The Role of Left Inferior Frontal and Superior Temporal Cortex in Sentence Comprehension: Localizing Syntactic and Semantic Processes

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An event-related functional magnetic resonance imaging (fMRI) paradigm was used to specify those brain areas supporting the processing of sentence-level semantic and syntactic information. Hemodynamic responses were recorded while participants listened to correct, semantically incorrect and syntactically incorrect sentences. Both anomalous conditions recruited larger portions of the superior temporal region than correct sentences. Processing of semantic violations relied primarily on the mid-portion of the superior temporal region bilaterally and the insular cortex bilaterally, whereas processing of syntactic violations specifically involved the anterior portion of the left superior temporal gyrus, the left posterior frontal operculum adjacent to Broca's area and the putamen in the left basal ganglia. A comparison of the two anomalous conditions revealed higher levels of activation for the syntactic over the semantic condition in the left basal ganglia and for the semantic over the syntactic condition in the mid-portion of the superior temporal gyrus, bilaterally. These data indicate that both semantic and syntactic processes are supported by a temporo-frontal network with distinct areas specialized for semantic and syntactic processes.

Introduction

A central question in modeling the mind–brain relationship is whether and to what extent different aspects of language processing can be separated. Linguistic theory holds that the language system is characterized by an internal modularity (Chomsky, 1965, 1986). A major delineation can be made between a rule-based grammatical system, i.e. syntactic knowledge, on the one hand and the mental lexicon containing lexical-semantic and lexically bound syntactic knowledge, i.e. word category and verb argument structure information, on the other (Pinker, 1994, 1999; Ullman, 2001). The two functionally distinct subsystems – syntactic knowledge and lexical knowledge – have been postulated to rely on distinct brain systems. A vast number of lesion studies indicated left anterior brain regions to be involved in syntactic processes and left temporal regions to support lexical-semantics (Caplan, 1992; Goodglass, 1993; Grodzinsky, 2000). A more recent view holds that the syntactic rule system is supported by a procedural memory circuit located in frontal cortex and the basal ganglia, whereas the lexicon is taken to be represented in a temporo-parietal circuit (Ullman *et al.*, 1997; Ullman, 2001). This latter neurotopographic description, however, is based solely on results from experiments comparing the processing of regular (rule-based) inflected verbs to irregular inflected verbs (represented in the lexicon) and it is open as to whether it holds for sentence-level syntactic and semantic processes as well.

A distinction between semantic processing and rule-based syntactic processing during sentence comprehension has also been reported in a number of studies using neurophysiological methods, such as event-related brain potentials (ERPs) and event-related magnetic fields. Semantic processes are reflected in a centro-parietal negativity around 400 ms (N400). This component of the ERP has been shown to vary as a function of lexical status (word versus non-word), lexical-semantic information (selectional restriction), thematic information (verb argument information), as well as pragmatic information (Kutas and Van Petten, 1994; Kutas and Federmeier, 2000). Syntactic processes have been correlated with an early and a late ERP component, namely a left anterior negativity (E/LAN) present between 150 and 400 ms (Neville *et al.*, 1991; Friederici *et al.*, 1993; Hahne and Friederici, 2002) and a late centro-parietal positivity (P600) present around 600 ms (Hagoort *et al.*, 1993; Osterhout *et al.*, 1994; Friederici, 2002). The two syntax-related ERP components have been attributed to two functionally different stages of syntax processing, i.e. an initial, automatized structure-building process and late, controlled processes of syntactic reanalysis and repair (Friederici *et al.*, 1996; Hahne and Friederici, 1999).

Attempts have been made to localize the neural generators underlying these different ERP components. It has been proposed that the N400 arises from a number of functionally and spatially distinct generators (Nobre and McCarthy, 1994, 1995). This suggestion is mainly based on data from intra-cranial depth recordings of ERPs during word reading. These data specify medial temporal structures close to the hippocampus as a possible location of the N400 generator. Data from intra-cranial recordings from less deep structures, however, suggest that cortical areas along the superior temporal sulcus are involved in the generation of the N400 (Halgren *et al.*, 1994). There have also been attempts to localize the sources of the N400 by means of magnetoencephalography or MEG (Papanicolaou *et al.*, 1998). Simos and collaborators (Simos *et al.*, 1997), measuring neuromagnetic signals over the left side of the scalp, identified the neural generator of the N400 in the left temporal lobe. Helenius and colleagues (Helenius *et al.*, 1998) used whole-head MEG recordings to identify the generators of the N400 and found structures in the immediate vicinity of the left auditory cortex bilaterally to be implicated in semantic aspects of sentence comprehension. Also using MEG, the neural generators of the early syntax-related ERP component (ELAN) were found to be localized in inferior frontal and anterior temporal cortices bilaterally with, however, a clear dominance in the left hemisphere (Friederici *et al.*, 2000b). The question remains as to which brain areas are responsible for the processes reflected in the P600, as attempts to localize P600-generators have so far failed to yield reliable source models. Additional information concerning the cerebral representation of on-line syntactic processing can be won from studies investigating language processing in neurological patients. Patients with circumscribed left anterior cortical lesions, who have difficulties in processing syntactic structures, do not show the early left anterior negativity seen in healthy adults (Friederici *et al.*, 1999). Patients with impaired basal ganglia function (i.e. patients suffering from

