Cerebral Cortex December 2006;16:1709-1717
doi:10.1093/cercor/bhj106
Advance Access publication January 4, 2006

Processing Linguistic Complexity and Grammaticality in the Left Frontal Cortex

Angela D. Friederici[1], Christian J. Fiebach[1,2], Matthias Schlesewsky[3], Ina D. Bornkessel[1] and D. Yves von Cramon[1]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, [2]Department of Psychology and Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA and [3]Research Group Neurolinguistics, Phillips-University Marburg, Marburg, Germany

We used event-related functional magnetic resonance imaging to directly compare the hemodynamic responses associated with varying degrees of linguistic complexity with those engendered by the processing of ungrammatical utterances. We demonstrate a dissociation within the left inferior frontal cortex between the deep frontal operculum, which responds to syntactic violations, and a core region of Broca's area, that is, the inferior portion of the left pars opercularis in Brodmann area 44, the activation of which is modulated as a function of the complexity of well-formed sentences. The data demonstrate that different brain regions in the prefrontal cortex support distinct mechanisms in the mapping from a linguistic form onto meaning, thereby separating ungrammaticality from linguistic complexity.

Keywords: Broca's area, fMRI, left frontal operculum, linguistic complexity, pars opercularis, syntax, ungrammaticality

Introduction

Successful language-based communication involves establishing real-time associations between sentences and their intended meaning (or vice versa). Sentence comprehension therefore presupposes the online implementation of a set of rules governing the mapping from form to meaning. In particular, one of the core aspects of sentence processing lies in reconstructing the relation between participants and events in a given sentence, that is, typically, the relation between arguments and verbs. However, this reconstruction of a sentence's underlying interpretation is not always straightforward, in particular in those cases where the correspondence between the form of a sentence and its meaning cannot be mapped directly. This is the case when the object linearly precedes the subject in the surface form, despite the fact that it is lower ranking in conceptual terms.

Empirical evidence accumulated over the past decades indicates that processing costs increase in sentences involving the permutation of event participants (arguments) in the sense described above, that is, typically, structures with an object-before-subject order. Sentences of this type are often referred to as "complex" because they require additional operations in order for their meaning to be reconstructed or as "noncanonical" because they require a nonstandard mapping from their actual form (word order) to meaning. Functional neuroimaging studies (e.g., Just and others 1996; Stromswold and others 1996; Caplan and others 1998, 1999; Röder and others 2002; Ben-Shachar and others 2004; Bornkessel and others 2005) have shown that differences in the complexity of sentences lead to a modulation of activation in one of the classical language areas of the brain, namely, Broca's region, suggesting that this region plays a crucial role in the mediation of the form-to-meaning mapping at the sentence level.

Increased complexity in the mapping from form to meaning has been modeled in a number of ways in the theoretical linguistic literature. Most commonly, it is assumed that a movement (transformation) operation derives the more complex (permuted or noncanonical) form from the base form (nonpermuted or canonical) (e.g., Haider and Rosengren 2003), thereby providing a direct link between the surface sentence form and the underlying interpretation. Note, however, that even in grammatical theories that do not assume transformations (e.g., Pollard and Sag 1994; Van Valin and LaPolla 1997; Bresnan 2001), these types of sentences are more complex because they require the application of some type of additional rule-based operation in order for a correct interpretation to be possible. However, rather than localizing the extra cost of this mapping in the syntax, these types of theories attribute it to other domains of the grammar, most often to the linking mechanisms mediating between syntax and semantics. From the latter perspective, object-initial sentences need not involve a higher degree of syntactic complexity, but rather a noncanonical assignment of thematic roles (i.e., the "Undergoer" of the event being described precedes the "Actor"). Indeed, we have argued previously that thematic information plays a crucial role in engendering increased activation of Broca's area during the processing of both noncanonical and canonical sentences (Bornkessel and others 2005). Thus, complexity-based neural responses likely result from the combination of a variety of factors (syntactic, thematic, and possibly semantic complexity). Hence, we use "linguistic complexity" as a cover term for these multiple influences throughout this paper, thereby avoiding stronger classifications that cannot be undertaken on the basis of the present manipulation.

Although there is widespread agreement that Broca's area crucially engages in the processing of sentences in which the form-to-meaning mapping is not straightforward, functional characterizations of the mechanisms involved in this process differ considerably. In essence, approaches to the function of Broca's area may be divided into 2 broad classes: those which attribute increased activation in this region to working memory (e.g., Caplan and others 2000; Kaan and Swaab 2002; Fiebach and others 2005) and those which associate this activation with language-inherent functions (e.g., Embick and others 2000; Grodzinsky 2000; Friederici 2002; Ben-Shachar and others 2003, 2004; Bornkessel and others 2005). Whereas working memory–based accounts assume that it is costly to maintain an initial object in memory until it can be integrated and interpreted, "language-internal" approaches attribute the higher activation of Broca's area to the need for more complex linguistic operations (e.g., transformations) in the comprehension of permuted sentences.

As working memory cost and linguistic complexity are often inherently confounded (e.g., in manipulations involving object-relative clauses in English: Just and others 1996; Stromswold and others 1996; Caplan and others 1998, 1999), dissociating between the competing approaches has proved difficult. However, more recent results indicate a possible involvement of both factors in accounting for activation patterns in Broca's area. When linguistic complexity and working memory demands were varied independently, both factors contributed to an increase of activation in the left inferior frontal gyrus (IFG) (Cooke and others 2001) or the factor of working memory was even dominant (Fiebach and others 2005). By contrast, other studies indicate that the increased activation of Broca's area engendered by at least certain types of argument permutations cannot be accounted for in terms of working memory (Bornkessel and others 2005; Grewe and others 2005).

However, all these previous studies are subject to the potential confound that the complex sentences examined were always in some sense more "difficult" than the control sentences. Thus, we cannot rule out that the neural response in Broca's area simply reflects the greater degree of difficulty associated with the mapping of a sentential form onto a conceptual representation, rather than of the particular types of linguistic operations in service to resolve the dependency relations between constituents.

In view of these considerations, the present study aimed to shed further light on the relationship between difficulty and linguistic complexity in the processing of permuted sentences. To this end, we manipulated the degree of language-internal complexity and compared this type of linguistic complexity with another type of difficult form-to-meaning mapping, namely, ungrammatical sentences. These manipulations were implemented by means of an experimental design (Table 1) that has already been subjected to extensive behavioral examination (Pechmann and others 1994, 1996; Röder and others 2000).

Example A in Table 1 illustrates the nonpermuted, that is, canonical, word order in German, in which the subject (S) precedes the indirect object (IO), which in turn precedes the direct object (DO). In example B, by contrast, the indirect object has been "scrambled" to a position preceding the subject, thus yielding a permuted (though grammatically licensed) word order. As is apparent from example C, in which both objects precede the subject, scrambling can apply iteratively, thus allowing for a parametric variation of complexity in grammatical sentences. In contrast to sentences A–C, example D is ungrammatical because the participle "geschenkt" (given) cannot intervene between the arguments and should rather be positioned clause finally. Previous behavioral studies showed that the acceptability of the 3 grammatical sentence types in Table 1 indeed decreases as a function of the number of argument permutations (Pechmann and others 1994, 1996; Röder and others 2000). Interestingly, the acceptability of the most complex condition (C) was reduced so dramatically that it did not differ significantly from that of the ungrammatical condition (D). This lack of an acceptability difference between conditions C and D is striking in view of the clear theoretical difference between them: whereas C is complex, but grammatically permissible (e.g., Lenerz 1977), D is not derivable on account of the constraints of the German grammar. Thus, these behavioral findings raise the question of whether the theoretically postulated difference between C and D is associated with distinct neural activation patterns for "grammatical" and "ungrammatical" structures, or whether there is no evidence for such a clear cutoff between the different structures.

