An fMRI Study of Canonical and Noncanonical Word Order in German

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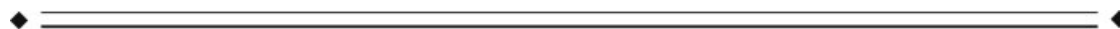
Abstract: Understanding a complex sentence requires the processing of information at different (e.g., phonological, semantic, and syntactic) levels, the intermediate storage of this information and the unification of this information to compute the meaning of the sentence information. The present investigation homed in on two aspects of sentence processing: working memory and reanalysis. Event-related functional MRI was used in 12 healthy native speakers of German, while they read sentences. Half of the sentences had unambiguous initial noun-phrases (masculine nominative, masculine accusative) and thus signaled subject-first (canonical) or object-first (noncanonical) sentences. Noncanonical unambiguous sentences were supposed to entail greater demand on working memory, because of their more complex syntactic structure. The other half of the sentences had case-ambiguous initial noun-phrases (feminine gender). Only the second unambiguous noun-phrase (eighth position in the sentences) revealed, whether a canonical or noncanonical word order was present. Based on previous data it was hypothesized that ambiguous noncanonical sentences required a recomputation of the sentence, as subjects would initially commit to a subject first reading. In the respective contrasts two main areas of brain activation were observed. Unambiguous noncanonical sentences elicited more activation in left inferior frontal cortex relative unambiguous canonical sentences. This was interpreted in conjunction with the greater demands on working memory in the former condition. For noncanonical ambiguous relative to canonical ambiguous sentences, an activation of the left supramarginal gyrus was revealed, which was interpreted as a reflection of the reanalysis-requirements induced by this condition. *Hum Brain Mapp 28:940–949, 2007.* © 2007 Wiley-Liss, Inc.

Key words: working memory; language processing; reanalysis; fMRI; word order; noncanonical sentences

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INTRODUCTION

One of the key questions to be solved by a reader/listener when confronted with a sentence is to determine "who did what to whom." To this end, the reader/listener must be able to unambiguously identify the different constituents of a sentence in order to assign thematic and syntactic roles. Interestingly, different languages draw on different sources of information for role assignment. MacWhinney et al. [1984], for example, have shown that English subjects rely primarily on word order, while Italian subjects used agreement information as the most important
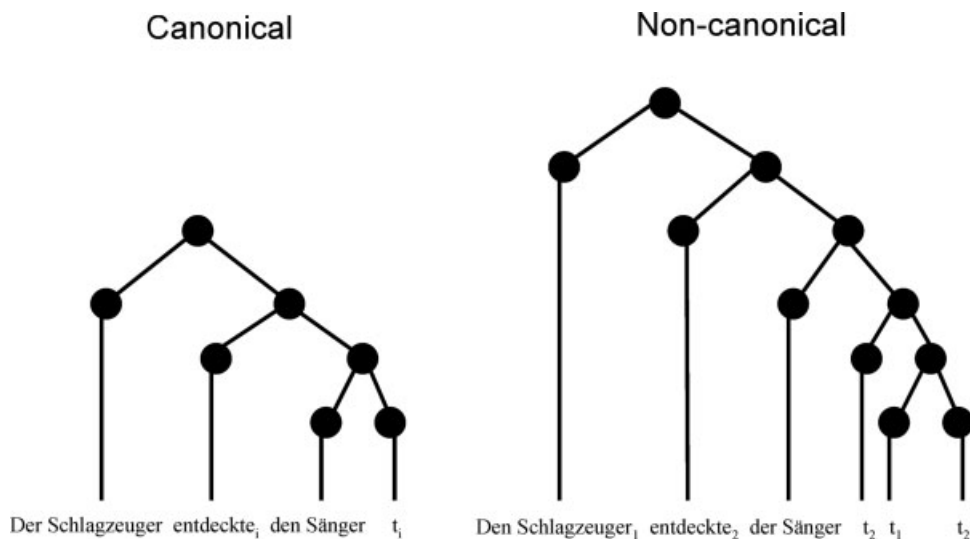
Canonical

Non-canonical

Der Schlagzeuger entdeckte$_i$ den Sänger t$_i$

Den Schlagzeuger$_1$ entdeckte$_2$ der Sänger t$_2$ t$_1$ t$_2$

Figure 1.

Simplified syntactic analysis of sentences with unambiguous masculine noun-phrases in the initial position (linguistic elements have been represented by filled circles, for a detailed description of the syntactic structure, see [Gorrell, 2000]). The canonical sentence on the left has a simpler structure than the noncanonical, object-first sentence on the right. At positions marked t$_x$ previous elements of the sentence (coindexed) have to be reactivated from working memory.

cue, and German subjects apparently employed agreement and animacy information.