Cerebral Cortex Feb 2003;13:170–177; 1047–3211/03/$4.00

subcortical lesions or degeneration caused by Parkinson's disease), on the other hand, do show an early negativity but only a reduced, if any, P600 (Friederici *et al.*, 1999; Friederici *et al.*, 2003). These latter results suggest that basal ganglia structures, in particular the caudate nucleus, the putamen and the globus pallidus, play an important role in the controlled syntactic processes underlying the P600.

Most recent studies using advanced brain imaging techniques to specify the functional significance of different brain areas for syntactic and lexical-semantic processes during sentence comprehension suggest that sentence processing is supported by a fronto-temporal network, with semantic and syntactic aspects specifically employing the following subregions. Semantic processes are assumed to be dependent upon posterior temporal areas (Caplan *et al.*, 1998; Kuperberg *et al.*, 2000; Ni *et al.*, 2000) as well as Brodmann's area (BA) 45/47 in the inferior frontal gyrus (IFG) (Dapretto and Bookheimer, 1999). Syntactic processing has been shown to activate frontal as well as temporal areas. With respect to the frontal cortex, a few studies (Ni *et al.*, 2000; Newman *et al.*, 2001) have reported an involvement of the superior frontal gyrus, while the majority (Just *et al.*, 1996; Stromswold *et al.*, 1996; Caplan *et al.*, 1998, 1999; Dapretto and Bookheimer, 1999; Embick *et al.*, 2000; Friederici *et al.*, 2000a) reported BA 44/45 in the left IFG as relevant areas supporting syntactic processing. With respect to the temporal cortex, it is in particular the anterior superior temporal gyrus (STG) which has been seen activated as a function of syntactic structure (Friederici *et al.*, 2000a; Meyer *et al.*, 2000; Friederici, 2002). There is tentative evidence that within the left IFG, a further functional separation can be made with respect to syntactic processes. The anterior portion of the IFG [i.e. BA 44 on the border to BA 45 (Fiebach *et al.*, 2001) and BA 47 (Cooke *et al.*, 2001)] seems to support aspects of syntactic memory as necessary in the processing of long antecedent-gap dependencies, whereas the posterior-inferior portion of BA 44, i.e. the inferior tip of the pars opercularis and deep frontal operculum on the border to ventral premotor cortex, is involved in on-line syntactic structure building processes (Friederici *et al.*, 2000a).

The functional description of the superior temporal region, which is implicated in both semantic and syntactic processing, is still a matter of debate. Scott and collaborators (Scott *et al.*, 2000) suggest that the processing of spoken language might be organized in the form of two separable pathways through the superior temporal lobe, starting from primary auditory cortex. These authors propose the presence of an anterolateral pathway specific for the comprehension of speech. This pathway projects to the anterior STG, which is activated only by intelligible speech stimuli (Scott *et al.*, 2000). As, however, other studies have demonstrated that the left anterior temporal region was not activated during the perception of auditorily presented word and pseudoword lists, but only for auditory stimuli with a syntactic structure (Friederici *et al.*, 2000a), the notion of intelligibility with respect to the anterior STG may not be as general as initially assumed. Friederici and colleagues (Friederici *et al.*, 2000a; Meyer *et al.*, 2000) proposed that the left anterior STG, together with the frontal operculum, is responsible for on-line syntactic processes. With respect to the posterior portion of the superior temporal lobe Wise *et al.* (Wise *et al.*, 2001) proposed that this region might be involved in the transient representation of phonetic sequences, independent of whether or not these sequences constitute intelligible speech. Based on this assumption, the posterior superior temporal lobe should be activated whenever words or sentences are processed. Despite these relatively specific assumptions regarding the function of STG areas, the specific functional description of the anterior and posterior portions of the superior temporal region is still a matter of debate.