In a recent functional magnetic resonance imaging (fMRI) study, Röder and others (2002) used a manipulation that was, in principle, identical to that of Pechmann and others (1994, 1996), but these authors only analyzed 2 levels of complexity, namely, "easy" (0 or 1 permutation) and "difficult" (2 permutations), and reported left inferior frontal activation for the contrast between the two. These results therefore provide an important foundation for the present study, although here we aim to analyze 3 levels of linguistic complexity. The experimental conditions of the current study displayed in Table 1 provide a manipulation of the difficulty of the form-to-meaning mapping in 2 dimensions. On the one hand, the 3 grammatical conditions are associated with a parametric increase of linguistic complexity, which can be motivated both theoretically (i.e., in terms of the number of permutations) and empirically (i.e., in terms of the acceptability pattern discussed above). On the other hand, the direct comparison between complex grammatical and ungrammatical structures allows us to examine whether increased difficulty in the form-to-meaning mapping differs between structures that are derivable by the grammar of the language being processed and those that are not. If this were the case, we would have reason to distinguish between higher difficulty due to the application of language-internal operations (e.g., the application of rules to reconstruct the basic word order) and higher difficulty due to the inability to apply language-internal operations.

Neuroanatomically, previous findings suggest that word order permutations in the grammatical structures indeed engender increased activation in Broca's area, specifically in the pars opercularis (Brodmann area [BA] 44) (Bornkessel and others 2005) or more generally in the left inferior frontal region (Röder and others 2002). With respect to more precise neuroanatomical predictions, it should be kept in mind that Broca's area in the IFG is traditionally thought to comprise BAs 44 and 45. These 2 subregions can be differentiated both on cyto- and receptor-architectonic grounds (Amunts and others 1999; Zilles and others 2004). Insofar, it is not surprising that a functional differentiation between BA 44 and the more anterior BA 45 has been proposed, in which syntactic processes in BA 44 are separated from more lexically based processes in BA 45 (Bookheimer 2002). Although this functional differentiation is likely, not all studies on processing syntactic complexity report

Table 1
Example sentences

Condition	Example sentence
A Canonical (S-IO-DO-V) (0 permuted objects)	Heute hat der Opa dem Jungen den Lutscher geschenkt. Today has the grandfather (nominative) the boy (dative) the lollipop (accusative) given (as a present)[a]
B Medium complexity (IO-S-DO-V) (1 permuted object)	Heute hat dem Jungen der Opa den Lutscher geschenkt. Today has the boy the grandfather the lollipop given[a]
C High complexity (IO-DO-SO-V) (2 permuted objects)	Heute hat dem Jungen den Lutscher der Opa geschenkt. Today has the boy the lollipop the grandfather given[a]
D Ungrammatical (S-V-IO-DO)	Heute hat der Opa *geschenkt dem Jungen den Lutscher. Today has the grandfather given the boy the lollipop[a]

Note: S, subject noun phrase; IO, indirect object argument; DO, direct object.
[a]Word-by-word translation. In a literal translation, sentences A, B, and C all translate into "Today the grandfather has given the lollipop to the boy."

inferior frontal patterns restricted to BA 44 (Caplan and others 1999; Röder and others 2002; Ben-Shachar and others 2003). As most of the relevant studies, however, report activation that includes BA 44, we shall therefore focus on BA 44 and its possible role in the processing of complex sentences.

With respect to the distinction between grammatical and ungrammatical sentences, it has recently been proposed that linguistic complexity and ungrammaticality are subserved by different brain areas, with the former recruiting Broca's area proper and the latter relying on the ventral premotor cortex, that is, the ventral part of BA 6, and the adjacent frontal operculum (Friederici 2004a). This region is located posteriorly to BA 44 and is cytoarchitectonically separable from it (Brodmann 1909; Sanides 1962). This proposal was based on the observation that studies using violation paradigms (i.e., a comparison between ungrammatical and grammatical sentences) to investigate syntactic processing have often failed to observe activation in BA 44 (e.g., Kuperberg and others 2000; Friederici and others 2003), thus supporting the perspective that BA 44 may be functionally related to language-internal processes involved in the reconstruction of a nondirect mapping between linear order and interpretation. However, in the studies in question, the ungrammaticality manipulation was at the level of local constituent structuring rather than touching upon the relative ordering between constituents at the sentence level. Thus, possible differences between these findings and those for permuted argument orders might result from differences with respect to the type of linguistic representation under examination rather than from a distinction between grammatical and ungrammatical structures per se. The present study circumvents this problem by employing a manipulation of grammaticality stemming from the same domain as the complexity manipulation, namely, constituent order.

Our hypotheses are as follows. First, if the activation of BA 44 observed for complex sentences is attributable to the application of additional linguistic operations (e.g., in terms of a reconstruction of word order rules), we expect to observe a parametric modulation of the activation of this region (i.e., condition C > B > A; see Table 1). Second, if BA 44 responds differently to complex grammatical as opposed to ungrammatical sentences, this result would support the idea that this brain area engages selectively in language-internal operations in the interpretation of a complex sentence. Third, in accordance with Friederici (2004a), we predict that ungrammatical sentences should engender increased activation in the ventral premotor cortex and/or the frontal operculum.

Materials and Methods

Participants

A total of 13 healthy, native German-speaking adults (6 males; mean age 23.1 years) participated in the fMRI study. All had normal or corrected-to-normal vision and were consistently right handed (mean laterality quotient 96.7%; Oldfield 1971). For the behavioral prestudy, 24 different individuals (10 males; mean age 24.3 years) were selected from the same pool of subjects.

Materials

Participants read ditransitive German sentences of the form in Table 1. For the examination of activation changes associated with linguistic complexity, a parametric approach was adopted by studying sentences with 0, 1, or 2 scrambled object noun phrases (see Fig. 1 and Table 1). The 3 grammatical conditions (A–C in Table 1) were compared with ungrammatical sentences of the form in D.

