Prominence vs. aboutness in sequencing: A functional distinction within the left inferior frontal gyrus

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**Abstract**

Prior research on the neural bases of syntactic comprehension suggests that activation in the left inferior frontal gyrus (lIFG) correlates with the processing of word order variations. However, there are inconsistencies with respect to the specific subregion within the IFG that is implicated by these findings: the pars opercularis or the pars triangularis. Here, we examined the hypothesis that the dissociation between pars opercularis and pars triangularis activation may reflect functional differences between clause-medial and clause-initial word order permutations, respectively. To this end, we directly compared clause-medial and clause-initial object-before-subject orders in German in a within-participants, event-related fMRI design. Our results showed increased activation for object-initial sentences in a bilateral network of frontal, temporal and subcortical regions. Within the lIFG, posterior and inferior subregions showed only a main effect of word order, whereas more anterior and superior subregions showed effects of word order and sentence type, with higher activation for sentences with an argument in the clause-initial position. These findings are interpreted as evidence for a functional gradation of sequence processing within the left IFG: posterior subportions correlate with argument prominence-based (local) aspects of sequencing, while anterior subportions correlate with aboutness-based aspects of sequencing, which are crucial in linking the current sentence to the wider discourse. This proposal appears compatible with more general hypotheses about information processing gradients in prefrontal cortex (Koechlin & Summerfield, 2007).

1. Introduction

During real-time communication, language unfolds over time, and, as a result, language understanding must proceed in a sequential manner. Hence, the order in which the words that make up a sentence occur crucially constrains the possible ways in which that sentence can be understood. In view of these considerations, it is not surprising that word order variations have played an exceptionally important role in investigations of the functional neuroanatomy of language processing. Over several languages (e.g., English, German, Hebrew and Japanese) and different sentence types (relative clauses, questions, declarative sentences), researchers have consistently observed increased activation in the left inferior frontal gyrus (lIFG) for sentences with object-before-subject orders in comparison to their subject-initial counterparts (e.g., Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996; Bahlmann, Rodriguez-Fornells, Rotte, & Münte, 2007; Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Ben-Shachar, Palti, & Grodzinsky, 2004; Caplan, Alpert, & Waters, 1998; Caplan, Alpert, Waters, & Olivier, 2000; Constable et al., 2004; Cooke et al., 2001; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Fiebach, Vos, & Friederici, 2004; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Keller, Carpenter, & Just, 2001; Kinno, Kawamura, Shioda, & Sakai, 2008; Röder, Stock, Neville, Bien, & Rössler, 2002). From these findings, it has been concluded that object-initial sentences are more complex to process, leading to measurably increased processing demands in healthy individuals and to comprehension deficits in patient populations (e.g., Caramazza & Zurif, 1976; Drai & Grodzinsky, 2006).

1.1. Prominence information and sequencing

Recent research suggests that, rather than being primary to the activation of the lIFG, the relative ordering of subject vs. object is only a subcase of more general requirements concerning the...
sequencing of information within a sentence. Thus, the degree of activation engendered by a particular word order depends on a variety of different information types that go beyond the mere subject–object dichotomy. For example, Chen, West, Waters, and Caplan (2006) found that the IIFG activation increase for object vs. subject-relative clauses in English depends on the animacy of the sentence participants (cf. example 1). Whereas object-relative clauses with an animate head noun and an inanimate relative clause subject (1a) engendered the typical pattern of increased IIFG activation (pars opercularis and pars triangularis) in comparison to minimally differing subject-relative clauses, object-relative clauses with an animate head noun and an animate relative clause subject (1b) did not.

Chen and colleagues’ results suggest that the increased inferior frontal activation observed for object-relative clauses in previous studies cannot be reduced to the (syntactic or general cognitive) ramifications of an object-before-subject order. Rather, other factors must also be taken into account. This perspective is supported by a range of studies on German, which revealed that the pars opercularis of the IIFG (POp) is sensitive to various linearization parameters such as “animate-before-inanimate” (Grewe et al., 2006), “pronoun before non-pronoun” (Grewe et al., 2005), “definite/specific before indefinite/non-specific” (Bornkessel-Schlesewsky et al., 2008), and “higher thematic role before lower thematic role” (Bornkessel et al., 2005). Whereas some of these findings showed that object-initial orders do not engender increased activation in the pars opercularis when other linearization preferences are fulfilled (Bornkessel et al., 2005; Grewe et al., 2005), others even demonstrated increased activation for subject-initial in comparison to object-initial orders (Grewe et al., 2006) or between subject-initial orders (Bornkessel-Schlesewsky et al., 2009). Notably, the information types which have been shown to influence word order-related activation in the left pars opercularis are not arbitrary. Rather, these so-called “prominence scales” are well-known from cross-linguistic investigations because they influence morphosyntactic phenomena (e.g. case marking) in a range of typologically different languages (cf. Comrie, 1989; Croft, 2003).

In summary, a number of fMRI findings are indicative of a correlation between the left POp and the sequencing of linguistic information. Crucially, sequencing-related activation is modulated by a range of different information types (cf. Bornkessel-Schlesewsky & Schlesewsky, 2009).

### 1.2. Linguistic sequencing: pars opercularis or pars triangularis of the IIFG?

The vast majority of the studies discussed in the previous section showed increased word order-related activation in the left pars opercularis (POp). However, the assumption of a specific correlation between this subregion of the IIFG and sequencing/linearization processes is called into question by a number of findings showing word order-related activation maxima in the pars triangularis of the IIFG (PTr). These observations stem from German (Bahlmann et al., 2007), Hebrew (Ben-Shachar et al., 2004), and Japanese (Kinno et al., 2008).\(^3\)

Interestingly, the sentence structures used in these studies suggest that there may be a principled reason for the distinction between POp and PTr activation in relation to word order variations. Whereas the many findings of POp activation in German all stem from studies which used clause-medial argument order permutations (Bornkessel et al., 2005; Bornkessel-Schlesewsky et al., 2009; Friederici et al., 2006; Grewe et al., 2005, 2007; Röder et al., 2002), the word order permutations in the studies reporting activation maxima in the PTr targeted the clause-initial position (Bahlmann et al., 2007; Ben-Shachar et al., 2004; Kinno et al., 2008). The distinction between these two types of word order permutations is illustrated on the basis of German in examples (2) and (3).