The Present Study

The present study set out to specify further the functional description of the different brain areas in the language-related network by localizing the neural basis of lexical-semantic and syntactic subprocesses which have been diagnosed to be functionally distinct using electrophysiological methods. To this end, event-related functional magnetic resonance imaging (fMRI) was used to identify those brain areas supporting (i) the processing of lexical-semantic information at the sentence level reflected in the N400 component and (ii) the processing of syntactic information in anomalous sentences reflected in the early left anterior negativity and the late centro-parietal positivity (P600). Changes in participants' hemodynamic response were measured during the auditory presentation of sentence stimuli identical to those used in a series of electrophysiological studies in which the N400, early left anterior negativity and P600 were observed (Friederici *et al.*, 1993, 1996, 1999; Hahne and Friederici, 2002). The sentence material consisted of spoken German sentences which were either correct, contained a selectional restriction violation (i.e. a semantic violation), or a syntactic phrase structure violation (see Table 1). As in the previous ERP studies, participants were required to perform an acceptability judgment after each sentence. On the basis of previous imaging studies and ERP studies with neurological patients, the following predictions were formulated: for the semantically anomalous condition we expected activation in the mid and posterior portions of the left superior temporal region and possibly in left inferior frontal cortex; for the syntactically anomalous condition we predicted activation in the anterior portion of the left STG, the left fronto-opercular cortex and the basal ganglia.

Materials and Methods

fMRI Data Acquisition

Eight axial slices (5 mm thickness, 2 mm inter-slice distance, FOV 19.2 cm, data matrix of 64 × 64 voxels, in-plane resolution of 3 × 3 mm) were acquired every 2 s during functional measurements [BOLD (blood oxygen level dependent) sensitive gradient EPI sequence, T_R = 2 s, T_E = 30 ms, flip angle = 90°, acquisition bandwidth = 100 kHz] with a 3 T Bruker Medspec 30/100 system. Prior to functional imaging, T_1-weighted MDEFT images (data matrix 256 × 256, T_R 1.3 s, T_E 10 ms) were obtained with a non-slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000). These were used to coregister functional scans with previously obtained high-resolution whole-head 3D brain scans — 128 sagittal slices, 1.5 mm thickness, FOV 25.0 × 25.0 × 19.2 cm, data matrix of 256 × 256 voxels (Lee *et al.*, 1995).

Participants

Fifteen native speakers of German (seven male, aged 23–30 years, mean

Table 1
Examples of sentence conditions used in the present study

Correct condition	Das Hemd wurde gebügelt The shirt was ironed
Syntactic violation condition	Die Bluse wurde am gebügelt The blouse was on ironed
Semantic violation condition	Das Gewitter wurde gebügelt The thunderstorm was ironed
Correct filler condition	Der Rock wurde am Freitag gebügelt The skirt was on Friday ironed

English translations retain German word order. A complete set of experimental materials is available from the authors.

age 24.8 years) participated in the study after giving informed consent. No participant had any history of neurological or psychiatric disorders. All participants had normal or corrected to normal vision and were right handed with laterality quotients of 90–100% according to the Edinburgh handedness scale (Oldfield, 1971).

Materials

The experimental material consisted of short sentences containing transitive verbs in the imperfect passive form. Participial forms of 96 different transitive verbs, all of which started with the regular German participial morpheme 'ge', were used to create the experimental sentences. For each participle, three different critical sentences and one filler sentence were constructed (see Table 1).

In the syntactically incorrect sentences, the participle immediately followed a preposition, thus yielding a phrase structure error. In semantically incongruous sentences, the meaning of the participle could not be satisfactorily incorporated into the preceding context of the sentence. The correct filler condition, which was not included in the final fMRI analysis, contained a completed prepositional phrase as well as the participle construction and was included to ensure that participants could not predict a syntactic violation based purely on the presence of a preposition. The sentences were spoken by a trained female native speaker, recorded and digitized, and presented auditorily to the participants. Sentence conditions differed slightly in average length (correct condition = 1747 ms; semantically incorrect condition = 1740 ms; syntactically incorrect condition = 1937 ms; filler condition = 2339 ms). The complete set of materials is available from the authors.

Experimental Procedure

Two differently randomized stimulus sequences were designed for the experiment. The 96 sentences from each of the four conditions were systematically distributed between two lists, so that each verb occurred in only two out of four conditions in the same list. Forty-eight null events, in which no stimulus was presented, were also added to each list. The lists were then pseudo-randomized with the constraints that (i) repetitions of the same participle were separated by at least 20 intervening trials, (ii) no more than three consecutive sentences belonged to the same condition and (iii) no more than four consecutive trials contained either correct or incorrect sentences. Furthermore, the regularity with which two conditions followed one another was matched for all combinations. The order of stimuli in each of the two randomized stimulus sequences was then reversed, yielding four different lists. These were distributed randomly across participants.

An experimental session consisted of three 11 min blocks. Blocks consisted of an equal number of trials and a matched number of items from each condition. Each session contained 240 critical trials, made up of 48 items from each of the four experimental conditions plus an equal number of null trials, in which no stimulus was presented and the BOLD response was allowed to return to a baseline state (Burock *et al.*, 1998).