Behavioral Prestudy

In order to ensure that the present sentence materials would indeed be suited to replicating the behavioral findings reported in previous studies (i.e., a reduction of acceptability as a function of the number of scrambled arguments and no acceptability difference between the most complex grammatical and the ungrammatical conditions), we conducted a behavioral prestudy. Here, 15 sentences of each of the 4 critical conditions were randomly interspersed with 165 distractor sentences and presented using rapid serial visual presentation (see Kieras and Just 1984). This presentation mode was chosen to avoid reading strategies and/or uncontrollable saccadic eye movements, as the identical presentation procedure was to be used during the fMRI study. Each word or phrase was presented for 400 ms with an interstimulus interval of 100 ms (analogous to the procedure of the fMRI study, but 100 ms faster). Stimuli were ordered in a random sequence. The participants task was to rate the acceptability of the sentences as quickly as possible using a 6-button response box. Participants were explicitly instructed not to base their judgments on the plausibility of the sentences' content, but rather to evaluate whether the sentence form constituted an acceptable way of expressing this content in German. Acceptability ratings and response times were analyzed by aggregating responses by subject and condition and then submitting these values to a repeated measures analysis of variance. The 165 distractor items consisted of 15 items for each of 11 other word orders (i.e., IO_{pron}-S-DO, DO_{pron}-S-IO,

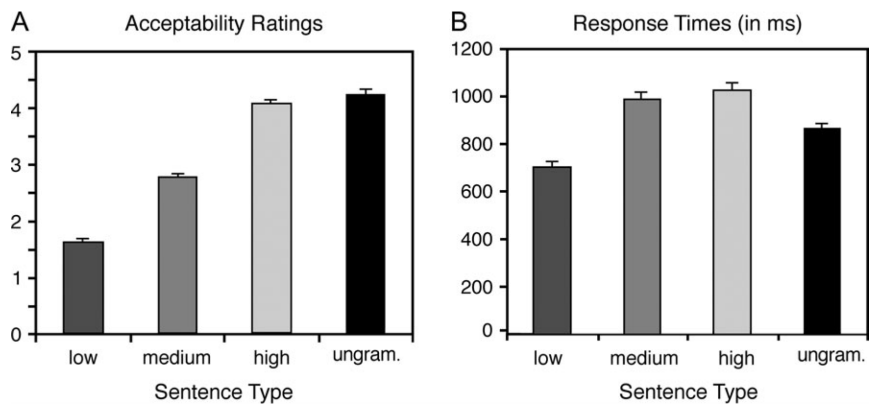

Figure 1. Results of the behavioral prestudy for the different sentence types. Condition low complexity refers to the sentences with 0 permutations, medium complexity to sentences with 1 permutation, and high complexity to sentences with 2 permutations. Ungram refers to ungrammatical sentences. (*A*) Speeded acceptability ratings ranging from 1 (perfectly acceptable) to 6 (totally unacceptable) reflect the unacceptability of complex and ungrammatical sentences. Displayed are mean ratings from 24 participants; error bars represent the standard error of the mean. (*B*) Mean response times for the speeded acceptability ratings, together with the standard error of the mean.

S_{pron}-IO-DO, DO_{pron}-IO-S, IO_{pron}-DO-S, S-DO_{pron}-IO, S-IO_{pron}-DO, IO_{pron}-S-DO_{pron}, DO-IO_{pron}-S, IO-S-DO_{pron}, *S_{pron}-V-DO-IO; "pron" indicates the use of a pronoun instead of a full noun phrase and "*" indicates ungrammatical sentences).

Behavioral Prestudy Results

The speeded acceptability ratings for the 4 critical sentence types (cf., Fig. 1) indicated a gradual decrease of acceptability with increasing complexity in the grammatically correct sentences ($F_{2,46}$ = 56.4, $P < 0.0001$; all pairwise contrasts: $t(24) > 5$, $P < 0.0001$). Response times also became longer with increasing complexity ($F_{2,46}$ = 19.3, $P < 0.0001$; 0 vs. 1 permuted object: $t(24) = 4.77$, $P < 0.0001$; 0 vs. 2: $t(24) = 5.36$, $P < 0.0001$; 1 vs. 2: $t(24) = 0.83$). Ungrammatical sentences showed a low acceptability, but this was equal to that of complex correct sentences ($t(24) = 0.63$). However, judgments were given faster for ungrammatical sentences than for grammatical sentences with 1 permuted object ($t(24) = -1.98$, $P = 0.059$) or grammatical sentences with 2 permuted objects ($t(24) = -3.92$, $P < 0.001$).

These data clearly indicate that the complexity variation was effective in the present sentence materials. The finding that acceptability decreases with an increasing number of scrambled arguments replicates earlier findings (Pechmann and others 1994, 1996; Röder and others 2000). The finding that the ungrammatical sentences were equally acceptable as the most complex sentences is also in agreement with previous results (Pechmann and others 1994, 1996). Thus, the relative acceptability differences observed between the critical conditions in this study are virtually identical to those reported previously. Importantly, the comparable acceptability between the most complex grammatical condition and the ungrammatical condition allows us to interpret possible differences between these 2 sentence types as reflecting differences in the processing of grammaticality rather than acceptability.

In addition to serving as a control for the efficacy of the experimental manipulation, the data from this behavioral experiment were used as an independent predictor of processing difficulty for the parametric analysis of the effect of increasing structural complexity on hemodynamic responses.

fMRI Study: Procedure

The experimental procedure for the fMRI session was analogous to that used in the behavioral study. Each word or phrase was presented for 500 ms with an interstimulus interval of 100 ms (cf., Fig. 2). A total of 40 critical sentences were presented for each condition (henceforth: "nontask trials") as well as another 8 items per condition for which participants had to perform a behavioral task, that is, answer a comprehension question, within 2 s. The comprehension questions (e.g., "Hat der Opa dem Jungen den Lutscher geschenkt?"/"Did the grandfather give the lollipop to the boy?") were constructed such that the participants had to pay attention to the relations between participants (thematic role assignments), as well as to the identity of every content word in the sentence. Comprehension of thematic role assignments was tested by creating incorrect items in which the grammatical functions of the arguments were exchanged between subject and indirect object. In addition, there were also incorrect questions in which either the verb or 1 of the 3 noun phrases was replaced by a different word of the same syntactic category. This was done to ensure that participants paid attention to the full length of the sentence's critical region. Half of the comprehension questions were correct and half incorrect with respect to the preceding critical sentence. Note that comprehension questions could also be used with ungrammatical sentences as the meaning of these sentences (i.e., the relations between the arguments and the verb) was extractable based on the case marking of the noun phrases (cf., Frisch and Schlesewsky 2001; Bornkessel and others 2002, 2003; Schlesewsky and Bornkessel 2004). Participants could answer the comprehension questions for ungrammatical sentences and did not report problems in doing so when questioned after the experiment. Finally, 40 null trials were included in the stimulus sequence (Burock and others 1998; Friston and others 1999).

The different trial types were presented in a pseudorandomly ordered sequence (with the constraint that transition frequencies between the different conditions were equated). Trials in which participants answered a comprehension question (presented 100 ms after the offset of the last word of the critical sentence) were randomly interspersed among the critical trials. Thus, participants could not predict whether or not they would actually have to perform the task until after reading a sentence. This procedure was chosen in order to ensure 1) that participants correctly processed sentences and 2) that the hemodynamic responses of the critical trials of interest, that is, the responses to nontask trials, exclusively reflected neural activity related to sentence processing, without being confounded by activity related to motor or decision components of the task. Based on experiences with earlier studies on sentence processing, we reasoned that answering the sentence comprehension question is likely to be cognitively more demanding than the highly overlearned task of processing a sentence. Given the systematic temporal coupling of the critical point in the sentences and the performance of the task (separated by less than 4 s), activation in response to the event of interest, which is embedded in the sentence, might be systematically confounded with the supposedly greater hemodynamic response during task performance (Zarahn and others 1997). The approach chosen here introduces a behavioral task that makes sure participants attend to the stimuli while at the same time allows one to analyze the hemodynamic responses elicited during sentence processing independent from those elicited during question answering. Nevertheless, it cannot be excluded that brain activation may be influenced by a specific task set as participants might have prepared for performing the task.