\(^2\) We have previously argued that this observation supports a “supra-syntactic” account of IIFG (and specifically pars opercularis) function in the processing of word order variations (Bornkessel, Zysset, Friederici, von Cra mom, & Schlesewsky, 2005; Bornkessel-Schlesewsky, Schlesewsky, & von Cronm, 2009; Grewe et al., 2005; Grewe et al., 2006). However, which information types are viewed as syntactic depends on the particular theory of grammar which one adopts. Thus, the question of whether information types such as animacy and definiteness/specificity are to be viewed as syntactic or non-syntactic is perhaps not of primary importance to understanding the function of Broca’s region in linguistic sequencing (word order). In this regard, we agree with Embick and Poppel (2003), who argued that the question of whether Broca’s region mediates syntactic computation is too coarse at both a cognitive and a neuroanatomical level, since “syntax” is not a single, monolithic task, nor is “Broca’s area” a single, monolithic area of the brain. In this paper, we therefore abstract away from questions regarding syntactic vs. non-syntactic processes or representations and rather focus on the specific requirements of different aspects of sequencing.

\(^3\) Two recent neuroimaging studies on English have also revealed word order-related activations in the POp (Santi & Grodzinsky, 2007a) and PTr (Santi & Grodzinsky, 2007b) of the left IFC, respectively. At a first glance, this variability across experiments appears difficult to explain because both studies were conducted in a highly comparable manner and, according to the authors, with a comparable manipulation. Nevertheless, these findings also indicate that it is important to shed further light on the precise functional role of the different subregions within the left IFC during the processing of word order.

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**Example stimuli from Chen et al. (2006)**

(a) The golfer that the lightning struck survived the incident.

(b) The wood that the man chopped heated the cabin.
1.3. What’s special about the clause-initial position?

As described in the previous section, German allows object fronting to either occur in the medial portion of the clause or to target the clause-initial position. These two scenarios are often referred to as “scrambling” (cf. example 3) and “topicalization” (cf. example 2), respectively. The two types of argument order permutations differ with regard to several properties, all of which could, in principle, be responsible for the apparent neuroanatomical distinction between the POp and the PTr.

1.3.1. Different types of syntactic properties/operations (double dissociation)

For German, the clause-initial (prefield) and clause-medial (middlefield) regions have often been associated with different syntactic properties.

Within the context of theoretical linguistic approaches which assume that word order permutations come about by means of movement operations (Chomsky, 1981), it has been debated whether scrambling and topicalization involve the same type of movement or different types of movement (for a discussion from a psycholinguistic perspective, see Friederici, Schlesewsky, & Fiebach, 2003). For example, Haider and Rosengren (2003) proposed that scrambling should be analyzed as “A movement”, while topicalization constitutes a case of “A-bar movement” (for an introduction to the difference between these two movement types, see Haegeman, 1994). If these different types of syntactic operations are implemented in a dissociable manner by the human brain (as proposed, for example, by Ben-Shachar et al., 2004), one should expect to observe a double dissociation between clause-medial and clause-initial word order permutations. On the basis of previous findings, this would most likely manifest itself in terms of increased POp activation for clause-medial object- vs. subject-initial orders as opposed to increased PTr activation for clause-initial object- vs. subject-initial orders.

A similar prediction can be derived from syntactic theories which assume a movement-independent differentiation between the prefield and middlefield. In Role and Reference Grammar (Van Valin, 2005), for example, the middlefield is analyzed as part of the “core” region of the clause, while the prefield is analyzed as a “pre-core slot” (Diedrichsen, 2008). While the core constitutes the minimal syntactic environment in which the verb and its arguments are realized, the pre-core slot is associated with information structural consequences (see below for more details on information structure and the prefield). From this movement-independent perspective, too, we could therefore predict a double dissociation between clause-initial and clause-medial word order permutations due to the differing syntactic environments in which they occur.

1.3.2. The clause-initial position and the notion of “aboutness”

Word order permutations in the clause-initial and clause-medial regions of the German clause also differ with regard to how they affect the “information structure” of a sentence. The term information structure refers to the fact that the same proposition can be expressed in different ways depending on which parts of the sentence the speaker wishes to emphasize (e.g. Lambrecht, 1994). As an illustration, consider the examples in (4).

\[(4)\]
\[
\text{(a) John accused Mary of murder.} \\
\text{(b) Mary was accused of murder by John} 
\]

Sentences (4a) and (4b) describe the same event. However, they differ in that this event is construed as being more strongly “about” John in (4a) and more strongly about Mary in (4b). This notion of aboutness is classically used to define the topic – comment structure of a sentence, i.e. what the sentence is about (its topic) and what is said about the topic (the comment). Reinhart (1981), for example, defines “[a] topic [as] an expression whose referent the sentence is about. The concept ‘topic’ is a category of pragmatic aboutness”. Note that, while the division between topic and comment overlaps to a certain degree with the distinction between old and new information, and thereby with the link between an individual sentence and the broader discourse, it is logically independent of it.

For German, it is often assumed that the clause-initial position (the so-called “prefield”) is more closely linked to aboutness than the medial portion of the clause (the “middlefield”) (e.g. Fenselov, Lenertová, & Lenertová, in press; Speyer, 2007; see also the discussion in Frey, 2007, and the references cited therein). In other words, the default interpretation of an argument in the prefield, whether it is a subject or an object, is as sentence topic. By contrast, clause-medial argument order is determined more closely by prominence considerations related to the arguments themselves such as thematic roles, animacy etc. (e.g. Lenerz, 1977; Müller, 1999). Notably, in the absence of additional information (e.g. further prominence distinctions between the arguments or a particular discourse context), object-before-subject orders pose a problem for both sentence-internal and aboutness or sentence topic-based ordering considerations: subjects are more prominent than objects and subjects rather than objects tend to convey old or “topical” information (e.g. Chafe, 1976; Keenan, 1976).

On the basis of these theoretical considerations, we hypothesize that the distinction between POp and PTr activation in previous studies of word order variations in German may reflect differing contributions of prominence-based and aboutness-based sequencing considerations, respectively. By analogy with the prefield results from German, the findings of PTr activation maxima for clause-initial word order permutations in Hebrew and Japanese could also be taken to reflect a strong contribution of aboutness-based processing considerations. Note that, if this hypothesized difference between prominence-based and aboutness-based sequencing is borne out, it could be due either to different cognitive operations or to a single cognitive operation (e.g. “selection for position”, see Thothathiri, Schwartz, & Thompson-Schill, 2010) which is applied to different kinds of sequence-related information. While this is difficult to specify a priori, we favor the second possibility for reasons of parsimony.

1.4. The present study

If our interpretation of the previous fMRI findings in German, Hebrew and Japanese is correct, differences between POp and PTr activation for word order permutations can be attributed to dissociable functional characteristics of the clause-initial and clause-medial regions rather than to cross-experimental differences in materials, task or methodology. Consequently, the two types of word order permutations should be expected to show a neuroanatomical distinction in a direct within-participants comparison. The present study aimed (a) to examine whether this assumption is indeed borne out and (b) to contrast the different functional hypotheses outlined above.