The 240 presented trials lasted 8 s each (i.e. four scans of $T_R = 2$ s). The onset of each stimulus presentation relative to the beginning of the first of the four scans was randomly varied between 0, 400, 800 and 1200 ms. The purpose of this jitter was to allow for measurements to be taken at numerous time points along the BOLD signal curve, thus providing a higher resolution of the BOLD response (Miezin *et al.*, 2000). After the initial jittering time a fixation cue, consisting of an asterisk in the center of the screen, was presented for 400 ms before presentation of the sentence began. Immediately after hearing the sentence, the asterisk was replaced by three question marks, which cued participants to make a judgment on the correctness of the sentence. Maximal response time allowed was 2000 ms. Identifying the type of error was irrelevant. Participants indicated their responses by pressing buttons on a response box. After the response, the screen was cleared. Incorrect responses and unanswered trials elicited a visual feedback. These trials, as well as two dummy trials at the beginning of each block, were not included in the data analysis.

Data Analysis

The functional imaging data processing was performed using the software package LIPSIA (Lohmann *et al.*, 2001). Functional data were corrected first for motion artifacts and then for slicetime acquisition differences using sinc-interpolation. Low-frequency signal changes and baseline drifts were removed by applying a temporal highpass filter to remove frequencies <1/60 Hz. A spatial filter of 5.65 mm FWHM was applied.

The anatomical images acquired during the functional session were co-registered with the high-resolution full-brain scan and then transformed by linear scaling to a standard size (Talairach and Tournoux, 1988). The transformation parameters obtained from this step were subsequently applied to the preprocessed functional images.

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston, 1994; Friston *et al.*, 1995a,b; Worsley and Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function (Friston *et al.*, 1998; Josephs *et al.*, 1997). The model equation, made up of the observed data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM. For each participant, three contrast images were generated, which represented the main effects of (i) correct sentences, (ii) syntactically violated sentences and (iii) semantically violated sentences. Subsequent group analysis consisted of a one-sample *t*-test across the contrast images of all participants that indicated whether observed effects were significantly distinct from zero (Holmes and Friston, 1998). The resulting *t*-statistics were transformed to standard normalized distribution. Statistical parametric maps [SPM{Z}] were thresholded at $Z > 3.09$ ($P < 0.001$, uncorrected). Only clusters of at least five connected voxels (i.e. 225 mm^3) are reported.

Results

Response accuracy rates were high in all conditions (correct sentences, 97.08%; semantic violations, 95%; syntactic violations, 95%; correct filler sentences, 96.25%) and not significantly different across conditions [$F(3,42) = 1.14$, $P > 0.3$]. In the following, we report main effects of increased activation for each experimental condition separately (see Table 2). Following this, we provide direct statistical comparisons between each violation condition and the correct condition, which we carried out in order to assess the extent to which the observed increases in activation could be directly attributed to a specific violation condition.

For the processing of syntactically and semantically well-formed sentences, we observed significantly increased activation along the STG bilaterally (see Table 2A and Fig. 1). In the left hemisphere, the maximum activation was found in the mid-portion of the STG, lateral to Heschl's gyrus. The activated area included more anterior parts of the STG as well, although this anterior activity was less pronounced than in mid-STG. In addition, a strong activation focus was found ($Z_{\max} = 4.24$) in the most posterior part of the frontal operculum (i.e. in premotor cortex inferior to the central sulcus) which, however, did not pass the cluster size threshold (see Table 2A). For the processing of correct sentences, no reliable activity was observed in classical inferior frontal areas such as BA 44 or in subcortical structures.

Similar to the pattern seen for the processing of correct sentences, grammatically violated sentences also strongly activated the mid-portion of the STG bilaterally. Additional activity specific for the processing of syntactic violations was observed primarily in the left hemisphere (see Table 2B and Fig. 1). These activations included a cluster in the posterior STG, as well as a strong activation increase in the most anterior aspect of the STG. Furthermore, syntax-specific activity was observed posteriorly in the frontal operculum, i.e. in the inferior precentral gyrus and spreading medially into insular cortex. Although not found exactly in BA 44 of the IFG, this activation was located in the direct vicinity of Broca's area. One small site of increased activation was further observed subcortically in the putamen of the left basal ganglia (see Fig. 1).

Table 2
Brain regions reliably activated by correct sentences and by sentences containing syntactic and semantic violations