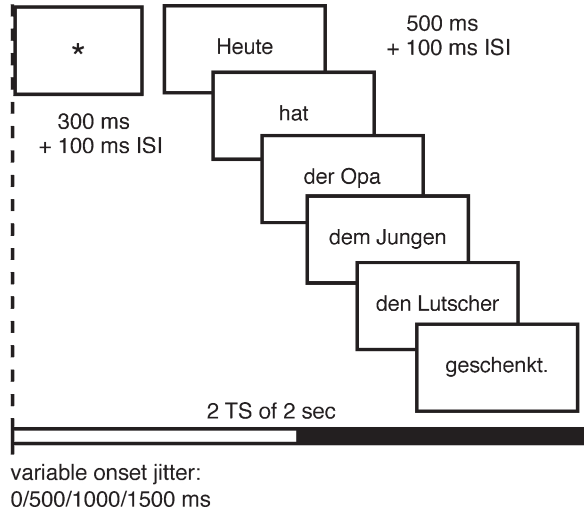

Figure 2. During the fMRI experiment, participants read sentences presented visually in 6 frames shown for 500 ms each (interstimulus interval 100 ms). Frames contained either a single word or a noun phrase (see fMRI Study: Procedure).

fMRI Data Acquisition and Analysis

Functional images were acquired from 20 axial slices (4 mm thickness, 1 mm skip) using a blood oxygen level dependent (BOLD) sensitive gradient echo planar imaging (EPI) sequence (echo time 30 ms, acquisition bandwidth 100 kHz, field of view 192 mm, in-plane resolution 3 × 3 mm) with a 3-T Bruker Medspec 30/100 scanner. One volume was acquired every 2 s (repetition time 2 s). Sentence onsets were jittered between 0, 500, 1000, and 1500 ms relative to the onset of the first acquired image of a trial. The mean stimulus onset asynchrony was 8 s (4 images). T_1-weighted modified driven equilibrium Fourier transform (MDEFT) structural images and anatomical EPI images were obtained for coregistration with previously acquired whole-head 3-dimensional MDEFT brain scans (Ugurbil and others 1993).

All analyses were carried out with the LIPSIA software package (Lohmann and others 2001). Preprocessing involved movement correction, slice-time correction, baseline correction, and a spatial smoothing using a Gaussian kernel of 5.6 mm full width half maximum (FWHM). After coregistration into stereotactic space (Talairach and Tournoux 1988), statistical analyses were performed using the identical statistical routines as implemented in the software package SPM99. Statistical modeling consisted of a random-effects model (treating subjects as random effects) in an event-related design. Design matrices were generated using a synthetic hemodynamic response function (Josephs and others 1997; Friston and others 1998). The model equation was convolved with a Gaussian kernel of dispersion of 4 s FWHM. A temporal high-pass filter with automatically determined cutoff frequencies was applied during parameter estimation.

The effects of interest in the present study were examined by modeling each sentence condition with an individual onset vector in order to be able to calculate contrasts between the 4 sentence conditions. In order to reduce noise in the estimate of the baseline, trials in which participants performed a task were modeled as nuisance covariate, but not considered further in the statistical analyses. For the analysis of linguistic complexity, empirically determined acceptability ratings for the 3 correct sentence conditions, obtained from the prestudy were used as predictors in a parametric model. These measures were used because 1) they stem from an independent sample of subjects, 2) they are consistent with previously reported data from behavioral studies, 3) they represent the fact that the increase between the 3 grammatically legal conditions is not linear (as it would be assumed if analyzing this complexity effect with, e.g., the predictor values 0, 1, and 2, representing the number of scrambled objects in the sentences), and 4) these performance data are a more reliable estimate than those acquired during the fMRI session, as they are based on more observations per participant and more participants. In this analysis, trials with ungrammatical sentences were modeled separately as a covariate of no interest. The ungrammaticality effect was assessed by directly contrasting ungrammatical with canonical grammatical sentences as well as with the most complex grammatical sentences, that is, those involving 2 permutations. To perform group statistics, individual contrast images were then submitted to a 1-sample *t*-test, testing at each voxel whether contrast values reliably differed from zero. Statistical parametric maps were thresholded at $P < 0.001$ (uncorrected at the voxel level). To protect against false-positive results, only clusters of a size of 14 voxels or more ($P < 0.05$ corrected for multiple comparisons; Worsley and others 1996; Kiebel and others 2000) are reported. Ungrammaticality effects were in addition evaluated at a reduced threshold of $P < 0.01$ in the a priori defined regions of interest, that is, in the ventral premotor region.

Time courses of the hemodynamic responses were extracted for all suprathreshold voxels in activated clusters from the preprocessed raw data sets, corrected by subtracting the response evoked by the null trials, and then averaged by condition and subject. For purposes of display, these aggregated time courses were averaged across subjects. Time course data were statistically analyzed in a time window between 9 and 11.5 s after onset. This time window was chosen as it encompasses the peaks from both regions of primary interest reported and therefore is best suited for a direct statistical comparison of the 2 brain regions. Statistical analyses were conducted using multiple paired *t*-tests and using an adjusted statistical threshold of $P < 0.05$, as determined using a modified Bonferroni correction described by Keppel (1991). This correction yielded a significance threshold of $P < 0.025$ for 6 statistical comparisons, the greatest number of comparisons made (medium vs. simple, complex vs. medium, complex vs. simple, ungrammatical vs. simple, ungrammatical vs. medium, and ungrammatical vs. complex). The *t*-tests were conducted as 1-sided tests to test our prediction of increased activations for complexity and ungrammaticality, relative to simple sentences. Where appropriate, 2-sided *t*-tests were used and indicated in the text.

Results

All trials were entered into the statistical analysis of the fMRI data. No participants had to be excluded as all participants performed above chance. The mean accuracy rates for the comprehension task were: low complexity (81% correct, SE = 3.9); medium complexity (75%, 5.4); high complexity (71%, 5.5); ungrammatical (79%, 4.9). Mean response times were: low complexity (1700 ms, 44.7); medium complexity (1758 ms, 72.3); high complexity (1778 ms, 53.3), ungrammatical (1665.9 ms, 47.8). The behavioral data thus showed a pattern that was consistent with the assumed effect of the sentence manipulations on processing difficulty, even though the effects were not significant due to the low number of comprehension trials during the scanning session. Moreover, the trend was consistent with the results from the behavioral prestudy.