4 Note that Frey (2004) proposed that the German middlefield also contains a designated position for sentence topics. However, in contrast to the prefield, which is identifiable in and of itself, the sentence-medial topic position can only be identified in the presence of a particular type of sentence adverbial, which a sentence topic must precede (e.g. zum Glück, ‘luckily’; anschneidend, ‘apparently’; wahrscheinlich, ‘probably’). Since neither previous fMRI studies of word order in German nor the present study employed such adverbs in the middlefield, no effects of the clause-medial topic position are to be expected.
To this end, the experimental design crossed the factors “permutation type” (TYPE: clause-medial, M vs. clause-initial, I) and “word order” (ORDER: subject-before-object, SO vs. object-before-subject, OS) in a 2 × 2 design. The resulting four critical conditions are illustrated in Table 1.

In order to allow for a comparison of the two permutation types under similar conditions, we employed matrix clauses containing so-called “bridge verbs” (Vikner, 1995). These verbs allow for an embedding of subordinate clauses introduced by the complemen-
tizer dass (and thus calling for a verb-final order; conditions SO-M and OS-M in Table 1) and of verb-second clauses (conditions SO-I and OS-I in Table 1). By comparing object- and subject-initial orders in these two types of sentence structures, we can contrast clause-medial (OS-M vs. SO-M) with clause-initial (OS-I vs. SO-I) word order permutations, while at the same time avoiding a con-
 founding influence of clause-type (subordinate vs. main).

In accordance with the previous findings cited above, we expected to observe an activation increase for object-initial orders in the pars opercularis (POp) and pars triangularis (PTr) of the lIFG. If hypothesis 1 (different syntactic operations/positions) is borne out, we should observe a double dissociation with clause-initial and clause-medial object-initial orders expected to engender activa-
tion increases in the PTr and POp, respectively, in comparison to their subject-initial counterparts. According to hypothesis 2 (prominence vs. aboutness), by contrast, the POp should be ex-
pected to show a main effect of word order, while the PTr should be expected to show a general effect of word order, since subjects are expected to observe an activation increase for object-initial orders (OS-I vs. SO-I) and also an effect of word order (since subjects are more typical instances of aboutness-based sentence topics.

2. Materials and methods

The experimental procedures were performed in accordance with the Declaration of Helsinki and were approved by the local ethics committee.

2.1. Participants

Eighteen students (11 women; mean age 26.0; age range 21–33 years) took part in the fMRI study. All participants were monolingually raised, native speakers of German, had normal or corrected-to-normal vision, and were right-handed as indicated by a German version of the Edinburgh Inventory (Oldfield, 1971).

<table>
<thead>
<tr>
<th>Condition</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>SO-M</td>
<td>Peter [teacher] behauptet, dass [der Lehrer] den Arzt [verfolgt] hat. Peter claims that [the teacher] has [the doctor] pursued has 'Peter claims that the teacher pursued the doctor.'</td>
</tr>
<tr>
<td>OS-M</td>
<td>Peter [teacher] behauptet, dass [der Arzt] den Lehrer [verfolgt] hat. Peter claims that [the doctor] has [the teacher] pursued has 'Peter claims that the doctor pursued the teacher.'</td>
</tr>
<tr>
<td>SO-I</td>
<td>Peter [teacher] behauptet, dass [der Lehrer] [hat] den Arzt [verfolgt]. Peter claims [the teacher] has [the doctor] pursued 'Peter claims the teacher pursued the doctor.'</td>
</tr>
<tr>
<td>OS-I</td>
<td>Peter [teacher] behauptet, dass [der Arzt] [hat] den Lehrer [verfolgt]. Peter claims [the doctor] has [the teacher] pursued 'Peter claims the teacher pursued the doctor.'</td>
</tr>
</tbody>
</table>

Table 1

Example sentences for each of the four critical conditions in the present study (stimulus segmentation for visual presentation indicated by vertical bars). Abbrevi-
tations: SO = subject-before-object; OS = object-before-subject; M = clause-medial argument order permutation (i.e. both arguments in the clause-medial region, the middlefield); I = clause-initial argument order permutation (i.e. first argument in the clause-initial prefield, second argument in the middlefield).

Informed written consent was obtained from all participants prior to the scanning session.

2.2. Materials

Four types of grammatically correct German declarative active sentences were used in the present study (see Table 1). Only unrelated noun phrase combinations were chosen in order to avoid lex-
ical-semantic biases with respect to the relation between subject and object. Each of the critical conditions contained 35 sentences, which were presented visually to every participant. In order to balance the acceptability for the behavioral task (see below), these critical sentences were interspersed with two types of grammatically incorrect filler sentences (70 in total). The fillers involved an incorrectly positioned verb, but were otherwise similar to the experimental sentences. Altogether, the participants read 210 sen-
tences, of which 70 were highly acceptable (the subject-initial sen-
tences), 70 were unacceptable (the ungrammatical fillers, SO and OS) and 70 were assumed to be of degraded acceptability (the ob-
ject-initial sentences). To improve statistical evaluation of the data (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000), 35 null events (empty trials) were introduced. Each participant was thus presented with a total of 245 trials.

2.3. Procedure

Stimuli were projected onto a screen and viewed by the partic-
ipant via a mirror mounted on the head-coil. In order to control for reading strategies, all sentences were presented in a segmented manner. Every segment was presented for 400 ms in the center of the screen with an interstimulus interval (ISI) of 100 ms (seg-
mentation indicated in Table 1). Each trial began with an asterisk, which was presented for 300 ms (plus 200 ms ISI) and ended with a 500-ms pause. Finally, a question mark signaled to participants that they were required to judge the acceptability of the preceding sentence. The participants accomplished this judgment task by pressing one of two push-buttons with their right index and middle fingers and were given maximally 1500 ms to respond. The assignment of fingers to acceptable and unacceptable was counter-balanced across participants.

Trials were presented with variable onset delays of 0, 400, 800, 1200, or 1600 ms, thereby leading to an oversampling of the actual image acquisition time of 2000 ms by a factor of five (Miezin et al., 2000). Every trial had a length of 8 s, resulting in a total measure-
ment time of 33 min, which was separated into two functional runs.

Each participant completed a short practice session before entering the scanner.

2.4. fMRI data acquisition

The experiment was carried out on a 3 T scanner (Siemens TRIO, Erlangen). Twenty axial slices (19.2 cm FOV, 64 by 64 matrix, 3 mm thickness, 0.6 mm spacing, 3 mm × 3 mm in-plane resolution) per-
allel to the AC-PC plane were collected using a single shot, gradient recalled sequence (TR 2000 ms, TE 30 ms, 90° flip angle). As the main focus of the experiment was on the activation of different subregions within the IFG, the slice thickness and spacing were chosen to allow for a relatively high spatial resolution for these regions of interest. For this reason, it was not possible to cover the whole head and no signal was acquired for superior parts of the frontal and parietal lobes as well as for inferior parts of the cerebel-
um. The exact slice coverage depended on individual brain size.