Area	BA	mm^3	*x*	*y*	*z*	Z_{max}
(A) Correct sentences						
Left superior temporal gyrus	22/42	2098	–54	–19	13	5.11
Right superior temporal gyrus	22	522	63	–40	17	4.07
	22/42	921	56	–16	8	4.68
Left posterior frontal operculum	6/43	141	–49	–8	10	4.24
(B) Syntactic violations						
Left posterior superior temporal gyrus	22/39/40	977	–61	–40	20	4.59
Left mid-superior temporal gyrus	22	769	–60	–29	10	3.77
Left anterior superior temporal gyrus	22/52	1110	–53	–1	0	4.36
Right superior temporal gyrus	22/42	961	59	–19	14	3.36
Left posterior frontal operculum	6/43	940	–41	–2	13	3.37
Left supramarginal gyrus	40	261	–40	–36	43	3.72
Left basal ganglia		124	–22	–5	13	3.55
(C) Semantic violations						
Left superior temporal gyrus	22	9154	–60	–42	20	5.29
Right post superior temporal gyrus	40/39	407	54	–56	16	3.93
Right mid-superior temporal gyrus	22	278	63	–40	20	3.81
	22	4723	58	–24	13	5.25
Right inferior premotor cortex	6	351	51	6	21	3.87
Left anterior insula		683	–37	9	8	4.04
Right anterior insula		696	40	14	5	3.74

BA, Brodmann's area; *x*, *y* and *z* represent Talairach and Tournoux (Talairach and Tournoux, 1988) coordinates.

Semantically anomalous sentences also brought on increased activation along the STG bilaterally. This activation extended, as in the syntactic condition, into more posterior regions than seen for the correct condition; however, it did not extend into the anterior STG regions observed for the syntactic condition (Table 2C and Fig. 1). Additional increases in activation specific to the semantic condition were observed in the anterior insula bilaterally, as well as in the right inferior premotor cortex (see Fig. 1).

We conducted direct statistical comparisons between the experimental conditions, in order to determine whether violation-specific activity in the regions described above did indeed differ reliably from activity elicited during the processing of correct sentences. To this end, spherical regions of interest (ROIs; radius 3 mm) were defined around the local maxima of each activation site, as reported in Table 2. For these ROIs, average contrast values were extracted for each participant and subjected to a repeated measures ANOVA (Bosch, 2000). A significantly greater increase in activation for the syntactic condition in comparison with the correct condition could be observed throughout the length of the left STG: posterior portion, $F(1,14) = 7.53$, $P < 0.05$; middle portion, $F(1,14) = 4.88$, $P < 0.05$; anterior portion, $F(1,14) = 9.37$, $P < 0.01$. The processing of syntactically violated sentences showed further tendencies towards greater activation increases than during processing of correct sentences in the left posterior frontal operculum [$F(1,14) = 3.26$, $P < 0.1$] and left basal ganglia [$F(1,14) = 3.69$, $P < 0.1$]. For the semantic condition in comparison to the correct condition, a significantly greater increase in activation was present in the mid-portion of the STG, bilaterally – left, $F(1,14) = 34.75$, $P < 0.01$; right, $F(1,14) = 20.19$, $P < 0.01$ – as well as in the anterior insula bilaterally – left, $F(1,14) = 15.62$, $P < 0.01$; right, $F(1,14) = 4.70$, $P < 0.05$.

The direct comparison of the two anomalous conditions showed greater levels of activation for the processing of syntactic errors over semantic errors in the left basal ganglia [$F(1,14) = 7.73$, $P < 0.05$]. The processing of semantically anomalous sentences brought on significantly increased levels of activation in comparison to the processing of syntactic errors in the mid-portions of the STG, bilaterally [left, $F(1,14) = 11.07$, $P < 0.01$; right, $F(1,14) = 10.76$, $P < 0.01$].

Discussion

The present study aimed to identify those cerebral areas specifically involved in the processing of semantic versus syntactic aspects of natural language. Semantic and syntactic processing were dissociated from one another through a violation paradigm. Several clear-cut results emerged from the study. First of all, sentences containing a semantic violation showed increased levels of activation in the mid-portion of the STG bilaterally and in the insular cortices bilaterally. Secondly, for sentences containing a syntactic violation, specific activation increase was seen in the anterior portion of the left STG, in the left posterior frontal operculum adjacent to BA 44 and in the putamen of the left basal ganglia. Thirdly, both the syntactically anomalous and the semantically anomalous conditions brought on increased levels of activation in the posterior portion of the left STG, though to a larger degree for the semantic condition. Lastly, it is interesting to note that this study did not observe classical Broca's area activation for sentence processing.

Semantic Processes

The results concerning semantic processing are, in general, in accordance with previous studies. Both the analysis of the semantically anomalous sentences as well as the comparison between the two violation conditions revealed higher activation in the STG bilaterally, suggesting a specialization of this area for semantic processes. The bilateral activation of the STG for semantically anomalous sentences in this study is in line with previous studies looking at the processing of semantic anomalies (Kuperberg *et al.*, 2000; Newman *et al.*, 2001; Ni *et al.*, 2000). A few studies have shown additional increased activation of inferior frontal cortex (Dapretto and Bookheimer, 1999; Newman *et al.*, 2001), which was not evident in our results. However, when trying to integrate our data into existing findings on language processing we should keep in mind that different