These different strategies appear to be related to the specific properties of a language. For example, relative to English, German possesses a comparatively rich morphology, thereby allowing deviations from the standard SVO word order that is needed (and therefore is mandatory) in English for identification of roles. This is illustrated by the following sentences:

1. Der begabte Sänger entdeckte den talentierten Gitarristen
   The gifted singer$_{(Masc. Nom.)}$ discovered the talented guitar player$_{(Masc. Acc.)}$.
2. Den begabten Sänger entdeckte der talentierte Gitarrist.
   "The gifted singer$_{(Masc. Acc.)}$ discovered the talented guitar player$_{(Masc. Nom.)}$."
   Meaning: The talented guitar player discovered the gifted singer.

In sentences (1) and (2), the first noun-phrase is of masculine gender and unambiguously marked for case: nominative, indicating a subject in the first position, in (1), and accusative, consistent with an object-first construction, in (2). Hemforth [1993] in a self paced reading experiment found longer reading times for unambiguous object first sentences. Therefore, it appears appropriate to consider the object-first word order "noncanonical". Linguistic analysis [Gorrell, 2000; Schlesewsky et al., 2000] has shown that sentences of type (1) are less complex than sentences of type (2) (see

Fig. 1). This is due to the fact that in object-first constructions more items have to be kept in syntactic working memory [Schlesewsky et al., 2000]. Now consider the next examples:

3. Die begabte Sängerin entdeckte den talentierten Gitarristen.
   The gifted singer$_{(Fem. Nom. Acc.)}$ discovered the talented guitar player$_{(Masc. Acc.)}$.
4. Die begabte Sängerin entdeckte der talentierte Gitarrist.
   "The gifted singer$_{(Fem. Nom. Acc.)}$ discovered the talented guitar player$_{(Masc. Nom.)}$."
   Meaning: The talented guitar player discovered the gifted singer.

Examples (3) and (4) differ from (1) and (2) in that an identical, case-ambiguous initial feminine noun-phrase was used, which is compatible with either a "subject first" or an "object first" interpretation.

A number of psycholinguistic studies [Bates et al., 1988; Hemforth, 1993; Meng and Bader, 1997; Schlesewsky et al., 2000] have indicated, however, that in such cases a "subject first" reading will be preferred. Under the assumption of a subject first interpretation, a reader should experience no difficulty upon the encounter of the second noun-phrase in (3), as this corroborates the initial interpretation. If, however, the object interpretation becomes necessary (sentence 4), a reanalysis of the input should be required including a complex recomputation of the syntactic representation of the object first reading (c.f. Fig. 1).

A variety of studies using readings times, grammaticality judgments, and ERPs have shown reliable subject-first advantages for sentences disambiguated via number mismatch of a verb [Friederici et al., 1998, 2001; Meng, 1997; Meng and Bader, 1997; Schlesewsky et al., 1999; Schriefers et al., 1994]. By contrast, costs for reanalysis for constructions, in which the ambiguity is resolved via the case information of the second NP, as in example (4) above, have been less consistently found. Although reading time measures [Meng, 1997; Schlesewsky et al., 1999] and grammaticality judgments [Meng and Bader, 1997] suggested no processing costs, our previous ERP study [Matzke et al., 2002] has shown a reliable P600 effect at the disambiguation point, i.e. the position of the second NP.

All in all, this suggests that two major differences between sentences (1) to (4) exist: First, noncanonical sentences are associated with the need to store items in syntactic working memory. Second, ambiguous noncanonical sentences (type 4) should be the only ones requiring reanalysis and reevaluation upon encounter of the second noun-phrase.

In a previous study, event-related brain potential (ERP) effects compatible with this analysis were obtained [Matzke et al., 2002]. In this study subjects watched sentences of types (1) to (4) word by word. Unambiguous sentences, i.e. those sentences with an initial masculine noun-phrase, were distinguished by a long-lasting negative frontal shift for the noncanonical sentences, which developed over the reading of the sentence. Such shifts have been found in a number of other ERP sentence reading studies and have been associated with working memory load [King and Kutas, 1995; Muller et al., 1997; Munte et al., 1998b]. A second effect distinguished ERPs to the ambiguous noncanonical sentences (type 4) from the other sentences: At the position of the second, disambiguating noun-phrase, a P600 component was observed in this condition only. This component has been found for a variety of syntactic violations, especially when reanalysis by the parser/subject is required [Brown et al., 2000; Friederici, 2004a; Friederici et al., 2001, 2002; Hagoort and Brown, 2000; Osterhout et al., 1994; van Herten et al., 2005]. In addition, it has also been found to reflect revision-processes that become necessary to reinterpret ambiguous phrases at the position of the disambiguating element [Friederici et al., 2002; Matzke et al., 2002; Osterhout et al., 1994].

Thus, our previous ERP study has shown qualitative differences between the four sentence types. With regard to the anatomical structures sensitive to the two different demands posited by the sentences, working memory, and reanalysis, the electrophysiological data were uninformative, however. Therefore, an event-related fMRI study was conducted to examine the BOLD response to the four different conditions described above.