Two functional runs of 490 time points were collected (includ-
ing two “dummy” trials at the beginning of each run, which did not enter the data analysis), with each time point sampling over the 20
slices. Prior to the functional runs, 20 anatomical T1-weighted MDEFT (Ugurbil et al., 1993) images (data matrix 256 × 256, TR 1.3 s, TE 7.4 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000). For registration purposes, a set of T1-weighted spin-echo EPI images (TE 14 ms, TR 3000 ms) were taken with the same geometrical parameters (slices, resolution) and the same bandwidth as used for the fMRI data. A slice-selective inversion pulse was applied with an inversion time of 1200 ms.

2.5. fMRI data analysis

The fMRI data were analyzed with the LIPSIA software package (Lohmann et al., 2001), which contains tools for preprocessing, registration, statistical evaluation and presentation of fMRI data.

In a first step, the functional data were corrected for motion using a matching metric based on linear correlation. A cubic-spline-interpolation based on the Nyquist–Shannon-Theorem was applied to correct for the temporal offset between the slices acquired in one scan. A temporal highpass filter with a cutoff frequency of 1/112 Hz and a spatial Gaussian filter with 5.65 mm full width half-maximum (FWHM) was used for the baseline correction of the signal. Furthermore, a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed to align the functional data slices onto a 3D stereotactic coordinate reference system. The rotational and translational parameters were acquired on the basis of the MDEFT and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data sets. This 3D reference data set was collected for each participant during a previous scanning session. The MDEFT volume data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach & Tournoix, 1988). The same rotational and translational parameters were normalized, i.e., transformed to a standard size via linear scaling. The resulting transformation parameters were then applied to the functional slices via trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. This linear normalization process was improved by a subsequent processing step that carries out an additional nonlinear normalization and serves to adjust structural–anatomical differences between different brains by using a procedure known as “demon matching” (Thirion, 1998). Here, an anatomical 3D data set is deformed so that it matches another 3D data set that serves as a fixed reference image.

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (see Aguirre, Zarah, & d’Esposito, 1997; Friston et al., 1995; Worsley & Friston, 1995; Zarah, Aguirre, & d’Esposito, 1997). The design matrix was generated with a box-car function convolved with the hemodynamic response function. The model equation, including the observation data, the design matrix as well as the error term, was convolved with a Gaussian kernel of dispersion 4 s FWHM to deal with the temporal autocorrelation (Worsley & Friston, 1995). In a next step, contrast maps were generated for each participant. The ungrammatical filler sentences were modeled as covariates of no interest such that only the four critical conditions entered the contrasts of interest. As the individual functional datasets were all aligned to the same stereotactic reference space, a group analysis was performed. The single-participant contrast-images were entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample t-test across the contrast images of all subjects that indicated whether observed differences between conditions were significantly distinct from zero (Holmes & Friston, 1998). Subsequently, t-values were transformed into Z-scores. The results were corrected for multiple comparisons using double thresholding: a single voxel probability level of p < 0.005 (z = 2.576) and a cluster-wise probability level of p < 0.05 (cluster size and cluster probability). Appropriate cluster sizes were computed using Monte Carlo simulations (Lohmann, Neumann, Mueller, Lepsien, & Turner, 2008).

3. Results

3.1. Behavioral data

For the analysis of the behavioral data, repeated-measures analyses of variance (ANOVA) were computed using the factors permutation type (TYPE: clause-medial, M vs. clause-initial, I) and argument order (ORDER: SO vs. OS).

The mean acceptability rates in the behavioral task were: SO-M (99%; sd = 0.14); OS-M (67%, sd = 0.33); SO-I (98%, sd = 0.02); OS-I (99%, sd = 0.01). The global analysis showed main effects of TYPE (F(1, 17) = 9.74; p < 0.007) and ORDER (F(1, 17) = 12.55; p < 0.004) as well as an interaction between the two factors (F(1, 17) = 10.58; p < 0.006). Subsequent pairwise comparisons revealed significant effects of ORDER for clause-medial (SO-M vs. SO-I: F(1, 17) = 14.66, p < 0.002) but not for clause-initial word order permutations (OS-I vs. SO-I: F(1, 17) = 2.99; p > 0.1).

The reaction times showed the following mean values per condition: SO-M (386 ms, sd = 119); OS-M (465 ms, sd = 170); SO-I (445 ms, sd = 136); OS-I (449 ms, sd = 156). The global analysis again revealed significant main effects of TYPE (F(1, 17) = 11.18, p < 0.004) and ORDER (F(1, 17) = 14.40, p < 0.001). However, the interaction between both factors was not significant (F(1, 17) = 3.12, p > 0.09).

The behavioral data provide converging support for the assumption that object-initial sentences are more difficult to process than their subject-initial counterparts, as evidenced by increased reaction times. Object-initial orders in the clause-medial region additionally gave rise to an acceptability drop, whereas clause-initial object-initial orders did not.

3.2. fMRI data

For the analysis of the fMRI data, we proceeded in two steps. First, we aimed to examine which of the regions that are sensitive to word order also respond to the difference between the two sentence types examined and which do not. To this end, we computed the ORDER contrast (i.e. OS-M/OS-I vs. SO-M/SO-I) and then masked this contrast inclusively and exclusively with the TYPE contrast (i.e. SO-I/OS-I vs. SO-M/OS-M). Inclusive masking allowed us to identify regions that showed increased activation for object-initial vs. subject-initial orders and also for clause-initial vs. clause-medial word order variations. Exclusive masking, by contrast, revealed regions that showed increased activation for object-initial vs. subject-initial orders but did not respond to the contrast of sentence type.

In a second step, we computed the interaction contrast ORDER × TYPE in order to examine the possibility that clause-medial and clause-initial word order permutations may show a double dissociation.

These analyses will be reported in turn in the following. Note that we will not consider main effects of TYPE (i.e. the contrast SO-M/OS-M vs. SO-I/OS-I) because these are potentially confounded by sentence length (the sentences with clause-medial permutations contained one additional word). Hence, effects of TYPE will only be considered when they co-occur with effects of ORDER or occur as part of an interaction.

3.2.1. Effects of ORDER and TYPE

The ORDER contrast (object-initial – subject-initial sentences) yielded activation in a widely distributed network of bilateral infero-
ior and middle frontal regions, bilateral subcortical regions (thalamus), left anterior cingulate cortex (ACC) and left middle and superior temporal regions (see Table 2).5

In order to further investigate the influence of sentence type within the overall network sensitive to word order permutations, we masked the ORDER contrast with the TYPE contrast. The results of the inclusive masking are shown in Fig. 1 and Table 3 and those of the exclusive masking are shown in Fig. 2 and Table 4.