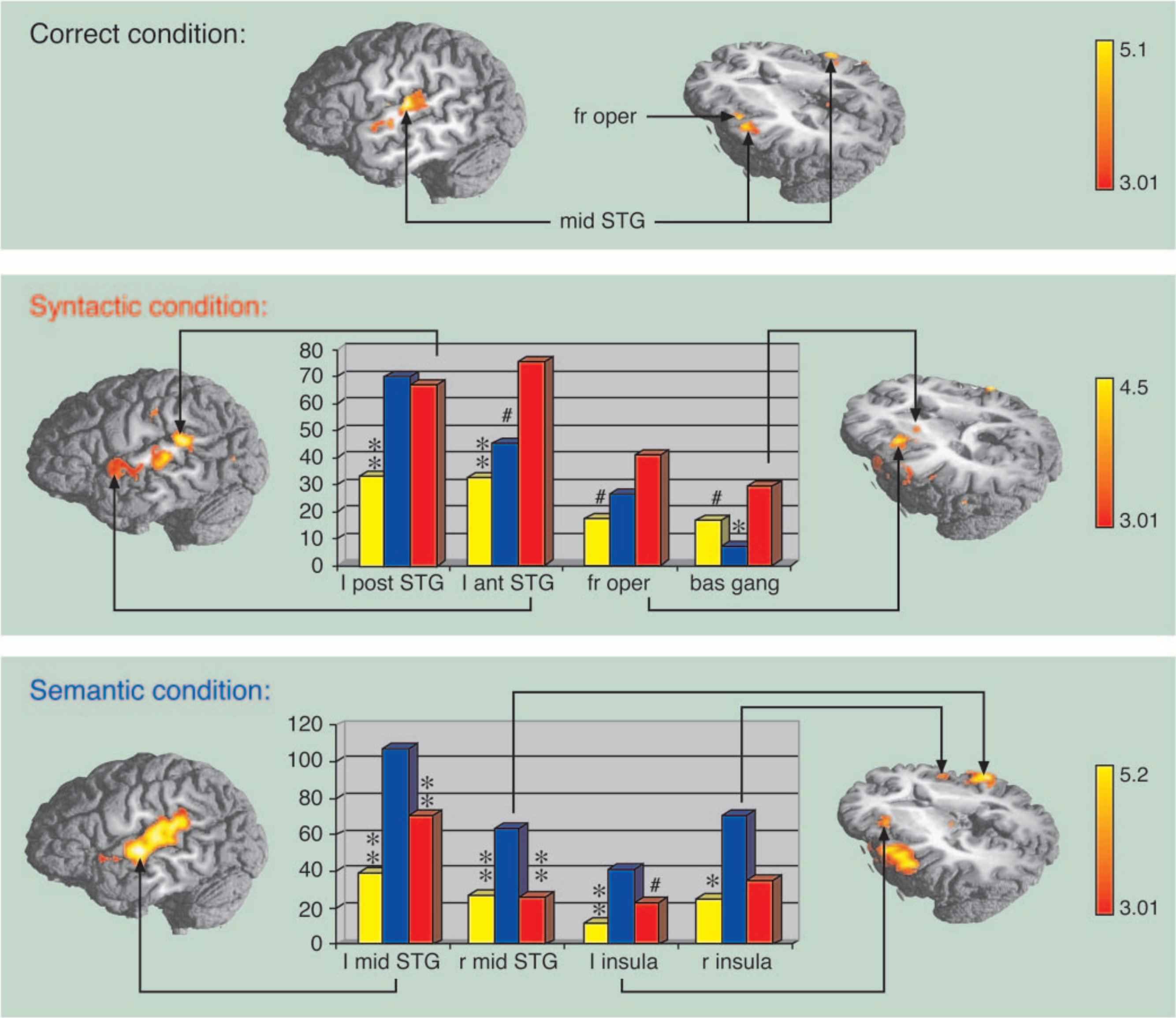

Figure 1. Neural activity elicited by correct, syntactically violated and semantically illegal sentences. Displayed are 3D renderings of significant activation effects onto a template brain. For sentences containing syntactic and semantic violations, bar charts are included which represent mean contrasts (in arbitrary values) for the spherical regions of interest on which the statistical comparison of correct and incorrect conditions was based (yellow = correct sentences, blue = semantic violations, red = syntactic violations; #$P < 0.1$; *$P < 0.05$; **$P < 0.01$). The statistical strengths which are shown in the bar charts always represent the difference between the respective violation condition and the two other conditions. Fr oper, frontal operculum; mid STG, mid-portion of superior temporal gyrus; l ant STG, left anterior superior temporal gyrus; bas gang, basal ganglia; r mid STG, mid-portion of right superior temporal gyrus; l STG, left superior temporal gyrus; l insula, left insular cortex; r insula, right insular cortex.

studies have relied upon a large variety of different types of stimuli modalities, tasks and languages. In particular, the majority of studies on semantic processing have investigated this issue at the word level (Démonet *et al.*, 1992; Fiez, 1997; Poldrack *et al.*, 1999), whereas only a few have looked at semantic processes at the sentence level. IFG activation for semantic processes at the word level was reported for tasks which included strategic aspects of processing (Fiez, 1997; Thompson-Schill *et al.*, 1997). Activation in the IFG for sentence level processes was reported by Dapretto and Bookheimer (Dapretto and Bookheimer, 1999) in a sentence-comparison task including aspects of working memory and by Newman *et al.* (Newman *et al.*, 2001) in a sentence-well-formed-judgment task, both using written stimulus material.