Note, that Fiebach et al. [2004] in a recent fMRI experiment have compared subject or object relative clauses in German sentences. In their study, all sentences featured a temporary ambiguity with different disambiguation points. Furthermore, subjects were split into high and low working memory span groups as assessed by a reading span test. A network of frontal, temporal, and sub-cortical brain areas was revealed during processing of the ambiguous sentences. Interestingly, a ROI analysis in these regions showed an interaction of working memory and ambiguity only for Broca's area (BA44). The authors therefore suggested that BA44 is responsive to increased processing demands, posited by the structures to be processed or by the individual limitations in working memory span.

As the present study uses a different approach to the exploration of long distance dependencies in sentences, i.e. a factorial manipulation of word order (canonical versus noncanonical) and ambiguity (ambiguous versus unambiguous sentences).

MATERIALS AND METHODS

All procedures were approved by the local institutional review board.

Subjects

Twelve right-handed, healthy volunteers (ages 20–28 years, 9 women) gave written consent to participate in the experiment. All were native speakers of German and handedness was determined using a standard handedness questionnaire [Oldfield, 1971].

Experimental Procedure

Materials were taken form Matzke et al. [2002] and were similar to the sentence examples (1)–(4). An additional prepositional phrase comprising three words (e.g. während der Weihnachtsfeier, *during the christmas celebration*; nach der Prüfung, *after the examination*) was inserted after the verb to increase working memory demands. For example, the sentence given as example (1) above, would now read

Der begabte Sänger entdeckte **während der Weihnachtsfeier** den talentierten Gitarristen.

The gifted singer$_{(Masc.\ Nom.)}$ discovered **during the christmas celebration** the talented guitar player$_{(Masc.\ Acc.)}$.

A total of 240 sentences were created. For each of these sentences four versions were prepared according to the four experimental conditions. During the experimental session, subjects read 60 sentences in each of the 4 experimental conditions. Four different scenarios were created such that, across subjects, each sentence was seen equally often in each of the four versions. The order of presentation of the sentences in each scenario was pseudo-randomized. In addition, a baseline condition was used presenting a row of X's with 2 s duration. Sentences were presented word by word in white letters on black background. Stimuli were back-projected onto a screen by an LCD-projector and could be viewed by the subject via a mirror mounted on the head-coil. Each sentence was preceded by a cross

TABLE I. Two-way factorial design of the present study

| Case ambiguity | Word order | |
	Canonical	Noncanonical
Unambiguous	CanNamb (a)	NcanNamb (b)
Ambiguous	CanAmb (c)	NcanAmb (d)

hair of 2 s duration, which was followed by the ten words (duration and SOA 500 ms). At the end of the sentence, the screen remained empty for 3 s. The onset asynchrony between sentences was fixed (10 s). The session was subdivided into 6 experimental runs each comprising 40 sentences (10 per experimental condition) and 10 baseline trials. At the end of each run, 8 test sentences were presented. Subjects were instructed to decide for each of these test sentences, whether or not it had been presented during the previous run and to indicate their decision by pressing one of two buttons (left index or left middle finger = "yes" or "no") on a magnet compatible response box. Half of the test sentences required a yes-response, while the other half was slightly modified and necessitated a "no-response." Incorrect sentences had a different role assignment in comparison to the previously presented sentences. This task was introduced to ensure subject's reading of the stimuli.

MRI Scanning Methods

Imaging was performed with a GE Medical Systems 1.5 Tesla Signa Neurovascular MR scanner with standard quadrature head coil. Conventional high-resolution structural images (rf-spoiled GRASS sequence, 60 sagittal slices, 2.8 mm thickness) were followed by functional images sensitive to blood oxygenation level-dependent contrast (echo planar T_2^*-weighted gradient echo sequence, TR/TE/FOV/flip angle = 1500 ms/40 ms/200 × 200 mm^2/90°, matrix size 64 × 64). Each functional run consisted of 310 sequential whole-brain volumes comprising 16 axial slices aligned to the plane intersecting the anterior and posterior commissures, 3.125 mm in-plane resolution, 7 mm thickness, 1 mm gap between slices, positioned to cover the entire brain. Volumes were acquired continuously and the four first volumes were discarded due to T1 equilibration effects. To allow precise coregistration of functional data a separate T1-weighted 2D spin echo-image was acquired in the same slice orientation as the functional scans covering the whole volume.

Analysis and visualization were performed using SPM99 software (http://www.fil.ion.ucl.ac.uk/spm/). The entire volume set of each subject was realigned to the first volume of the first sequence. A sinc-interpolation was applied to correct for the temporal offset between the slices acquired in one scan. Structural and functional data were spatially normalized to an EPI template based on the Montreal Neurological Institute (MNI) reference brain [Cocosco

et al., 1997], an approximation of canonical space [Talairach and Tournoux, 1988], using a 12-parameter affine transformation along with a nonlinear transformation using cosine basis functions. Functional EPI volumes were resampled into 4 mm cubic voxels and then spatially smoothed with an 8 mm FWHM isotropic Gaussian Kernel to accommodate residual anatomical differences across volunteers.