fMRI Data

Linguistic Complexity

The effect of complexity on hemodynamic responses was investigated using a parametric approach. Empirically determined mean acceptability ratings for each of the 3 grammatically correct sentence types (Fig. 1) were entered into the general linear model as a parametric predictor for hemodynamic responses elicited during the processing of well-formed sentences. This analysis should therefore serve to identify brain areas that display stronger activity for linguistically more complex, and therefore less acceptable, sentences. A significant positive relation between increased difficulty/reduced acceptability due to the increased number of permutations in the sentences (i.e., 0, 1, or 2) and the measured hemodynamic responses was observed in 2 brain regions (Fig. 3). First, parametric complexity effects are seen in Broca's area proper, more specifically on the free surface of the inferior–posterior portion of the pars opercularis of the IFG (BA 44), anterior to the ventrolateral premotor cortex, and extending into the frontal operculum (49 voxels; $x = -49$, $y = 10$, $z = 4$; $t(12) = 16.41$; $Z = 6.06$; P corrected = 0.001). This area will henceforth be referred to as left BA 44i (inferior portion of BA 44). Examination of trial-averaged hemodynamic response time courses reflects the systematic sensitivity of the left BA 44i to the structural complexity of the sentences (Fig. 3). Paired *t*-tests on the peak of the hemodynamic response, conducted using a time window of 9–11.5 s after trial onset, show that activity elicited by medium-complexity sentences is significantly greater than that elicited by low-complexity sentences (1-sided paired *t*-test, $t(12) = 2.4$, $P = 0.017$) and activity for high-complexity sentences is greater than that for medium-complexity sentences ($t(12) = 3.02$, $P = 0.005$). In addition, differences in BA 44i grammatical and ungrammatical sentences were analyzed. Ungrammatical sentences show BA 44i activation that is comparable with the medium-complexity condition (2-sided *t*-test; $t(12) = 0.3$, $P = 0.79$), but weaker than the most complex correct sentence condition ($t(12) = 2.3$, $P = 0.019$). Thus, BA 44i activation appears to systematically increase as a function of linguistic complexity with most complex/most difficult grammatical sentence leading to highest activation, whereas the ungrammatical sentence, for which form-to-meaning mapping is equally difficult, does not show an equally large activation in BA 44i. This suggests that BA 44i activation varies as a function of linguistic complexity rather than difficulty.

Second, a mapwise parametric complexity effect, with a weaker peak activation strength, was observed also in the anteriormost portion of the presupplementary motor area (preSMA; 19 voxels; $x = 7$, $y = 22$, $z = 44$; $t(12) = 5.77$; $Z = 0.92$; P uncorrected < 0.001). Trial-averaged BOLD responses, however, reveal that this result is in fact due to equally increased activation for the medium- and high-complexity conditions, relative to the low-complexity condition (Fig. 3). Furthermore, the ungrammatical condition clusters with the 2

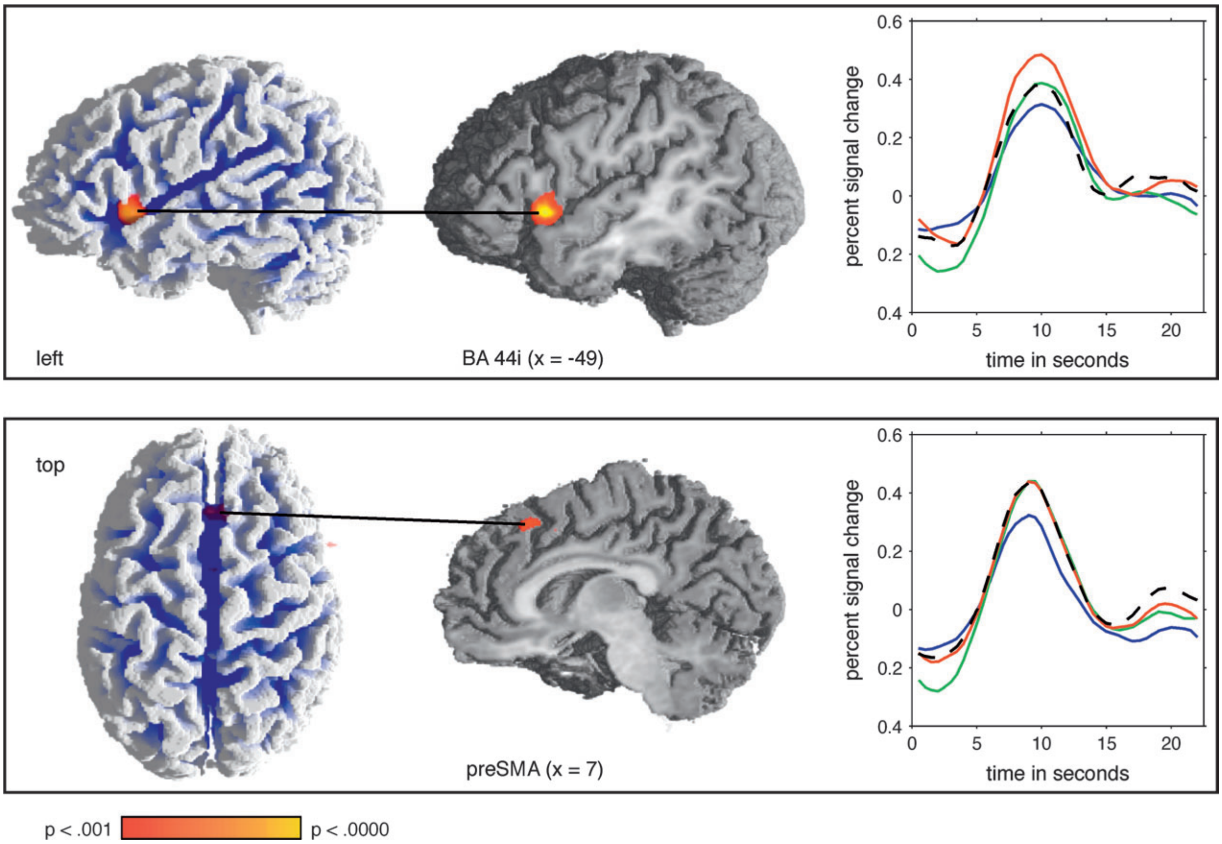

Figure 3. Linguistic complexity effect. Brain regions sensitive to linguistic complexity, as identified in the parametric analysis of the 3 grammatical sentence conditions (low complexity, blue; medium complexity, green; high complexity, red). As a comparison, activation timelines for ungrammatical sentences are presented as well (broken black line). (Left) Lateral and top views of a white matter–segmented brain from which the cortical gray matter layer was removed for display of functional data. (Middle) Activated areas displayed in parasagittal sections. (Right) Trial-averaged hemodynamic responses of the 3 correct sentence conditions, corrected for activity elicited during the null trials. BA 44i, inferior pars opercularis of the left IFG; preSMA, presupplementary motor area. *P* uncorrected < 0.001.

more complex correct sentence conditions in the preSMA. This is supported by the statistical analysis of the specified time window using paired *t*-tests. Medium- and high-complexity sentences as well as ungrammatical sentences elicited greater activity in the preSMA than low-complexity sentences (all $t(12) > 3.6$, all $P < 0.002$). In addition, there were no significant differences in activation strength between medium-complexity, high-complexity, and ungrammatical sentences (all $t(12) < 0.25$).