The masking analyses reported in Tables 3 and 4 revealed disso-
ciations in both frontal and temporal regions. Whereas superior and anterior portions of the left IFG, right PTr and IFS and left STS/STG showed a sensitivity to both word order and sentence type, posterior and inferior portions of the left IFG extending into the IFS, right IFJ, and a slightly more posterior portion of left STS/STG only showed an effect of word order. The thalamus and left ACC also only showed an ORDER effect but were not sensitive to sentence type. For the IIFG, the dissociation between subregions showing only an ORDER effect (revealed via exclusive masking) and subregions showing effects of both ORDER and TYPE (revealed via inclusive masking) is readily apparent in Fig. 3.

In order to examine whether the activation patterns in posterior and anterior IIFG (as identified via the masking procedure) indeed differ significantly from one another, we conducted an additional analysis in which we directly compared the activation patterns across the two regions. To this end, we extracted the time course of the underlying BOLD signal for the voxel with the highest z-value (in the group contrast) in the two masked contrasts (exclusive masking: maximum in the PO; inclusive masking: maximum in the PTr). The percent signal change (relative to the mean signal intensity) was averaged for each condition and participant. The extracted time courses (mean percent signal change for a time window from −2 to +2 s relative to the maximal signal change) were subjected to repeated measures ANOVAs involving the within-participant factors word order (ORDER; subject–object vs. object–subject) sentence type (TYPE; clause-medial vs. clause-initial word order permutation) and region (REG; posterior vs. anterior). This analysis revealed main effects of ORDER (F(1, 17) = 3.105; p < 0.001) and TYPE (F(1, 17) = 5.92; p < 0.03) as well as an interaction REG × TYPE (F(1, 17) = 6.73; p = 0.01). The interaction reflected the fact that the anterior subregion showed an effect of TYPE (F(1, 17) = 7.90; p < 0.02), whereas the posterior subregion did not (p > 0.11).

3.2.2. Interaction ORDER × TYPE

The interaction contrast ORDER × TYPE revealed increased activation in the left insula and right parahippocampal gyrus (see Table 5). In order to determine the source of these interactions, separate ANOVAs were computed over the time courses of the BOLD signal for clause-medial and clause-initial sentence types in each of these three regions (extraction of the time course signal as described for the cross–regional analysis above). All regions showed an ORDER effect for clause-medial word order permutations (L posterior insula: F(1, 17) = 9.67, p < 0.01; L mid insula: F(1, 17) = 11.15, p < 0.01; R parahippocampal gyrus: F(1, 17) = 4.50, p < 0.05), but none showed a significant ORDER effect for clause-initial word order permutations (L posterior insula: p > 0.26; L mid insula: F < 1; R parahippocampal gyrus: p > 0.72). Crucially, all of the order effects for the clause-medial word order permutations resulted from increased activation for subject- vs. object-initial orders.

4. Discussion

Previous fMRI studies of word order permutations have shown activation maxima in the pars opercularis and pars triangularis of the left IFG. Here, we investigated the hypothesis that this distinction may be due to differences between the clause-initial vs. clause-medial nature of the order permutation by examining the processing of subject- and object-initial orders in clause-medial and clause-initial regions of the German clause. Our results revealed a broadly distributed network of regions which showed increased activation for object- vs. subject-initial orders, including bilateral inferior frontal (IFG, IFS, IFJ) and subcortical regions (thalamus) as well as left superior temporal (STS/STG) and left anterior cingulate cortex (ACC). Within this overall network, posterior and inferior portions of the IFG, the ACC, thalamus and mid STS showed only an effect of word order. By contrast, reliable effects of word order and sentence type (increased activation for object-initial vs. subject-initial sentences and for clause-initial vs. clause-medial word order permutations, respectively) were observed in a slightly more posterior portion of left mid STS and in superior and anterior portions of the IFG. The two factors interacted in left middle and posterior insular cortex and in the right parahippocampal gyrus.

In the following, we first discuss these findings in relation to the hypotheses formulated in the introduction. We then go on to consider possible functional–neuroanatomical interpretations of the neural regions sensitive to both word order and sentence type (e.g. superior and anterior IIFG) and how they differ from regions sensitive only to word order (e.g. posterior and inferior IIFG). On the basis of these considerations, we propose a functional dissociation between aboutness and prominence-based sequencing within the left inferior frontal gyrus.

4.1. A neuroanatomical dissociation within the left IFG between different types of object-initial sentences?

The present findings do not support the apparent double disso-
ciation between different types of object-initial orders in German that was suggested by the comparison of Bahlmann et al.’s (2007) results on clause-initial word order permutations and previous findings on clause-medial permutations (e.g. Bornkessel et al., 2005; Bornkessel-Schlesewsky et al., 2009; Friederici et al., 2006; Grewe et al., 2005, 2007; Röder et al., 2002). Thus, the entire IIFG showed increased activation for both types of word order permutations (as did a wide range of further regions). Furthermore, we could not identify any regions that only showed increased

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Table 2

<table>
<thead>
<tr>
<th>Region Activation</th>
<th>Max. z-value</th>
<th>Volume (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. IFG (POp, PTr, PO); deep frontal operculum, anterior insula</td>
<td>−47 14 6</td>
<td>4.03</td>
</tr>
<tr>
<td>R. IFS/IFJ/PMC/IFG (POp, PTr, PO); deep frontal operculum, anterior insula</td>
<td>34 −1 30</td>
<td>3.84</td>
</tr>
<tr>
<td>L. ACC</td>
<td>−8 20 39</td>
<td>3.36</td>
</tr>
<tr>
<td>L. STS/STG</td>
<td>−47 −43</td>
<td>3.82</td>
</tr>
<tr>
<td>L/R. thalamus (nucleus medialis thalami)</td>
<td>12</td>
<td>5 −25 12</td>
</tr>
<tr>
<td>L/R. thalamus (nucleus anterior thalami)</td>
<td>−11 −16 3</td>
<td>3.72</td>
</tr>
</tbody>
</table>

---

5 Note that, in addition to the increased activation for object- vs. subject-initial sentences reported in Table 2, the ORDER contrast identified three regions that showed increased activation for subject- vs. object-initial sentences: the left postcentral gyrus (−50 −13 12), the right mid STS/MTG (49 −34 −3) and the right inferior parietal lobule (55 −31 27).
activation for object- vs. subject-initial orders in either clause-medial or clause-initial word order permutations. Those regions which only showed a word order difference for clause-medial sentences (left mid and posterior insula, right parahippocampal gyrus) showed increased activation for subject- vs. object-initial sentences. These findings therefore clearly speak against Hypothesis 1, i.e. against the assumption that clause-medial and clause-initial word order permutations constitute dissociable linguistic operations (e.g. different types of movement operations) which are processed in distinct brain regions.