The present semantic violation condition, moreover, revealed activation of the insular cortex bilaterally. A similar insular activation in the left hemisphere related to semantic processing was, for example, reported for a positron emission tomography (PET) study focusing on automatic semantic mechanisms during semantic word priming (Mummery *et al.*, 1999).

Syntactic Processes

The analysis of the syntactic violation condition revealed increased activation in the posterior and most anterior portion of the STG, as well as in the frontal operculum and the left basal ganglia. The comparison between the two violation conditions only showed higher activation in the left basal ganglia for the syntactic violation over the semantic violation, supporting the notion of a special role of this structure during syntactic processing.

With respect to the processing of syntactic violations, two of the activation sites, namely the left frontal operculum and the left anterior portion of the STG, are similar to those reported in earlier studies. On-line syntactic phrase structure building processes during auditory comprehension have been reported to involve the left frontal operculum as well as the temporal pole (Mazoyer *et al.*, 1993), or the anterior STG (Friederici *et al.*, 2000b; Meyer *et al.*, 2000); Humphries *et al.* (Humphries *et al.*, 2001) report this latter area to play an important role in sentence-level comprehension. In particular, the left frontal operculum in the inferior frontal lobe was found to be activated in previous studies investigating the processing of syntactic information (Stromswold *et al.*, 1996; Friederici *et al.*, 2000a). The present data are in complete agreement with these last findings.

Additional activation for the processing of syntactically anomalous sentences was seen in the putamen of the left basal ganglia. There is evidence in the literature for the notion that some basal ganglia structures play a role in on-line syntactic processing. Ullman (Ullman, 2001) points to the involvement of basal ganglia structures in a so-called procedural memory system — a system which has been implicated in controlling well-established cognitive skills and which is thought to be involved in rule-based syntactic procedures. The involvement of left basal ganglia structures in syntax processing was predicted on the basis of the finding that patients with Parkinson's disease have problems in the application of grammatical rule processes in verb inflection (Ullman *et al.*, 1997; Ullman, 2001) and on the basis of earlier ERP studies with brain-lesioned patients, suggesting an involvement of these structures in controlled syntactic processes (Friederici *et al.* 1999, 2003). In these latter studies, in which the same sentence material as in the present study was used, impaired function of the basal ganglia affected the late syntactic processes, as evidenced by a reduction or absence of the P600. Although the present data can not speak to the issue of syntactic on-line procedural versus late syntactic processes, they clearly indicate an involvement of the putamen in the left basal ganglia in syntactic processes. A recent fMRI study comparing the processing of syntactic versus morpho-syntactic violations (Moro *et al.*, 2001) also found structures within the left basal ganglia to be particularly involved in syntactic processing. Taken together, the data discussed here and the present results suggest that areas within the basal ganglia are involved in the processing of syntax during language comprehension. Structures of the basal ganglia obviously play an important role in syntactic processing. Moreover, their specific role appears to lie in the support of late controlled processes rather than early syntactic processes of phrase-structure building.

Posterior STG

One area in particular, namely the posterior STG, brought on a greater increase in activation for both anomalous conditions in comparison to correct sentences. This finding suggests that the functionality of the posterior STG is not domain-specific, but may rather be related to processes of sentence evaluation or processes of sentential integration. But what is the particular function of this brain area during language comprehension as realized in the present study? Sentence acceptability judgments, which participants had to make in all experimental conditions, may be more difficult in anomalous than in correct sentences, leading to a higher activation for incorrect than for correct conditions. However, as there was no behavioral difference between correct and incorrect conditions, this judgment-related interpretation is unlikely. Rather, it appears that increased activation in the posterior STG is a result of the increased effort involved in integrating an anomalous structure into a sentence. This presumably unsuccessful integration process is the only shared delineating feature between incorrect and correct conditions, leading us to believe that the shared posterior STG activation observed for both violation conditions in some way reflects the additional costs of attempted integration. Thus we propose that the posterior STG supports a processing stage during which different types of information, e.g. semantic, syntactic and pragmatic, are mapped onto each other to achieve a final interpretation.