For the statistical model a block design matrix including all conditions of interest was specified using the canonical hemodynamic response function for all event types [Friston et al., 1998]. The data was high-pass filtered, smoothed temporally with a 4 s full-width half-maximum Gaussian kernel and rescaled to the global mean. Significant differences in hemodynamic responses were validated using the linear model approach as implemented in SPM99. Effects were estimated using a subject-specific fixed-effects model. Linear contrasts were used to obtain subject-specific estimates for each effect. A factorial design matrix was employed, which comprised contrasts modeling the two main effects (see Table I) noncanonical vs. canonical [(b + d) − (a + c)] and ambiguous versus unambiguous [(c + d) − (a + b)] and the interaction between word order and ambiguity [(a−b) − (c−d)].

Also, in order to delineate those structures that are commonly activated across all syntactic conditions, an average activation of all conditions compared to the baseline condition (row of Xs) was obtained. For group analysis, these estimates were entered in a second-level analysis treating subjects as a random effect. Unless mentioned otherwise, contrasts were thresholded at $P < 0.001$ and only activations involving contiguous clusters of at least twenty significant voxels are reported. The maxima of suprathreshold regions were localized by rendering them onto the MNI reference brain [Cocosco et al., 1997] and are reported in MNI coordinates, as used by SPM99.

Regions of interests (ROI) definition and signal extraction was performed using the ROI toolbox available at http://spm-toolbox.sourceforge.net/toolboxes.html. Selective averaging was computed upon a finite impulse response (FIR) model. ROIs were defined functionally and their extent was set at 8-mm radius. On the basis of the activations in the contrast of all conditions against baseline/fixation, three different regions of interest (ROI) were analyzed: (1) left inferior frontal gyrus, (2) the posterior portion of the medial and superior temporal gyrus, and (3) the left inferior temporal gyrus. These ROIs have been identified by earlier functional neuroimaging studies as important sites of the neural bases of syntactic processing: (i) the LIFG is the area most likely related to grammatical processing in the literature and also appeared to be related to the main contrast of Word order (see [Caplan, 2001; Ben-Shachar et al., 2003; Indefrey, 2004; Friederici, 2004b]). In a similar vein, previous studies using scrambling in ambiguous and unambiguous sentences showed activation in the IFG [Bornkessel et al., 2005]; (ii) The supramarginal gyrus (BA40) was highlighted by a previous study of Kuperberg et al. [Kuperberg et al., 2003b]. These authors encountered that morphosyntactically anomalous sentences
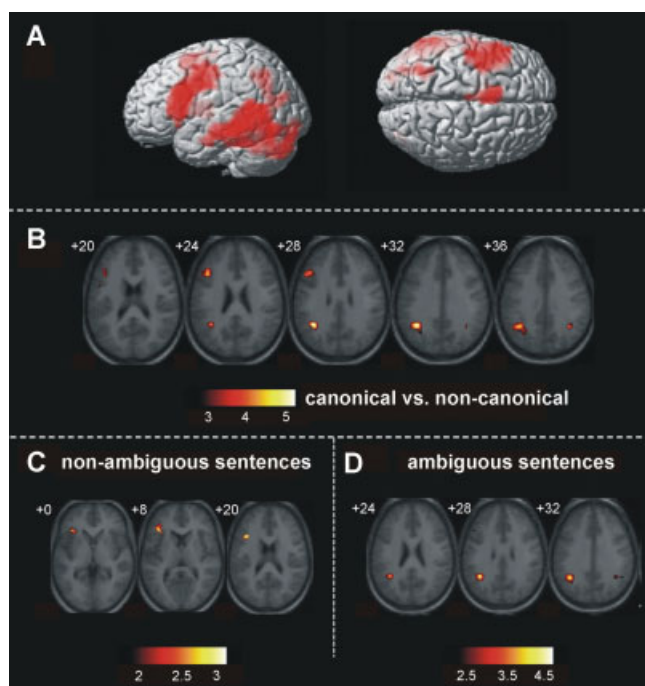
Figure 2.

A: Comparison of all sentence conditions against fixation/baseline. Activations are rendered on a T1-weighted single subject MNI template as provided by SPM. For all differences shown, P < 0.01, cluster extent 20 voxels. B: Main effect of Word order: noncanonical against canonical sentences. An activation of the left anterior inferior frontal region (BA44/45) and the left supramarginal gyrus is seen. C: Effects of word order in the unambiguous sentences: noncanonical sentences are more active in the left anterior frontal region. D: Effects of word order in the ambiguous sentences: noncanonical sentences yield an activation of the left supramarginal gyrus. The axial views presented in this figure were superimposed on the mean anatomical image formed by averaging the T1 structural MRI scans mapped into normalized MNI space across all subjects.

(which typically elicited a P600 in ERP studies) were associated with larger activation in this region; (iii) the posterior part of the middle temporal regions has been shown by a recent meta-analysis [Indefrey, 2004] to play a role in syntactic processing.