Rather, our results suggest that the apparent dissociation between the two types of order permutations in previous studies may be attributable to differences in the maximal point of activation within the IIFG rather than to non-overlapping activations in distinct subregions. Indeed, at least two previous fMRI studies on clause-medial word order permutations in German observed activation that extended partially into the superior portion of the PTr (Bornkessel et al., 2005; Röder et al., 2002). Conversely, Bahlmann et al. (2007) also observed increased activation in the POp for clause-initial object-initial orders in a ROI analysis based on the activation maxima of the all sentence conditions vs. baseline contrast. These observations suggest that, in at least several previous studies, the inferior frontal activation for object-initial sentences encompassed both the superior portion of the left POp and the superior portion of the left PTr, even though the activation maxima differed for clause-medial and clause-initial word order permutations.

The present findings provide an indication of how these previous patterns of results may have come about. Recall that posterior and inferior portions of the IIFG (including the POp) only showed a main effect of word order (OS vs. SO), whereas superior and anterior portions of the IIFG (including the superior PTr) showed effects of both word order (OS vs. SO) and permutation type (clause-initial vs. clause-medial). This region was therefore most highly activated for sentences involving clause-initial objects. Hence, it appears plausible that the activation maximum for clause-initial object-before-subject orders in the study by Bahlmann et al. (2007) was located in superior PTr rather than in POp because both the object-before-subject order and the permutation type contribute to activation in this region.

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Table 3

Activated regions in the word order contrast masked inclusively by the sentence type contrast. Results were corrected for multiple comparisons at the cluster level ($p < 0.05$).

<table>
<thead>
<tr>
<th>Region</th>
<th>Activation maximum</th>
<th>Max. z-value</th>
<th>Volume (mm$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. IFG (anterior/superior)</td>
<td>47 20 3</td>
<td>3.70</td>
<td>3537</td>
</tr>
<tr>
<td>L. STS</td>
<td>47 – 40 6</td>
<td>3.68</td>
<td>540</td>
</tr>
<tr>
<td>R. IFG (anterior/superior)</td>
<td>43 23 6</td>
<td>2.82</td>
<td>135</td>
</tr>
<tr>
<td>R. IFS</td>
<td>43 20 21</td>
<td>3.82</td>
<td>297</td>
</tr>
</tbody>
</table>

---

Fig. 1. Group-averaged activations for the ORDER contrast (OS-M/OS-I vs. SO-M/SO-I) inclusively masked by the TYPE contrast (SO-I/OS-I vs. SO-M/OS-M). Activations are shown on sagittal slices of an individual brain normalized and aligned to the Talairach stereotactic space. In addition, the figure shows BOLD time courses for all four conditions for selected activation maxima. Results were corrected for multiple comparisons at the cluster level ($p < 0.05$).

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6 For this study, however, it cannot be excluded that the order effect in the POp is, in fact, prominence-based. In addition to placing an object in the clause-initial position, Bahlmann and colleagues’ object-initial sentences included a permuted prepositional phrase (PP) within the middlefield (cf. example 2; the basic word order would require the subject to precede the PP “during the Christmas party”). For a similar argument with respect to other previous reports of word order-related POp activation in German, see Bornkessel et al. (2005).
The observation that the POP does not differentiate between clause-initial and clause-medial word order permutations supports the hypothesis that this region engages in the processing of sentence-internal (i.e. prominence-based) linearization principles (Bornkessel et al., 2005; Grewe et al., 2005, 2006, 2007; see also Bornkessel-Schlesewsky & Schlesewsky, 2009; Bornkessel-Schlesewsky et al., 2009). Since these principles only govern the positioning of sentence participants (arguments) relative to one another (e.g. subject-before-object, animate-before-inanimate, definite-before-indefinite), they are independent of whether the permuted object resides in the clause-medial or clause-initial region.7

These assumptions are further supported by the behavioral results from the present study. Recall that the acceptability judgments showed an interaction between sentence type and word order, with only clause-medial object-initial orders engendering a significant acceptability drop in comparison to their subject-initial counterparts. This is compatible with the assumption that, in principle, any argument can be the aboutness-based sentence topic, thus rendering clause-initial object-initial orders highly acceptable. Clause-medial word order, by contrast, depends on the inherent prominence of the arguments themselves; since the

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**Table 4**

Activated regions in the word order contrast masked exclusively by the sentence type contrast. Results were corrected for multiple comparisons at the cluster level \((p < 0.05)\).

<table>
<thead>
<tr>
<th>Region</th>
<th>Activation maximum</th>
<th>Max. z-value</th>
<th>Volume ((\text{mm}^3))</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. IFG (posterior/inferior), IFS, IFJ</td>
<td>-47 14 6</td>
<td>4.03</td>
<td>10,071</td>
</tr>
<tr>
<td>R. IFS, IFG (posterior/inferior)</td>
<td>34 – 1 30</td>
<td>3.84</td>
<td>7722</td>
</tr>
<tr>
<td>L. ACC</td>
<td>-8 20 39</td>
<td>3.36</td>
<td>2214</td>
</tr>
<tr>
<td>L. STS/STG</td>
<td>-47 – 43 12</td>
<td>3.82</td>
<td>1917</td>
</tr>
<tr>
<td>L./R. thalamus (nucleus medialis thalamus)</td>
<td>-5 – 25 12</td>
<td>3.26</td>
<td>1566</td>
</tr>
<tr>
<td>L./R. thalamus (nucleus anterior thalamus)</td>
<td>-11 – 16 3</td>
<td>3.72</td>
<td>3105</td>
</tr>
</tbody>
</table>

---

7 Note that, while the direct influence of prominence information on clause-medial word order permutations is undisputed (see Lenerz, 1977; Müller, 1999, for theoretical arguments; and Bornkessel et al., 2005; Bornkessel-Schlesewsky et al., 2009; Grewe et al., 2005, 2006, for previous fMRI results), there are two scenarios as to how prominence-based sequencing could affect the clause-initial position. On the one hand, the influence could be direct in the sense of a general prominence evaluation of co-arguments that applies independently of whether the clause-initial position is filled or not. On the other hand, it could be due to the fact that, for an argument to occupy the clause-initial position, it must first have occupied the left edge of the middlefield. This assumption is made by derivational approaches which assume that topicalization (occupation of the clause-initial position) presupposes scrambling (permutation to the left-edge of the middlefield) (Fanselow and Lenerzová, to appear; Fanselow, 2002; Frey, 2005; Müller, 2003; Speyer, 2007). The present study does not allow us to distinguish between these two theoretical scenarios.
sentence materials used here did not provide an additional prominence-based motivation for the object-initial order, this was judged to be degraded in acceptability. Crucially, however, note that the acceptability of the different sentence types cannot account for the activation pattern observed in the lIFG: no region within the lIFG showed the interaction between ORDER and TYPE that was apparent in the acceptability judgments. (For detailed analyses and discussions of the relation between lIFG activation for German word order permutations and acceptability patterns/other behavioral parameters, see Bornkessel-Schlesewsky et al., 2009.)

