Word order and Broca’s region: Evidence for a supra-syntactic perspective

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**A R T I C L E  I N F O**

**A B S T R A C T**

It has often been suggested that the role of Broca’s region in sentence comprehension can be explained with reference to general cognitive mechanisms (e.g. working memory, cognitive control). However, the (language-related) basis for such proposals is often restricted to findings on English. Here, we argue that an extension of the database to other languages can shed new light on the types of mechanisms that an adequate account of Broca’s region should be equipped to deal with. This becomes most readily apparent in the domain of word order variations, which we examined in German verb-final sentences using event-related fMRI. Our results showed that activation in the pars opercularis – a core subregion of Broca’s area – was not only modulated by the relative ordering of subject and object, but also by a further factor known to affect word order in a number of languages, namely referentiality. Notably, the finding provides the first demonstration of a word order-related activation difference within subject-initial sentences in this region. Additional parametric analyses using individual behavioral data as predictors further attest to the independence of the pars opercularis activation from: (a) sentence acceptability, and (b) difficulty in performing the experimental (judgment) task. We argue that these and related findings attest to the need for a processing mechanism that can manipulate predicate-independent, interacting and hierarchically structured relational representations during real time comprehension. These properties pose a challenge to existing accounts of pars opercularis function.

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1. Introduction

Of the language-related areas of the human brain, Broca’s area (comprising the pars opercularis and triangularis of the left inferior frontal gyrus, IFG) is arguably the most famous. In recent years, the precise role of this region in language comprehension has been subject to a heated debate, the primary focus of which has been its increased activation during the comprehension of sentences in which the object precedes the subject. An example for a “non-canonical” or “permuted” sentence of this type is the (italicized) object-relative clause in ‘Bill caught the burglar who the detective chased’.

The involvement of Broca’s area in the processing of word order permutations has been demonstrated in a large number of neuro-imaging studies. While increased activation of this region for object-initial sentences was first reported for relative clauses in English (e.g. Caplan, Alpert, Waters, & Olivieri, 2000; Constable et al., 2004; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Keller, Carpenter, & Just, 2001; Stromswold, Caplan, Alpert, & Rauch, 1996), it has also been observed for clause-medial word order permutations (“scrambling”) in German (e.g. Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Grewe et al., 2005, 2006, 2007; Röder, Stock, Neville, Bien, & Rösler, 2002) and for object-initial sentences in Hebrew (Ben-Shachar, Palti, & Grodzinsky, 2004) and Japanese (Kinno, Kawamura, Shioda, & Sakai, 2008).

In view of these very consistent results, it is undisputed that Broca’s area – and particularly the pars opercularis of the left IFG – plays an important role in the processing of varying word orders. This function (“linearization”) is very important for the comprehension of natural language for at least two reasons: (a) since language unfolds over time, the order in which sentence constituents are encountered in the speech stream imposes crucial constraints on how the comprehension process can proceed; and (b) because an estimated 70% of natural languages exhibit a significant degree of word order freedom (Steele, 1978), the possibility of variations...
in this order should be considered the rule rather than the exception. Approaches to the function of Broca’s region/the left pars opercularis differ as to whether they attribute its role in the processing of permuted word orders to language-internal (e.g. syntactic movement: Ben-Shachar et al., 2004; Grodzinsky, 2000; Grodzinsky & Friederici, 2006; Grodzinsky & Santi, 2008) or domain-general operations (e.g. working memory: Caplan et al., 2000; Fiebach, Schlesky, Lohmann, von Cramon, & Friederici, 2005; Kaan & Swaab, 2002; Müller, Kleinhans, & Courchesne, 2003; or cognitive control: Thompson-Schill, Bedny, & Goldberg, 2005). From a somewhat more general perspective, it has also been proposed that the language-related function of Broca’s region can be subsumed under broader cognitive mechanisms related to “action understanding” (Rizzolatti & Arbib, 1998). Language-specific approaches are often criticised (e.g. Müller & Basho, 2004) because they fail to account for the observation that Broca’s region is also activated by non-linguistic tasks, e.g. motor imagery (Binkofski et al., 2000) and the processing of complex relational information (Kroger et al., 2002). One of the main challenges in accounting for the involvement of the pars opercularis in the processing of word order permutations thus lies in determining whether it can be derived from some more general function of this cortical region within higher cognition.

Here we will argue that, at least with respect to word order variations, domain-general approaches and highly specific language-internal approaches to pars opercularis function have more in common than is typically acknowledged. In our view, both types of approaches underestimate the complexity of the activation patterns that this region shows in response to fine-grained linguistic differences. Specifically, we will argue that, while the basic finding of increased activation for object-before-subject orders can be derived by all models in a relatively straightforward manner, they are equally challenged by more complex word order patterns. In the following, we first provide a brief summary of previous findings which suggest that the relative ordering of subject and object may not be the key to explaining pars opercularis activation for word order variations before describing an fMRI study which further corroborates this perspective.