The BOLD response for each contrast was averaged separately for each subject across the six runs for a 16 s epoch. Since a TR of 1.5 s was used, time points at every 1.5 s were measured. Serial t tests were conducted for each time-point comparing the canonical and noncanonical sentences separate for ambiguous and unambiguous conditions. A significant difference between conditions was considered when at least two consecutive t tests showed a significant difference from zero ($P < 0.05$). The time course data were also used to perform repeated measures analyses of variance (ANOVA) with factors word order (2 lev-

els), ambiguity (2 levels), and time-point (4 levels). Scans selected for the ANOVA were centered upon the peak value of the bold signal (between 10.5 s and 15 s; scans 11, 12, 13, 14). The ROI's resulting from the baseline contrast were chosen and not from the main effects (canonicity or ambiguity). This type of analysis represents a more conservative method, since in the baseline contrast, a common activation pattern within the four conditions was calculated by the general linear model and differences between the conditions within these common activations were calculated in the ANOVA.

RESULTS

The performance in the recognition task was about 75% correct. Figure 2A and Table II illustrate the significant peak activations for all conditions against baseline. The following regions showed a significant increase: superior portion of the left inferior frontal gyrus (BA44/45), supplementary motor area, left inferior temporal gyrus, and the superior part of the left middle temporal gyrus. The crucial comparison between noncanonical and canonical sentences showed activation in the supramarginal gyrus (BA40) and the left inferior frontal gyrus (BA45) (Fig. 2B, Table II). No significant activations were observed for the main effect of ambiguity at the specified threshold ($P < 0.001$, 20 voxels). In addition, no significant activations were obtained for the interaction between Word order and Ambiguity.

To study the effect of word order separately for ambiguous and unambiguous sentences pair-wise comparisons were carried out. The comparison between noncanonical and canonical unambiguous sentences, which should reflect the working memory demands presented by the noncanonical unambiguous sentences, yielded a significant activation in the left inferior frontal gyrus (BA45, $T = 3.18$, $P < 0.004$, peak coordinates −40, 28, 8). By contrast, the same comparison for the ambiguous sentences, presumably related to the need for reanalysis, revealed an activation of the left supramarginal gyrus (BA40; $T = 5.4$, $P < 0.001$, peak coordinates −40, −52, 28).

Time Course of the BOLD Response in Specific Regions of Interest

On the basis of the comparison of all conditions against baseline (Fig. 2A, Table II), three ROIs were identified. The time course of the activations is shown in Figure 2 in terms of percent signal change.

In the *inferior frontal region* (Broca) differences in the BOLD response to canonical and noncanonical sentences were seen for both the ambiguous and unambiguous conditions (Fig. 3, upper panel). These differences were assessed by serial t tests (Table III). While in the unambiguous sentences the BOLD responses of the canonical and noncanonical sentences differentiated as early as 7.5 s, this

TABLE II. Brain regions showing significant changes in the specified contrasts

| Brain region | ~BA | Stereotactic coordinates | | | T peak | P < |
		x	y	z		
All conditions vs. baseline						
Left inferior temporal G	20	−56	−32	−16	6.7	0.001
L middle temporal G (posterior superior temporal G)	21/37/22	−48	−60	8	4.4	0.001
L inferior frontal G	44	−44	12	20	6.0	0.001
SMA	6	−8	8	60	3.6	0.001
R Cerebellum		36	−80	−28	3.5	0.001
Noncanonical vs. Canonical						
L supramarginal G	40	−40	−52	28	5.7	0.001
L inferior frontal G	45	−44	24	28	4.6	0.001

MNI coordinates and T value for the peak location in a particular anatomical cluster ($P < 0.001$; 20 voxels spatial extent). BA, approximate Brodmann's area; L, left hemisphere; R, right hemisphere; G, gyrus.

was not the case for the ambiguous sentences. Here, the BOLD response to canonical and noncanonical sentences started to diverge significantly only at 13.5 s. Furthermore, a repeated measures ANOVA, introducing Word order, Ambiguity, and Time-point (4 levels: 10.5, 12, 13.5, and 15 s) was performed. The time points were selected, because they encompass the peak of the BOLD response. The increased BOLD response associated with the noncanonical sentences was reflected by a main effect of Word order ($F(1,11) = 18.6$, $P < 0.001$). No main effect of Ambiguity ($F(1,11) < 1$) and no interaction between Word order and Ambiguity ($F(1,11) < 1$) were seen. A main effect of Time-point ($F(3,33) = 16.8$, $P < 0.001$) as well as a Word order × Time-point interaction ($F(3,33) = 9.9$, $P < 0.001$) were obtained, the latter reflecting the differential effect of Word-order across time. The interaction between Ambiguity and Time-point ($F(3,33) < 1$) as well as the triple interaction of all factors ($F(3,33) = 1.35$, $P > .27$) were not significant.[1]

The time course of the BOLD response in the posterior part of the middle temporal cortex (GTM, Fig. 3 middle panel, Table III) suggests that this region is exclusively sensitive to variations of Word-order in ambiguous sentences. This is reflected by the serial t tests between canonical and noncanonical sentences at each time-point. The ANOVA design showed a main effect of Word order ($F(1,11) = 11.5$, $P <$

0.006) and Time ($F(3,33) = 10.5$, $P < 0.004$), but no interaction between these factors (Word order × Time, $F(3,33) < 1$). There was no main effect of Ambiguity ($F(1,11) = 2.6$, $P > 0.13$) but an Ambiguity × Time interaction ($F(3,33) = 6.9$, $P < 0.005$). The Word order × Ambiguity interaction approached significance ($F(1,11) = 3.1$, $P > 0.104$). The three-way interaction was not significant.