Grammaticality

Applying the same statistical threshold as that for the analysis of the complexity effect, no brain area in the left inferior frontal region showed greater activation for ungrammatical as compared with simple correct sentences (cf., Table 2 for a list of activated regions). In order to evaluate the hypotheses that syntactic complexity and ungrammaticality should activate distinct inferoposterior frontal subregions, we explored brain activation responses to ungrammatical sentences in the left ventral premotor region and in the left inferior frontal cortex more generally at a reduced statistical threshold $P < 0.01$. Using this hypothesis-driven approach, we observed increased activity in a deep posterior portion of the left frontal operculum (pFO) which was located about 2 cm posterior to BA 44i (Fig. 4; 24 voxels; $x = -46$, $y = -7$, $z = 17$; $t(12) = 4.2$; $Z = 3.23$; *P* uncorrected < 0.001). The analysis of hemodynamic response time courses (Fig. 4) indicates that in pFO indeed the greatest

Table 2
Brain regions modulated by grammaticality at $P < 0.001$

Region	BA	t_{max} (Z_{max})	*P* cluster (corrected)	Location *x*	*y*	*z*
Incorrect > correct sentences						
Left postcentral gyrus	1/2	5.03 (3.62)	0.017	−43	−23	52
Right intraparietal sulcus	40	4.56 (3.41)	0.049	46	−43	52
Right intraparietal sulcus	7/40	5.29 (3.73)	<0.001	34	−65	44
Left cerebellum		5.85 (3.95)	0.002	−31	−70	−17

Note: The *t*- and *Z*-values are reported for voxels of greatest activity within activated clusters. Locations of these voxels are given in Talairach and Tournoux (1988) coordinates.

activation is elicited by the ungrammatical sentence condition. The time course analysis supports the observed difference between ungrammatical and simple grammatical sentences ($t(12) = 3.47$, $P < 0.0025$). Medium- and high-complexity sentences do not differ from each other ($t(12) = 0.23$, $P > 0.8$, 2-sided *t*-test) and are therefore averaged for the purposes of the present analysis. These noncanonical sentences elicited significantly stronger pFO activity than simple sentences ($t(12) = 2.3$, $P = 0.02$) and significantly less pFO activity than ungrammatical sentences ($t(12) = 3.23$, $P < 0.004$). Ungrammatical sentences elicited significantly stronger activation in pFO than all grammatically correct sentence conditions (all $t(12) > 2.7$, $P < 0.01$).

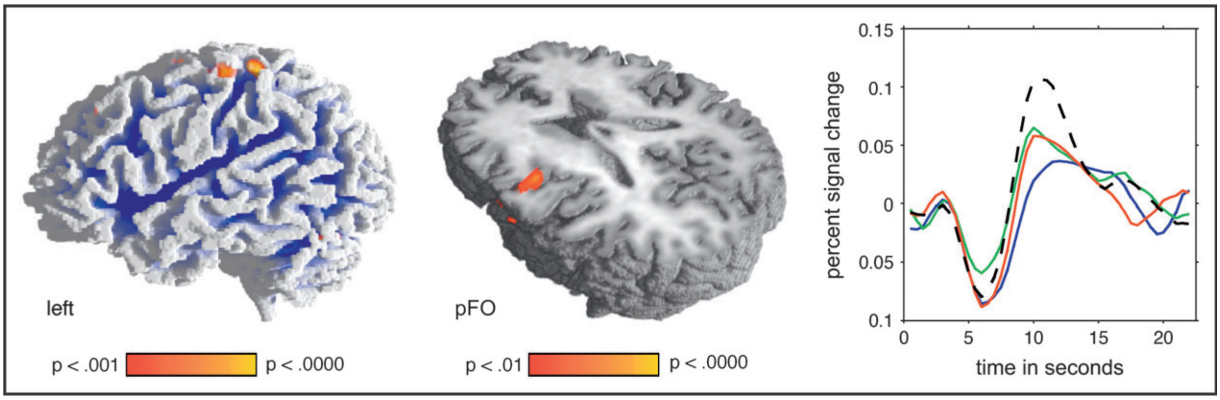

Figure 4. Ungrammaticality effect. Brain regions exhibiting greater activity for grammatically illegal than for canonical sentences. (Left) Rendering of activation onto a white matter segmentation of a template brain; *P* uncorrected < 0.01. (Right) Trial-averaged hemodynamic responses of the ungrammatical condition (black broken line) relative to the 3 correct sentence conditions (blue, green, and red); pFO, left deep posterior frontal operculum.

The time course analyses demonstrate that pFO is not only modulated by ungrammatical sentences but also activated by medium- and high-complexity sentence conditions, as compared with the canonical sentences; similarly, BA 44i is not only activated by complex sentences but also, to a lesser degree, by ungrammatical sentences. To ensure that the differential inferior frontal activations seen for complexity and ungrammaticality in these areas were indeed specific to argument permutations versus violation processing, a region (BA 44i vs. pFO) by experimental condition (complexity vs. grammaticality) interaction was examined. This analysis was performed by conducting a 2-sided paired *t*-test on the region-specific difference scores between the high-complexity condition and the ungrammatical sentence condition. This analysis resulted in a significant region-by-condition interaction ($t(12) = 3.02$, $P = 0.01$), indicating that BA 44i was indeed selectively more active for complexity than for ungrammaticality, whereas pFO was more active for ungrammaticality than for complexity.

Discussion

The present fMRI study provides the first direct demonstration of a functional–neuroanatomical distinction between brain areas involved in the processing of ungrammaticality and brain areas engaging in the comprehension of sentences that are well formed but differ in linguistic complexity. Both the complexity and the grammaticality manipulation were realized within the domain of word order variations in German. Whereas a core region of Broca's area—the inferior portion of the pars opercularis (BA 44i)—shows a parametrical sensitivity to a sentence's structural complexity, the pFO shows increased activity for syntactically incorrect sentences. The dissociation between the 2 inferior frontal areas observed with respect to syntactic processing in the present study is of particular importance, as these results suggest a more fine-grained functional dissociation between BA 44i and the pFO within the boundaries of the broad region of the IFG usually involved in motor aphasia (e.g., Mohr and others 1978).

The activation observed in the left BA 44i area for linguistically complex sentences is consistent with other studies investigating the brain bases of syntactic complexity (e.g., Just and others 1996; Stromswold and others 1996; Caplan and others 1998, 1999; Röder and others 2002; Ben-Shachar and others 2003, 2004), although the center of activation differs somewhat from study to study and is sometimes located more anteriorly than the one observed in the present experiment. The study that can be compared most directly with the present one is that by Röder and others (2002), which used very similar German sentence structures. However, as discussed in the Introduction, these authors only reported a comparison between "easy" (subject first) and "difficult" (object first) sentences without further separating the number of permutations involved for each sentence. For this comparison, which was conducted across participants, they reported activations for different regions of interest, with the inferior frontal regions comprising both BA 44 and BA 45 (with the center of activation at the coordinates $x = -41$, $y = 10$, $z = 20$). The center of the activation observed in the present study ($x = -46$, $y = 8$, $z = 0$) is clearly located in BA 44 and differs from that reported by Röder and others (2001), which, in contrast, includes parts of BA 45. (The study of Röder and others [2002] further differs from the present experiment in that it additionally contrasted "normal" sentences containing both syntactic and semantic information with sentences consisting of pseudowords [i.e., sentences devoid of semantic content but retaining relevant morphosyntactic information]. The inferior frontal region of interest examined by these authors showed an interaction of syntactic and semantic information, thus raising the possibility that the maximum of the activation may have been shifted somewhat by this enhanced focus on semantic information in comparison with the present study. Further converging support for an explanation along these lines stems from the results reported by Bornkessel and others [2005], who combined a manipulation of syntactic complexity with one of the verb class, thereby also incorporating a critical semantically based factor. The maximal activation observed in this study was located at –43, 14, 18, and thereby much more comparable with that reported by Röder and others [2002] in terms of *y* and *z* coordinates.)