Left Inferior Frontal Gyrus

It is interesting to note that the present study does not indicate any increased levels of activation in Broca's area (BA 44) in the left IFG, an area classically thought to support several general aspects of language processing. We argue, however, that this is a result of differences in task and material presentation between our study and previous studies. Specifically, we propose that activation in Broca's area may reflect a greater involvement of language-related working memory rather than on-line language processes. It appears that the pars opercularis of the left IFG (i.e. BA 44) may not be a necessary part of the network supporting on-line, sentence-level semantic and syntactic processes, but may only come into play under particular task demands. We will discuss this in more detail below.

With respect to semantic processing, activation in anterior inferior frontal cortex has previously been reported for sentence-level semantic aspects in combination with tasks requiring the comparison of two consecutively presented sentences, thus involving aspects of working memory (Dapretto and Bookheimer, 1999). Various studies have located specific subprocesses of verbal working memory in structures of the left IFG (Paulesu *et al.*, 1993; Gabrieli *et al.*, 1998), whereas others have described the left IFG to be involved in strategic semantic processes (Fiez, 1997; Thompson-Schill *et al.*, 1997; Gabrieli *et al.*, 1998). While the present study did not reveal specific involvement of the IFG for semantic processing, bilateral activation of insular cortex was observed. Similar activation has been reported for studies focusing on automatic semantic aspects of word priming paradigms (Mummery *et al.*, 1999). It is possible that insular cortex activity in the present study reflects automatic aspects of semantic processing, while antero-lateral IFG activation reflects strategic aspects of semantic processing.

A similar distributional difference emerges from a comparison of studies within the syntactic domain. Inferior frontal activation in Broca's area has often been tied to syntactic processing. However, such activation was mostly elicited in studies examining the processing of complex sentences with long-distance syntactic dependencies (Just *et al.*, 1996; Stromswold *et al.*, 1996; Inui *et al.*, 1998; Caplan *et al.*, 1998, 1999, 2000; Cooke *et al.*, 2001), whereas studies investigating on-line syntactic processes of phrase-structure building have reported fronto-opercular activation (Friederici *et al.*, 2000a). Thus, it can be concluded with respect to the results of the present study that the activation observed in the posterior portion of the left fronto-opercular cortex most likely is related to the on-line detection of the word category mismatch in syntactically violated sentences during the initial syntactic analysis (Friederici *et al.*, 2000b).

Recent studies have demonstrated that the involvement of Broca's area is not a function of syntactic complexity as such, but seems to be related more specifically to syntactic working memory necessary to maintain a displaced element in working memory over a prolonged distance while processing a syntactically complex sentence (Cooke *et al.*, 2001; Fiebach *et al.*, 2001). Note that natural languages allow the displacement of an element from its original sentential position to another and that when encountering such a displaced element (e.g. a sentence initial object), the processing system keeps this element in working memory until its original sentential position is reached (Fiebach *et al.*, 2002). The manipulation of the sentences undertaken in the present experiment did not cause an increased load for working memory processes. Therefore, if increased IFG activation is indeed a product of increased utilization of working memory resources, it should not be expected in the present study.

The combined data from the various studies suggest that the deep left frontal operculum is involved in local on-line processes of syntactic structure building, whereas the more laterally located pars opercularis of the IFG appears to support the working memory required during processing of long-distance syntactic dependencies. It may be interesting to note that the latter process is reflected in the ERP in a sustained frontal negativity, with a maximum over the left hemisphere and spanning the time from the perception of the displaced element to its original position (King and Kutas, 1995; Kluender *et al.*, 1998; Fiebach *et al.*, 2002). The former process, i.e. on-line syntactic structure building, is correlated with the observation of a local, short-lived early left anterior negativity (Neville *et al.*, 1991; Friederici *et al.*, 1993; Kluender *et al.*, 1998; Hahne and Friederici, 2002). Taken together, it appears that the two functionally distinct processes of local syntactic structure building and syntactic working memory also have a distinct neural basis.

Conclusion

The present results indicate interesting differences and similarities for the processing of sentences containing a semantic violation and those containing a syntactic violation. Both conditions recruited larger portions of the superior temporal region than correct sentences and elicited activity extending to the most posterior part of the STG. This posterior STG activation appears to be correlated with processes of sentential integration. The processing of semantic violations in a sentence mainly relies on the mid-portion of the superior temporal region bilaterally and the insular cortex bilaterally. The processing of syntactic violations, in contrast, specifically involved the anterior portion of the STG, the left posterior frontal operculum and the left basal ganglia (i.e. the putamen). These findings are compatible with the view that both semantic and syntactic processes rely on a temporo-frontal network, each with distinct specific areas.

Notes

The authors are indebted to Yves von Cramon for his support. We further wish to thank Stefan Zysset and Karsten Müller for helpful comments regarding the fMRI data analysis. This study was supported by the Leibniz Science Prize awarded to A.F. and by research grant FI 848/1 awarded to C.F. by the Deutsche Forschungsgemeinschaft (German Research Foundation, DFG).

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