The last ROI, located in the inferior temporal gyrus (GTI, Fig. 2, lower panel, Table III) , showed only a main effect for Word order ($F(1,11) = 9.1$, $P < 0.011$) and Time ($F(3,33) = 12.6$, $P < 0.001$). Neither the main effect of ambiguity ($F(1,11) = 1.05$, $P > 0.33$) nor the interactions between Word order × Ambiguity ($F < 1$), Word order × Time ($F < 1$), Ambiguity × Time ($F < 1$), and the interaction between the three factors ($F < 1$) were significant.

DISCUSSION

The analysis of the stimulus materials and the results of our previous brain potential study [Matzke et al., 2002] suggested different processing demands for noncanonical sentences in the unambiguous and ambiguous conditions. While the noncanonical sentences should lead to an increased working memory load in the unambiguous sentence from the sentence onset onwards, the noncanonical sentences in the ambiguous condition call for a reanalysis of the sentence at the position of the disambiguating case-marked second noun-phrase.

These processing differences were reflected by the brain activation patterns: Noncanonical word order led to activation in the left anterior inferior frontal region and the left supramarginal gyrus (Fig. 2B). Moreover, separate examination of the word-order effects in unambiguous and ambiguous sentences revealed that the inferior frontal region was responsive mainly in the former comparison (Fig. 2C), while the supramarginal gyrus was activated in the latter comparison (Fig. 2D). With respect to our task analysis, this would imply that the anterior region is related to the working memory demands posited by the noncanonical

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[1] We further analyzed the LIFG ROI in order to inspect for the existence of a possible Word Order × Ambiguity or Word Order × Ambiguity × Time interaction. Notice that the word-order effect begins earlier in the nonambiguous sentences. We chose two time-points that cover the onset and the peak value of the BOLD response difference, 9 s and 12 s (see Fig. 3). In this analysis, the interaction between Word Order × Ambiguity × Time was marginally significant ($F(1,11) = 3.97$, $P = 0.072$) indicating that noncanonical sentences in the unambiguous conditions differed at an early time-point when compared to ambiguous sentences. Also, there were main effects of Word Order ($F(1,11) = 10.3$, $P < 0.008$) and Time-point ($F(1,11) = 21.8$, $P < 0.001$), but neither a main effect of Ambiguity ($F < 1$) nor a significant interaction between Word Order × Ambiguity ($F(1,11) = 1.9$, $P < 0.19$) was obtained.
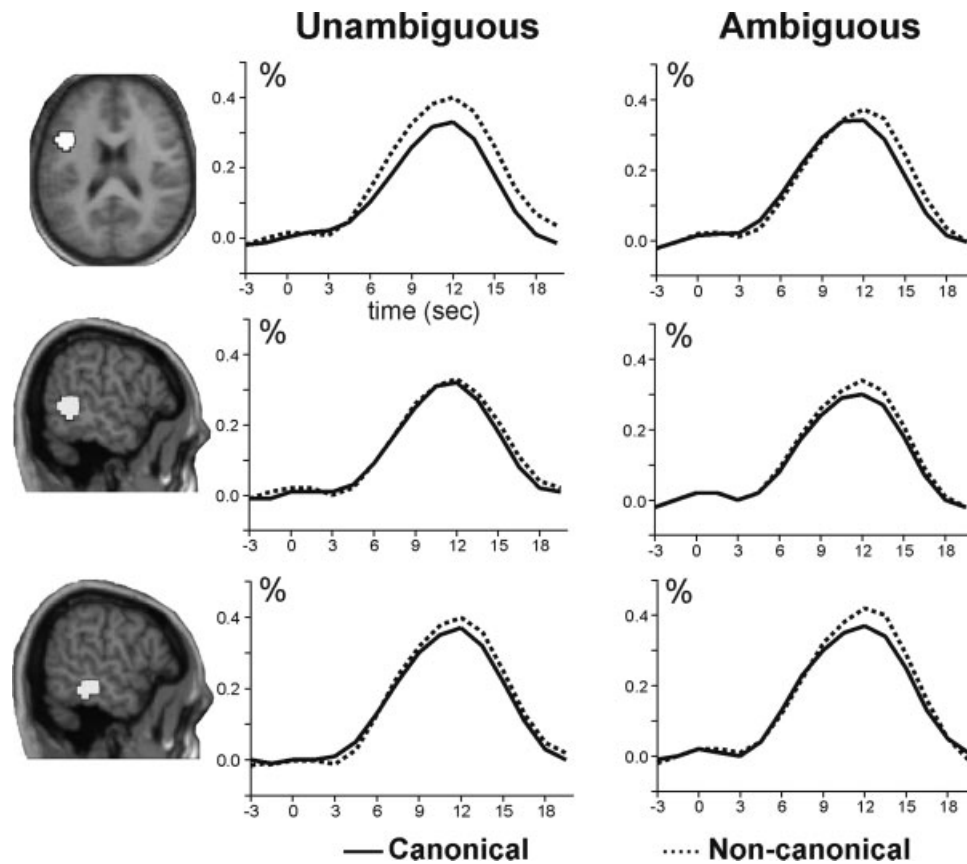
Figure 3.