Crucially, the present results extend previous findings by demonstrating that the activation of the left BA 44i is modulated parametrically as a function of the number of permutation operations that need to be reconstructed. As such, this activation appears to reflect those language-internal operations that must be applied in complex, grammatical sentences in order to reconstruct the underlying hierarchical dependencies between arguments. This finding is in good agreement with recent fMRI studies on the processing of argument hierarchies in German

(Bornkessel and others 2005; Grewe and others 2005), which also found increased BA 44 activation when demands on the mapping from the sentence form onto hierarchical interpretative dependencies increased. Note that the modulation of BA 44i activation observed in the present study cannot be taken to reflect a frequency effect as the least frequent sentence condition is the ungrammatical condition, which does not show a strong response in this brain area.

In contrast to examinations of complexity, neuroimaging studies of syntactic violations have hitherto failed to reveal a consistent neuroanatomical correlate of the processing of syntactic anomalies (e.g., Embick and others 2000; Kuperberg and others 2000, 2003; Meyer and others 2000; Indefrey and others 2001; Moro and others 2001; Newman and others 2001; Friederici and others 2003; for a recent review, see Friederici 2004b). Only 2 of these studies described an involvement of Broca's area. These, however, compared syntactic violations to sentences with other violation types rather than ungrammatical with grammatical sentences. Moro and others (2001) reported activation in the medial portion of the left IFG (BA 45) and the anterior insula, as well as in the right BA 44/45, for syntactic violations as compared with phonotactic violations, and Embick and others (2000) reported an activation increase in Broca's area (BA 44/45) for grammatical errors as compared with spelling errors. By contrast, a recent study that compared ungrammatical with grammatical sentences reported activation in the pFO, which was very similar in its localization to the activation observed in the present study (Friederici and others 2003). Given the fact that, in this study, ungrammaticality was realized as a word category violation, it can be concluded that pFO involvement is not specific to the kind of violation used in the present study, but may rather reflect more general operations involved in the processing of ungrammatical sentences.

With respect to the mechanism involved in the processing of the ungrammatical sentences, the present pFO activation could reflect the detection of an unexpected element in the incoming sequence given the grammar in use. This would hold for the ungrammatical sentences in particular, but, moreover, it could explain the observed increase of activation in the medium- and high-complexity sentence condition.

It is of interest to note that the 2 functionally distinct fronto-opercular regions of the left hemisphere, which were identified in the present study, were not activated in isolation but within distinct networks for ungrammatical and linguistically complex sentences. Whereas the processing of complex sentences only activated the preSMA in addition to the left BA 44i, fronto-opercular activity for ungrammatical sentences covaried with activation in the left postcentral gyrus, the left cerebellum, and the right intraparietal sulcus. The latter finding is consistent with some of the previous neuroimaging studies examining syntactically anomalous sentences (Embick and others 2000; Kuperberg and others 2003), suggesting that regions of the parietal lobe play a role in the detection or resolution of structural problems during sentence processing.

Finally, the observation that different neural networks engage in the processing of complex and ungrammatical sentences appears most striking in view of the fact that it also implicates distinct neural bases for the most complex grammatical condition as compared with the ungrammatical condition in the present experiment. Recall that, in terms of their acceptability, these 2 sentence types are indistinguishable, thus raising the question of whether linguistic well formedness should be considered a graded, rather than a categorical property. The fMRI data clearly differentiate between the 2 sentence conditions in question, thereby showing that the surface acceptability pattern must be attributed to different underlying neural sources and, hence, to different cognitive processes. Whereas the ungrammatical sentences are unacceptable because there is no language-internal rule to derive them, the unacceptability of the complex sentences stems from the very high degree of difficulty involved in reconstructing the basic word order.

Conclusion

The present study contrasted the brain activation effects associated with sentence grammaticality with activations due to parametric variations in linguistic complexity. The results indicate that 2 distinct subregions of the posterior portion of the left inferior frontal lobe selectively respond to those two aspects of language comprehension. Hemodynamic responses in a core region of Broca's area, that is, BA 44i, were modulated by increasing linguistic complexity but not by the presence of a syntactic anomaly, whereas the more posterior deep frontal operculum selectively engaged in the processing of sentences with an ungrammatical word order. These data demonstrate that brain activation effects in the inferior portion of BA 44 are indeed specific to the processing of linguistic hierarchies.

Notes

The authors wish to thank Ricarda Schubotz and Markus Ullsperger for the intensive discussion of the present data. This research was supported by grants FI848/1 awarded to CJF and ADF and FOR 309/3-1 by the German Research Foundation.

Address correspondence to Angela D. Friederici, Max Planck Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, Stephanstrasse 1a, 04103 Leipzig, Germany. Email: angelafr@cbs.mpg.de.

References

Amunts K, Schleicher A, Burgel U, Mohlberg H, Uylings HB, Zilles K. 1999. Broca's region revisited: cytoarchitecture and intersubject variability. J Comp Neurol 20:319–341.

Ben-Shachar M, Hendler T, Kahn I, Ben-Bashat D, Grodzinsky Y. 2003. The neural reality of syntactic transformations: evidence from functional magnetic resonance imaging. Psychol Sci 14:433–440.

Ben-Shachar M, Palti D, Grodzinsky Y. 2004. Neural correlates of syntactic movement: converging evidence from two fMRI experiments. Neuroimage 21:1320–1336.

Bookheimer S. 2002. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. Annu Rev Neurosci 25:151–188.

Bornkessel I, Schlesewsky M, Friederici AD. 2002. Beyond syntax: language-related positivities reflect the revision of hierarchies. Neuroreport 13:361–364.

Bornkessel I, Schlesewsky M, Friederici AD. 2003. Eliciting thematic reanalysis effects: the role of syntax-independent information during parsing. Lang Cognit Process 18:269–298.

Bornkessel I, Zysset S, Friederici AD, von Cramon DY, Schlesewsky M. 2005. Who did what to whom? The neural basis of argument hierarchies during language comprehension. Neuroimage 26:221–233.

Bresnan J. 2001. Lexical-functional syntax. Oxford: Blackwell.

Brodmann K. 1909. Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Leipzig: J. A. Barth.

Burock MA, Buckner RL, Woldorff MG, Rosen BR, Dale AM. 1998. Randomized event-related experimental designs allow for extremely

