than activation foci obtained by the same group with comparatively small paradigm variations (Stromswold *et al.*, 1996, $-38, 20, 8$; Caplan *et al.*, 2000, $-46, 36, 4$).

For meaningful stimulus material, higher syntactic complexity has been reported to yield additional activations in Broca's area (Stromswold *et al.*, 1996; Just *et al.*, 1996; Inui *et al.*, 1998; Caplan *et al.*, 1998, 1999, 2000). The behavioral data obtained during the PET measurement were in line with previous reports on greater complexity of sentences with object-relative clauses compared to sentences with subject-relative clauses (e.g., Ford, 1983; Waters *et al.*, 1987; King and Just, 1991; Just and Carpenter, 1993). The absence of significant differences between the two syntactic correction conditions, involving different degrees of syntactic variability, was therefore unexpected. A possible explanation is that as a result of the greater difficulty of pseudoword material there was a ceiling effect, because the relatively easier condition already recruited syntactic processing resources maximally. It remains to be examined whether hemodynamic effects related to degrees of syntactic complexity can be shown for syntactically simpler pseudoword material.

The syntax-related regional cerebral blood flow increases did not significantly interact with sex. This finding is in line with recent large-scale studies on the location of brain lesions in aphasic patients finding no or only very small differences between men and women (Hier *et al.*, 1994; Pedersen *et al.*, 1995). On the other hand, Shaywitz *et al.* (1995) reported fMRI data showing a sex difference for a phonological task. Although it should be kept in mind that the sample size in the present study is smaller than that of Shaywitz *et al.* (1995), our data suggest that possible sex differences in phonological processing do not necessarily hold for other language processes.

There are several alternative interpretations of the observed left posterior frontal activation. First, this activation focus might not be related to syntactic processing, but rather to a difference in task difficulty between the syntactic conditions and the control con-

ditions. This interpretation finds some support in the behavioral data showing that the phonotactic judgment condition had a lower error rate than the syntactic judgment condition, suggesting insufficient control in this respect. As explained in the previous section, however, we identified the neural correlates of the task components related to error detection in general by comparing all tasks involving error detection to the pseudoword pronunciation task, which did not involve error detection at all. The resulting set of areas did not comprise the activation area discussed here, which, therefore, does not seem to be sensitive to general aspects of error detection tasks, including their difficulty.

Second, the overt responses in the syntactic tasks required the planning of sentence-level prosody, which might be considered a potential confound. Although sentence-level prosody is different from the prosody of sequences of single pseudowords, it is not plausible that the processing load should be higher, particularly considering the higher rate of overt responses in the pseudoword pronunciation condition. The same argument can be made with respect to the objection that the observed activation might be due to subjects processing the prosody of their own utterances. Furthermore, the processing of prosody in the acoustic input seems to be related to temporal rather than frontal lobe activations (Meyer *et al.*, 2000b). This latter observation may also explain a discrepancy between our finding and a PET study by Mazoyer *et al.* (1993), who reported temporal rather than frontal activations when subjects listened to auditorily presented pseudoword sentences. In a recent fMRI study, Friederici *et al.* (2000) confirm temporal activations during auditory presentation of pseudoword sentences, but report also activations in a frontal opercular region of interest. Interestingly, frontal activations were not observed when subjects listened to meaningful sentences. The authors suggest that for auditory presentation of sentences frontal areas may be observable only when syntactic processing becomes more difficult (as with pseudoword material). Indeed, two of the four above-mentioned studies that failed to find frontal activations (Kuperberg *et al.*, 2000; Meyer *et al.*, 2000a) used auditory sentence presentation.

Although explanations of the observed activation in terms of nonsyntactic task components, such as task difficulty or prosody, are improbable, this does not imply that within the domain of syntactic processing the functional role of the observed activation focus is exactly clear. One question here concerns the relative contributions of syntactic production and comprehension. The syntactic correction tasks required the production of a syntactically correct sentence while the syntactic judgment task did not. In direct comparisons, one might, therefore, have expected additional activations in the correction conditions due to syntactic en-

coding. Interestingly, there was no significant difference, suggesting one of two alternative explanations. Subjects may have covertly produced a correct version of the stimulus sentences in the syntactic judgment task, but suppressed it in order to just repeat the incorrect version according to the instructions. Consequently, no differences would be observable, since in all syntactic tasks "syntactic processing" was a combination of syntactic parsing and encoding. This explanation finds some support in the observation that a few subjects occasionally produced corrected sentences in the syntactic judgment condition. Alternatively, and more interestingly, syntactic encoding might not have taken place in any of the three conditions. This would mean that the syntactic structure built up during syntactic comprehension was used for the subsequent sentence production. Experiments on syntactic priming (Bock, 1986; Bock and Griffin, 2000) suggest that this is possible. In sum, an interpretation of the observed activation focus as being partly related to syntactic production cannot be excluded, although a relation to syntactic parsing only would be the sparser explanation.