In summary, the present findings are highly compatible with the assumption that the occupation of the clause-initial position involves two separable aspects: prominence-based and aboutness-based sequencing. Argument order in the medial region of the clause, by contrast, only involves the prominence-based sequencing component. From a functional-neuroanatomical perspective, prominence-based sequencing correlates with activation in posterior and inferior subregions within the lIFG (and activation in left frontomedian, bilateral superior temporal, and bilateral subcortical regions), whereas aboutness-based sequencing additionally modulates activation in superior and anterior portions of the lIFG (bilaterally) and in the left mid STS. We discuss possible interpretations of these activations in the following section.

4.2. Filling the clause-initial position: The role of anterior/superior IFG

In addition to an order effect, anterior and superior regions of the IFG (bilaterally) showed a type effect, i.e. generally higher activation for sentences with an argument in the clause-initial position, the prefield. The differentiation between these subportions of the lIFG and posterior/inferior subregions was further supported by the finding of a TYPE × REGION interaction in a follow-up analysis. As outlined in the introduction, the positioning of an argument in the prefield serves to establish it as an aboutness-based sentential topic. Hence, the more anterior and inferior portions of the lIFG, which show an effect of sentence type, appear to engage more strongly in this aboutness-based sequencing function than more posterior and inferior portions of the lIFG, which appear to be involved primarily in prominence-based linearization processes. Note that, on the basis of the present findings, we cannot differentiate between accounts of aboutness-based sequencing that characterize the occupation of the German prefield in terms of movement (i.e. proposals formulated within Chomskyan frameworks; for the notion of movement to a clause-initial topic position, see Rizzi, 1997) and accounts that assume a movement-independent structural differentiation between the prefield and the middlefield (e.g. Role and Reference Grammar; see Diedrichsen, 2008). Importantly, however, the general assumption of a link between the prefield and the information structural notion of aboutness not only accounts for the present results, but is also in line with the many empirical findings which suggest that the PTr and POr are involved in semantic and pragmatic aspects of sentence processing (see Bookheimer, 2002; for a review of neuroimaging findings on semantic processing, and Hagoort, Hald, Bastiaansen, & Petersson, 2004, for initial evidence with respect to pragmatics/world knowledge).

However, why should clause-medial word order permutations also have activated anterior portions of the lIFG in the present study in contrast to previous experiments? One possible explanation is that the use of bridge verbs (i.e. main clause verbs permitting the embedding of both verb-second and verb-final) may have led the processing system to evaluate the sentences without a clause-initial argument more strongly with respect to their discourse-related function. Thus, in contrast to previous studies, which did not employ bridge verbs, these sentences could alternatively have been expressed with an argument in the prefield in the current experiment. Hence, it appears plausible that the system may have evaluated why the speaker chose not to position the first argument clause-initially but rather behind the complementizer dass (‘that’). This discourse-related evaluation is more pressing for object- than for subject-initial sentences, since, in the absence of sentence-internal motivations for an object-initial order (based e.g. on animacy or thematic roles, see above), these require a particular context in order to be felicitous (e.g. Lenerz, 1977). Though this explanation appears plausible in view of the differences between the present experiment and previous studies, it is clearly post hoc and thus requires further testing in future research.

4.3. A neuroanatomical dissociation between different aspects of sequencing: consequences for the neurobiology of syntax

On the basis of the discussion in the preceding two sections, we propose that the processing of linear order in language comprises at least two separable subprocesses, which yield dissociable activation patterns within the left IFG.

On the one hand, order permutations involve prominence-based sequencing, which correlates with activation differences in posterior portions of the lIFG (i.e. typically with the POp). As we have proposed previously (see Bornkessel-Schlesewsky & Schlesewsky, 2009, for an overview), this type of sequencing involves an evaluation of the inherent prominence features of the sentential arguments (e.g. in terms of animacy, definiteness/specificity, pronominality and thematic role), with posterior IFG activation reflecting a deviation from the general rule “more prominent should precede less prominent”.

On the other hand, the processing of word order involves aboutness-based sequencing. This aspect of processing is tied primarily...
to the sentence-initial position and the element residing in it (Li & Thompson, 1976; cf. Tomlin, 1986) and correlates with activation differences in anterior–superior portions of the left IFG. Though we have focused on the role of aboutness in isolated sentences, in which it serves to define the sentence’s topic-comment structure, we assume that there is a close connection between aboutness-based sequencing and linking individual sentences to the broader discourse: a sentence topic is often also a discourse topic (cf. Asher, 2004; Kehler, 2004; Oberlander, 2004).

Overall, this account thus suggests that sentence-level comprehension processes are supported by a gradient of information processing within the left IFG, with posterior–inferior portions engaging in sentence-internal (prominence-based) sequencing operations and anterior–superior portions involved in the establishment of relations between the current sentence and the broader discourse (via aboutness). This proposal is partly compatible with Hagoort’s (2005) assumption of a “unification gradient” within the left IFG, though the specific functional designations of the individual subregions differs between the two approaches. Like Hagoort’s proposal, it is also compatible with the notion of a single cognitive operation (e.g. selection for position; Thothathiri et al., 2010) that applies to different types of information across the gradient in question. Notably, the explanation proposed here could be extended beyond the sentence-level in order to account for the involvement of the POp and PTr in phonological processing and processing of semantic information at the word level, respectively (cf. Bookheimer, 2002). Whereas phonological processing clearly requires segmentation and sequencing, most lexical semantic processing tasks require the retrieval of associated words or concepts from the mental lexicon or semantic memory. Hence, even with respect to units below the sentence-level, the functional subdivision between sequencing of the current input and establishing relations between the current input and external representations of some type can be maintained.