Time course of the BOLD response in several regions of interest. The time-points on the x-axis are relative to sentence onset (0 s.) The ROI in the inferior frontal gyrus (upper panel, coordinates −44, 12, 20) showed a pronounced and early difference in the BOLD time course between noncanonical and canonical sentences for the unambiguous sentences. The corresponding difference for the ambiguous sentences was smaller and delayed. The second ROI encompassed the posterior part of the middle temporal gyrus (−56, −48, 0, middle panel) and showed a difference between noncanonical and canonical sentences in the ambiguous conditions only. The third ROI was located in the left inferior temporal gyrus (−56, −32, −16, lower panel): The difference between noncanonical and canonical sentences was more pronounced in the ambiguous sentences (see also Table III).

unambiguous sentences, while the posterior activation should be related to the reanalysis processes entailed by the noncanonical ambiguous sentences.

The Left Inferior Frontal Gyrus

Working memory account for this activation is supported by the time-course analyses. The ROIs were determined by the overall contrast of all conditions against baseline and not based on the results of the specific contrasts discussed before. Hence, the coordinates of the baseline contrast in Broca's area (−44, 12, 20) are close but not identical to those of the activation found for noncanonical unambiguous sentences (peak coordinates −40, 24, 28). Clearly, word-order effects appeared earlier (onset 6 s, Table III) and were more pronounced in the unambiguous sentences (c.f. Fig. 3). The onset of the BOLD differences in the unambiguous sentences suggests that the effect is triggered upon the encounter of the first noun-phrase, which in these sentences determines a subject or object first construction. In contrast, the onset of the BOLD word-order effect for the ambiguous sentences was later. This is due to the fact that up to the 8th word, or $t = 3.5$ s at the chosen presentation rate, noncanonical and canonical sentences are completely identical in the ambiguous sentences. Inferior frontal activations have also been found in studies examining the processing of complex sentences with long-distance syntactic dependencies [Ben-Shachar et al., 2003; Caplan, 2001; Caplan et al., 1998, 1999, 2002; Inui et al., 1998; Just et al., 1996; Keller et al., 2001; Röder et al., 2002; Stromswold et al., 1996]. Also, similar frontal regions have been found to be activated for tasks requiring the comparison of two consecutively presented sentences, thus involving aspects of working memory [Dapretto and Book-heimer, 1999]. Indeed, various verbal working memory tasks have been shown to activate the left IFG [Gabrieli

TABLE III. Pairwise serial t tests noncanonical vs. canonical word order in three regions of interest (c.f. Fig. 3 and corresponding legend for coordinates)

Seconds	Broca		GTM		GTI	
	Unamb.	Ambiguous	Unamb.	Ambiguous	Unamb.	Ambiguous
4.5	−0.2	1.2	0.7	−1.4	1.5	−0.5
6	−1.6	0.7	0.2	−2	0.3	−0.1
7.5	−2.7*	0.5	−1.6	−0.2	−0.6	−0.3
9	−3.1*	0.3	−0.4	−0.4	−1	−1.7
10.5	−2.8*	−0.1	−0.5	−0.7	−1.2	−2.8*
12	−2.9*	−1.2	−0.7	−2	−1.4	−3.5**
13.5	−3.5**	−2.4*	−1.1	−2.6*	−1.3	−2.8*
15	−4.4***	−2.4*	−1.5	−2.4*	−1.1	−2.3*
16.5	−3.4**	−1.8	−1.3	−1.8	−0.5	−1.8
18	−2.4*	−0.8	−1.3	−0.7	−0.5	−0.9

All ROI are left hemisphere
*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

et al., 1998; Paulesu et al., 1993]. Investigating the neural effects of filler-gap dependencies, i.e. syntactic constructions that require the maintenance of an item (filler) in working memory until the position, from which it has been displaced (gap), is encountered, Fiebach et al. [2001] found left inferior frontal activity for conditions with greater working memory demands.[2]

The present data and the aforementioned studies can be accommodated by a recent psycholinguistic model [Gibson, 1998]. This model describes how the limited resources of the parser are distributed during the on-line comprehension of speech and allows quantitative predictions for different types of structural configurations, such as subject relative versus object relative clauses. Syntactic complexity is a function of the integration costs and the memory costs of a sentence. To apply this to the noncanonical sentences of the present study, the higher integration costs in the object-first sentences results from the fact that the predicted category must be kept in memory until the prediction of the element is satisfied. This implies greater working memory demands on object-fist sentences, due to the greater cost for maintaining the category prediction. In terms of the ambiguity effects, Gibson's model assumes that the parser chooses the structure with the less memory costs. In the present study this would result in a subject-fist strategy. The parser has to reevaluate the structure at the first position of the last NP, which in our view is reflected by the increased Broca activity for ambiguous sentences in comparison to the unambiguous

sentences (in the ROI analysis at $t = 13.5$ s, approximately at the 8th word).