Given that the reported activation area had a close spatial relation to both Broca's area and the dorsolateral prefrontal cortex as known neural substrates of working memory (Paulesu, 1993; Ungerleider, 1995; Goldman-Rakic, 1996), we must finally consider an interpretation in terms of a relatively stronger working memory recruitment during the syntactic conditions. Most importantly, we must distinguish between a recruitment of working memory resources for syntactic processes and a recruitment of working memory resources for the generation and short-term maintenance of verbal material in general. According to Baddeley (Baddeley and Hitch, 1974; Baddeley, 1986, 1992), the system engaged in the latter processes comprises a controlling instance, the central executive, and a slave system, the phonological loop. The phonological loop consists of a phonological store and a subvocal rehearsal system. Given that there is evidence for an involvement of Broca's area in subvocal rehearsal (Paulesu *et al.*, 1993; Fiez *et al.*, 1996; Smith *et al.*, 1996), a possible contribution of this process to our reported activation cannot be excluded on anatomical grounds with certainty. Subvocal rehearsal, furthermore, may be used in off-line sentence judgment tasks (Caplan *et al.*, 2000), such as the syntactic judgment task. In our experiment, however, this task involved reading out the written stimulus, which is equivalent to massive concurrent articulation, a condition that is known to block subvocal rehearsal (Baddeley, 1986). It seems, therefore, highly unlikely that subvocal rehearsal might have been reflected in the posterior frontal activation we report.

The central executive has been associated with the dorsolateral prefrontal cortex (Shallice, 1988). Activa-

tion of this area has been reported for tasks that are considered to recruit central executive functions, such as the production of self-generated sequences of digits or words (Petrides *et al.*, 1993) or the letter *n*-back task, in which the content of working memory has to be continually updated (Cohen *et al.*, 1997; Nystrom *et al.*, 2000). The requirements of such tasks bear some resemblance to those of our sentence correction and judgment tasks. The corrected sentences were in part self-generated, and subjects may have used a strategy of storing an increasing number of words for later retrieval as they proceeded through the sentence. What makes it nonetheless unlikely that such nonsyntactic working memory processes resulted in the observed activation is its strict left-lateralization. In a review of various working memory tasks activating the dorsolateral prefrontal cortex, Fiez *et al.* (1996) found right-sided or at least bilateral activations in all studies, including the study of Petrides *et al.* (1993). Cohen *et al.* (1997) and Nystrom *et al.* (2000) also report right-sided activations of the dorsolateral prefrontal cortex for the letter *n*-back task.

Although we believe that a contribution of nonsyntactic working memory to the observed dorsal prefrontal activation can be rejected for good reasons, this does not mean that there is no working memory involvement in the processing of syntax. On-line syntactic processing during both comprehension and production of sentences clearly requires the short-term maintenance of syntactically relevant information such as number or gender features until this information is used in later parts of the sentence. Listeners or readers easily detect violations of subject-verb agreement, even if subject and verb are separated by many intervening words. Speakers (at least in most cases) inflect the main verb correctly, even if they have produced intervening subordinate clauses. Moreover, the working memory load can be predicted for different syntactic structures and thus be used as a criterion defining syntactic complexity (Lewis, 1996; Gibson, 1998). There are, however, conflicting views on the exact nature of the working memory resources engaged in the processing of syntactic information. On the one hand, they are seen as general working memory resources which can also be used for syntactic information (Just and Carpenter, 1992), on the other hand they are conceived of as a subsystem that is dedicated to syntactic processing (Caplan and Waters, 1999). In our view, the observed activation focus may very well be due to the short-term storage of syntactic features or structural information built up during the parsing process. In this case the strict left-lateralization of the observed activation and the absence of activation in parietal regions known to be involved in general verbal storage (Paulesu *et al.*, 1993, Becker *et al.*, 1999) may rather support the assumption of a dedicated working memory component. Alternatively, our results are also com-

patible with a role of the reported dorsal prefrontal area in syntax-related computations rather than storage.

In conclusion, the observed pattern of responses has at least two implications. The first is a methodological one. It has become clear that both implicit and explicit error detection or judgment components in syntactic tasks lead to right and anterior left prefrontal activations that are not syntax-specific. Reports about these areas being related to syntactic processing (Nichelli *et al.*, 1995; Just *et al.*, 1996; Meyer *et al.*, 2000a) must, therefore, be interpreted with caution if a judgment task is involved. Second, our results on pseudoword material clarify the role of the left posterior prefrontal cortex in sentence-level processing, by showing that it is indeed syntax-related processing rather than a syntactically mediated semantic integration of word meanings that activates this cortical region.

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