Intriguingly, the gradient of information processing proposed here with regard to linguistic sequencing operations corresponds well to current information theoretical proposals about the function of prefrontal cortex. Specifically, Koechlin and colleagues have proposed a cascaded model of cognitive control in which different types of control signals are processed along an anterior–posterior gradient within prefrontal cortex (Koechlin, Ody, & Kouneiher, 2003; Koechlin & Summerfield, 2007; see also Egner, 2009, for a recent overview). This model differentiates between control processes related to the immediate context in which a stimulus occurs (“contextual control” in their terminology) and control processes tied to a temporally distal event (“episodic control”). As an example, Egner (2009) describes the event of dining at a restaurant. Though you would normally proceed to eat as soon as the waiter places your food in front of you, contextual control can serve to override this tendency under the circumstance that your fellow diner has not yet been served. If, however, the person with whom you are dining has previously indicated that he/she will not be eating, episodic control would enable you to start eating anyway by adjusting your response to the contextual cue. This differentiation between contextual control (driven by the immediate context) and episodic control (related to past events) mirrors the requirements of prominence-based and aboutness-based sequencing which we have described in relation to the present study. Whereas prominence-based sequencing involves an assessment of local cues, namely of the relative prominence of the co-arguments, aboutness-based sequencing is more closely tied to the requirements of the broader discourse (since sentence topics are also likely to be discourse topics, see above). This distinction, which correlated with activation in posterior (and inferior) vs. anterior (and superior) subregions of the lIFG in the present study, thus corresponds nicely to the anterior–posterior gradient assumed to differentiate between episodic and contextual cues. In addition, the external information provided by aboutness-based sequencing can override sentence-internal (prominence) properties just as an episodic cue can modulate the response to a contextual cue. This is shown by our acceptability ratings, which revealed an acceptability drop for object-initial orders only for clause-medial word order permutations, i.e. when there was no additional influence of aboutness. These considerations thus suggest that different types of sequencing operations during language comprehension constitute a specific case of more general neural mechanisms of information processing in prefrontal cortex.

Interestingly, however, there appears to be a discrepancy between the direction of information flow predicted by Koechlin and colleagues’ model of cognitive control and electrophysiological findings on the temporal interplay between aboutness and prominence in word order processing. Koechlin and Summerfield (2007, p. 233) describe a “hierarchically ordered executive system lying along the anterior–posterioraxis of the lateral PFC […] , with control signals owing to events which occurred in the more and more distant past arising from successively more anterior cortical regions” and note that “[i]nformation thus flows in a ‘cascade’ from anterior to posterior regions […] .” This would make the prediction that aboutness-based cues should be able to modulate the response to prominence-based cues. While this assumption appears to be borne out from a behavioral perspective (see above), electrophysiological findings suggest that the time course of information processing proceeds in the opposite direction. For example, Bornkessel and Schlesewsky (2006a) found that the characteristic local event-related potential (ERP) response engendered by a scrambled object (cf. example 3) was not modulated even when the discourse context supported the object-initial word order and rendered it highly acceptable (as shown by sentence-final acceptability judgments). We have previously concluded from this observation and related findings that the computation of argument prominence hierarchically precedes the influence of discourse information during language comprehension (Bornkessel & Schlesewsky, 2006b; Bornkessel-Schlesewsky & Schlesewsky, 2009).

Assuming that the cartographic parcellation of the information gradient proposed within the cascade model is correct and can be applied to sequencing in language processing as we have suggested, these seemingly conflicting findings about the direction of information flow could be interpreted in at least two ways. Firstly, one might consider the possibility that information can, in fact, flow in both directions depending on the type of input being processed. This is not, however, a preferable option, since it would go against the output direction assumed within the cascade model, in which “multiple control signals owing to temporally distinct events arriving from the PFC […] govern response selection within the premotor cortex” (Koechlin & Summerfield, 2007, p. 233).

A second possibility is that the inferior frontal contributions to sequencing on which we have focused in this paper do not correlate with incremental linguistic information processing per se, but that they rather reflect evaluative aspects of linguistic processing. From this perspective, the prominence-based activation observed here would reflect a global evaluation of relative argument prominence as opposed to a local, word-by-word assessment of prominence features.8 It would thus correspond to

---

8 The difference between word-by-word and global prominence assessments can be illustrated with reference to the prominence-based linearization rule “animate-before-inanimate” (see Gewe et al., 2006, for more details). This rule is not yet violated at the position of an initial inanimate argument, since it could be the only argument in the sentence. Once an animate argument is encountered in the second position, however, prominence-based sequencing becomes suboptimal and, thereby, more effortful. Thus, the inanimate-before-animate order is disadvantageous from a global perspective even though this disadvantage is not yet apparent at the position of the initial argument during incremental processing.
sequence evaluation rather than to sequence processing. If this view turned out to be correct (for a related proposal based on the notion of “selection”, see Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), the findings on word order processing could be reconciled with the direction of information flow proposed by the cascade model. Within this scenario, incremental sequence processing would correlate with brain regions other than the lIFG. In this regard, superior temporal cortex presents itself as a plausible candidate (cf. also Thompson-Schill et al., 2005): recall that the present study revealed distinct activation foci within mid left STS/STG, one of which showed only a word order effect and the other of which showed effects of both word order and sentence type. Thus, the two activation patterns within the lIFG mirror those observed in the mid STS/STG, as one would predict under the assumption that the output of incremental sequencing in superior temporal cortex provides the input for sequence evaluation in lIFG. This account leads to the testable prediction that it should be possible to modulate prominence-related activation within the left POp and that this modulation should be predictable via the activation pattern of more anterior portions of the lIFG (and possibly superior temporal regions). Whether this prediction is indeed borne out will need to be demonstrated in future research.

5. Conclusions

By contrasting two types of object-before-subject word orders in an event-related fMRI study, we were able to show that, in functional-neuroanatomical terms, the processing of word order permutations is not a unitary phenomenon. Activation in posterior–inferior portions of the lIFG correlates with prominence-based aspects of argument sequencing and is thus independent of sentence type. By contrast, activation in anterior–superior portions of the lIFG is additionally modulated by whether an argument (either subject or object) resides in the sentence-initial position. We have argued that this modulation reflects aboutness-based aspects of argument sequencing which serve to establish a sentence topic and to link the current sentence to the broader discourse. We thus proposed a gradation of linguistic sequence processing in the lIFG, with posterior–superior portions engaging primarily in prominence-based (local) aspects of sequencing and anterior–inferior portions governing aboutness-based aspects of sequencing (requiring, in part, the integration between current and past representations). This proposed information processing gradient correlates well with more general hypotheses about a hierarchically organized executive control system which operates along an anterior–posterior dimension within prefrontal cortex (Koechlin & Summerfield, 2007).

Finally, while we believe that these “cartographic” correlations between particular brain regions and certain aspects of syntactic processing constitute an important first step in furthering our insights on the neurobiology of syntax, a true understanding of these correlations will likely require the use of new, biologically-inspired approaches. In this regard, the proposed link between dissociable aspects of linguistic sequencing and neurobiological gradients of cognitive control processes could constitute a move in the right direction.

Acknowledgments

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