Another recent, interesting development is the new version and computational implementation of the unification model by Vosse and Kempen [2000]. According to the account, incoming words activate "lexical frames," conceptualized as elementary trees attached to the input and a number of candidate "unification links" is set up between the different frame nodes. Importantly, these links represent tentative attachments that are graded rather than all-or-none. With regard to classical garden path sentences, the model mimics the performance of human comprehenders: the less preferred reading has a lesser initial attachment strength and its activation level is rapidly reduced by lateral inhibition from the preferred attachment.

In a neurophysiological extension of the Vosse and Kempen [2000] account, Hagoort [2005] proposes that the inferior frontal cortex subserves the *unification* of the independent elements of the hierarchical structure of a sentence into a coherent overall representation drawing on phonological, semantic and syntactic information. Critically, he argues, language comprehension is extended over time and therefore the lexical building blocks need to be kept activated for some time in working memory while unification operations take place. Inspired by recent neuroimaging research Friederici [2004b] suggested that "Broca's area (BA44/45) is most obviously activated during language processing when long-distance dependencies and transformational structures (i.e. hierarchical structures) are processed," which would be in line with the present data set.

These extended working memory accounts fit the present data and go also well with our previous ERP study using the same materials [Matzke et al., 2002]. With regard to the Vosse and Kempen [2000] model the fact that there was no noticeable difference in across sentence averages between unambiguous canonical and ambiguous sentences our ERP data would imply that the activation of the object first reading is declining very rapidly.

[2]We would like to point out, however, that a working memory view of the role of the pars opercularis of the left IFG has recently been challenged by Bornkessel et al. [2005]. These authors manipulated word order (subject first versus object first), ambiguity (ambiguous case marking versus unambiguous case marking), and verb type (active verb versus dative object-experiencer verb). Their study showed word order effects in the left inferior frontal region which were modulated by the verb-type used in a particular sentence.

The Left Temporal Lobe

The word order effect seen for the ambiguous sentences (left BA40) echoes recent findings in the literature. For example, using a standard violation paradigm ("My parents couldn't sleep because the baby would cry/cries/phone"), Kuperberg et al. [2003b] reported activation of the morphosyntactically anomalous sentences ("cries") for left (and right) BA40 relative to correct ("cry") and pragmatically ("phone") anomalous sentences. Critically, this condition was also associated with a P600 effect in an ERP experiment conducted in parallel with the same materials. Because in their study BA40, as well as the cuneus and the posterior cingulate cortex, showed a deactivation for all sentence conditions relative to the resting baseline, Kuperberg et al. [2003b] discussed the differences between conditions in the sense of "differential deactivations." They point out that "it is unlikely that the increased BOLD parietal response in association with morphosyntactically anomalous sentences relative to normal sentences or pragmatically anomalous sentences is a specific marker of linguistic syntax." Following Raichle [1998] the differential deactivation of this region was interpreted to reflect the differential attentional demands of the various conditions. To the extent that these regions are related to the generation of the P600 response of the ERP, such an interpretation would go well with accounts of this component that put less emphasis on its syntactic specificity [Coulson et al., 1998; Hagoort, 2003; Kolk et al., 2003; Kuperberg et al., 2003a; Munte et al., 1998a; van Herten et al., 2005]. In line with these studies and with our task analysis we propose that the activation of BA40 is related to the recomputation demands necessitated by the ambiguous noncanonical sentences.

In addition, based on the overall activation pattern of sentence conditions relative to fixation control a region of interest in the posterior part of the middle temporal cortex was determined, which showed a modulation of activity in ambiguous sentences (noncanonical > canonical), only (c.f. Fig. 3, Table III). The posterior part of the medial temporal gyrus has been found active in 6 (of 26) brain-imaging studies addressing syntactic processing surveyed by Indefrey [2004] in a recent meta-analysis. It thus has been observed previously in conjunction with syntactic processing. Both, the fact that a canonicity-effect was seen in the ambiguous but not in the unambiguous sentences and its timing (significant at 13.5 and 15 s, see Table III), suggest that this region, as the supramarginal gyrus discussed above, is involved in the reanalysis of the noncanonical sentences triggered by the second noun-phrase.

CONCLUSION

To summarize, the present investigation revealed distinct activations reflecting (syntactic) working memory and reanalysis aspects of sentence comprehension. While the former is subserved by the left inferior frontal cortex including Broca's (BA44), areas in the temporal lobe including the left supramarginal (BA40) and medial temporal gyrus (BA21/37) are involved in the latter.

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