rapid presentation rates using functional MRI. Neuroreport 9:3735–3739.
Caplan D, Alpert N, Waters G. 1998. Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. J Cogn Neurosci 10:541–552.
Caplan D, Alpert N, Waters G. 1999. PET studies of syntactic processing with auditory sentence presentation. Neuroimage 9: 343–351.
Caplan D, Alpert N, Waters G, Olivieri A. 2000. Activation of Broca's area by syntactic processing under conditions of concurrent articulation. Hum Brain Mapp 9:65–71.
Cooke A, Zurif EB, DeVita C, Alsop D, Koenig P, Detre J, Gee J, Pinango M, Balogh J, Grossman M. 2001. Neural basis for sentence comprehension: grammatical and short-term memory components. Hum Brain Mapp 15:80–94.
Embick D, Marantz A, Miyashita Y, O'Neil W, Sakai KL. 2000. A syntactic specialization for Broca's area. Proc Natl Acad Sci USA 97: 6150–6154.
Fiebach CJ, Schlesewsky M, Lohmann G, von Cramon DY, Friederici AD. 2005. Revisiting the role of Broca's area in sentence processing: syntactic integration vs. syntactic working memory. Hum Brain Mapp 24:79–91.
Fiebach CJ, Vos SH, Friederici AD. 2004. Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers. J Cogn Neurosci 16:1562–1575.
Friederici AD. 2002. Towards a neural basis of auditory sentence processing. Trends Cogn Sci 6:78–84.
Friederici AD. 2004a. Processing local transitions versus long-distance syntactic hierarchies. Trends Cogn Sci 8:245–247.
Friederici AD. 2004b. The neural basis of syntactic processes. In: Gazzaniga MS, editor. The cognitive neurosciences. 3rd ed. Cambridge, MA: MIT Press. p 289–302.
Friederici AD, Rüschemeyer S-A, Hahne A, Fiebach CJ. 2003. Localization of syntactic and semantic processing networks: an event-related fMRI study. Cereb Cortex 13:170–177.
Frisch S, Schlesewsky M. 2001. The N400 reflects problems of thematic hierarchizing. Neuroreport 12:3391–3394.
Friston KJ, Fletcher P, Josephs O, Holmes A, Rugg MD, Turner R. 1998. Event-related fMRI: characterizing differential responses. Neuroimage 7:30–40.
Friston KJ, Zarahn E, Josephs O, Henson RNA, Dale AM. 1999. Stochastic designs in event-related fMRI. Neuroimage 10:607–615.
Grewe T, Bornkessel I, Zysset S, Wiese R, von Cramon DY, Schlesewsky M. 2005. The emergence of the unmarked: a new perspective on the language-specific function of Broca's area. Hum Brain Mapp 26:178–190.
Grodzinsky Y. 2000. The neurology of syntax: language use without Broca's area. Behav Brain Sci 23:1–71.
Haider H, Rosengren I. 2003. Scrambling: nontriggered chain formation in OV languages. J Germanic Linguist 15:203–267.
Indefrey P, Hagoort P, Herzog H, Seitz RJ, Brown CM. 2001. Syntactic processing in left prefrontal cortex is independent of lexical meaning. Neuroimage 14:546–555.
Josephs O, Turner R, Friston K. 1997. Event-related fMRI. Hum Brain Mapp 5:243–248.
Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR. 1996. Brain activation modulated by sentence comprehension. Science 274:114–116.
Kaan E, Swaab TY. 2002. The brain circuitry of syntactic comprehension. Trends Cogn Sci 6:350–356.
Keppel G. 1991. Design and analysis. 3rd ed. Englewood Cliffs (NJ): Prentice Hall.
Kiebel SJ, Poline JB, Friston KJ, Holmes AP, Worsley KJ. 2000. Robust smoothness estimation in statistical parametric maps using standardized residuals from the general linear model. Neuroimage 10:756–766.
Kieras DE, Just MA. 1984. New methods in reading comprehension research. Hillsdale, MI: Lawrence Erlbaum Associates.
Kuperberg GR, Holcomb PJ, Sitnikova T, Greve D, Dale AM, Caplan D. 2003. Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. J Cogn Neurosci 15:272–293.
Kuperberg GR, McGuire PK, Bullmore ET, Brammer MJ, Tabe-Hesketh S, Wright IC, Lythgoe DJ, Williams SCR, David AS. 2000. Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study. J Cogn Neurosci 12:321–341.
Lenerz J, editor. 1977. Zur Abfolge nominaler Satzglieder im Deutschen. Tübingen: Narr
Lohmann G, Mueller K, Bosch V, Mentzel H, Hessler S, Chen L, Zysset S, von Cramon DY. 2001. Lipsia—a new software system for the evaluation of functional magnetic resonance images of the human brain. Comput Med Imaging Graph 25:449–457.
Meyer M, Friederici AD, von Cramon DY. 2000. Neurocognition of auditory sentence comprehension: event-related fMRI reveals sensitivity to syntactic violations and task demands. Cogn Brain Res 9:19–33.
Mohr JP, Pessin M, Finkelstein S, Funkenstein H, Duncan G, Davis K. 1978. Broca aphasia: pathological and clinical. Neurology 28: 311–324.
Moro A, Tettamanti M, Perani D, Donati C, Cappa SF, Fazio F. 2001. Syntax and the brain: disentangling grammar by selective anomalies. Neuroimage 13:110–118.
Newman AJ, Pancheva R, Ozawa K, Neville HJ, Ullman MT. 2001. An event-related fMRI study of syntactic and semantic violations. J Psycholinguist Res 30:339–363.
Oldfield RC. 1971. The assessment and analysis of handedness. The Edinburgh inventory. Neuropsychologia 9:97–113.
Pechmann T, Uszkoreit H, Engelkamp J, Zerbst D. 1994. Word order in the German middle field: linguistic theory and psycholinguistic evidence. Computational Linguistics, University of Saarland, Report No. 43.
Pechmann T, Uszkoreit H, Engelkamp H, Zerbst D. 1996. Wortstellung im Deutschen Mittelfeld: Linguistische Theorie und psycholinguistische Evidenz. In: Habel C, Kanngießer S, Rickheit G, editors. Perspektiven der kognitiven Linguistik. Wiesbaden: Westdeutscher Verlag. p 257–299.
Pollard C, Sag I. 1994. Head-driven phrase structure grammar. Chicago: University of Chicago Press.
Röder B, Rosler F, Neville HJ. 2001. Auditory memory in congenitally blind adults: a behavioral-electrophysiological investigation. Cogn Brain Res 11:289–303.
Röder B, Schicke T, Stock O, Heberer G, Rösler F. 2000. Word order effects in German sentences and German pseudo-word sentences. Sprache Kognit 19:3–12.
Röder B, Stock O, Neville H, Bien S, Rösler F. 2002. Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: a functional magnetic resonance imaging study. Neuroimage 15:1003–1014.
Sanides F. 1962. Die Architektonik des menschlichen Stirnhirns. In: Müller M, Spatz H, Vogel P, editors. Monographien der Gesamtgebieten der Neurologie und Psychiatrie. Berlin: Springer.
Schlesewsky M, Bornkessel I. 2004. On incremental interpretation: degrees of meaning accessed during sentence comprehension. Lingua 114:1213–1234.
Stromswold K, Caplan D, Alpert N, Rauch S. 1996. Localization of syntactic comprehension by positron emission tomography. Brain Lang 52:452–473.
Talairach J, Tournoux P. 1988. Co-planar stereotaxic atlas of the human brain. Stuttgart: Thieme.
Ugurbil K, Garwood M, Ellermann J, Hendrich K, Hinke R, Hu X, Kim SG, Menon R, Merkle H, Ogawa S, Salmi R. 1993. Imaging at high magnetic fields: initial experiences at 4 T. Magn Reson Q 9:259–277.
Van Valin RD Jr, LaPolla RJ. 1997. Syntax: structure, meaning and function. Cambridge: Cambridge University Press.
Worsley KJ, Marrett S, Neelin P, Vadal AC, Friston KJ, Evans AC. 1996. A unified statistical approach for determining significant signals in images of cerebral activation. Hum Brain Mapp 4:58–73.
Zarahn E, Aguirre G, D'Esposito M. 1997. A trial-based experimental design for fMRI. Neuroimage 6:122–138.
Zilles K, Palomero-Gallagher N, Schleicher A. 2004. Transmitter receptors and functional anatomy of the cerebral cortex. J Anat 205: 417–432.