1.1. Beyond subjects and objects: interacting information types in word order variations

Despite differing viewpoints on precisely which mechanism should be held responsible for the additional processing costs in object-before-subject orders, virtually all approaches appeal to the inherent dependency between objects and subjects in deriving these costs. For example, it is commonly assumed that comprehending an object-initial sentence involves reconstructing the canonical subject-initial order and that an initial object cannot be interpreted until either the subject or the verb is encountered (see, for example, Kaan & Swaab, 2002). One might therefore assume that it is this type of dependency that engenders the increased activation of the pars opercularis in object-initial orders. If this were indeed the correct functional characterization of word order-related pars opercularis activation, it would provide a candidate mechanism which domain-general models would need to explain. It is, of course, easily derived in a movement-based, language-internal approach, since object-initial orders can be modeled theoretically as involving an additional movement operation which places the object in front of the subject. However, recent results from German indicate that matters are somewhat more complex: under certain circumstances, object-initial orders systematically fail to show increased pars opercularis activation in comparison to their subject-initial counterparts. This is the case, for example, when the object bears a higher-ranking thematic role than the subject, as in (1) (from Bornkessel et al., 2005).

(1) Gestern wurde erzählt, dass dem Jungen die Lehrer auffallen that [the boy]DAT.OBJ.SG [the teachers]NOM.SUBJ.PL be.striking.TOPL
Yesterday, someone said that the boy finds the teachers striking.

In (1), the verb auffallen (‘to be striking to’) assigns the higher-ranking Experiencer role to the grammatical object, the boy, whereas the grammatical subject, the teachers, bears the lower-ranking role of Theme (or Stimulus) (cf. Grimshaw, 1990; Primus, 1999, for theoretical arguments; and Bornkessel, Schlesky, & Friederici, 2003, for empirical evidence). Thus, in sentences such as (1), the object-initial order allows for an independent preference to be upheld, namely that arguments bearing higher-ranking thematic roles should precede arguments bearing lower-ranking thematic roles. This ordering tendency has been assumed to hold for German (Fanselow, 2000; Haider & Rosengren, 2003; Wunderlich, 1997) as well as across a wide range of languages (Tomlin, 1986). It has also been confirmed empirically (see Haupt, Schlesky, Roehm, Friederici, & Bornkessel-Schlesky, 2008 for the results of a rating study with 1120 native speakers of German). In an fMRI study, Bornkessel et al. (2005) demonstrated that subject-object order interacts with the order of thematic roles in the left pars opercularis: increased activation for object- vs. subject-initial orders was only observed for sentences with action verbs (in which the subject bears the higher-ranking thematic role than the object), but not for sentences with “object-experiencer” verbs of the type in (1).

Further converging evidence that object-initial orders do not engender increased pars opercularis activation when the non-canonical order is motivated by an independent word order rule was provided by Grewe et al. (2005). Here, the independent rule was one of pronoun placement, namely that pronouns should precede non-pronominal arguments in the medial region of the German clause (Bierwisch, 1963; Lenerz, 1977; Müller, 1999). Similarly to Bornkessel et al.’s (2005) results on thematic roles, Grewe et al.’s (2005) findings showed that object-initial orders only engendered increased activation in the left pars opercularis when both subject and object were non-pronominal noun phrases, but not when the initial noun phrase was realized by a pronoun.

On the basis of these findings, Bornkessel et al. (2005) and Grewe et al. (2005) concluded that pars opercularis activation in the domain of word order variations cannot be reduced to a single factor, but rather results from the interaction of multiple information types. They thus put forward the “linearization hypothesis”, according to which activation in the left pars opercularis is modulated by a range of non-syntactic “prominence scales”, with activation increasing whenever a less prominent argument precedes a more prominent argument. The relevant scales, which are given

1 The idea that integration of the object is triggered by the subject has been proposed for verb-final languages such as German, in which the base position of the object intervenes between the subject and the verb (see Fiebach, Schlesky, & Friederici, 2002). In English, by contrast, the integration of the object can be assumed to be triggered by the verb, irrespective of whether this integration is mediated by a trace or by the direct association between the object and its subcategorizer (Pickering & Barry, 1991). Importantly, however, the processing of the subject is assumed to be a necessary prerequisite for the integration and interpretation of the object in all cases.2 But note that this is only one possible theoretical characterization of object-before-subject orders. By contrast, a number of theories of grammar do not assume movement operations (e.g. Lexical Functional Grammar: Bresnan, 2001; “Simpler Syntax”: Culicover & Jackendoff, 2005; Role and Reference Grammar: Van Valin, 2005; Construction Grammar: Goldberg, 2006).
in (2), are well-known from cross-linguistic research as they serve to constrain grammatical phenomena in a range of languages (cf. Comrie, 1989; Croft, 2003). It has recently been argued that they also play an important role in language processing, for example in the assignment of thematic interpretations (“who is acting on whom”) during online comprehension (Bornkessel-Schlesewsky & Schlesewsky, 2006; Bornkessel-Schlesewsky & Schlesewsky, 2009) or in the avoidance of similarity-based interference (Lee, Lee, & Gordon, 2007). Furthermore, all of the prominence scales in (2) have been argued to influence word order preferences both in German (Lenerz, 1977) and cross-linguistically (Tomlin, 1986), i.e. speakers find sentences more acceptable when a more prominent argument precedes a less prominent argument rather than vice versa.

(2) Prominence scales relevant to word order processing (from Wolff, Schlesewsky, Hirotani, & Bornkessel-Schlesewsky, 2008).

Note that “>” should be read as “is more prominent than”.

* nominative > - nominative
* pronoun > - pronoun
* animate > - animate
* [specific/definite] > [specific/definite]
* actor > - actor (i.e. higher thematic role > lower thematic role)

In accordance with the linearization hypothesis, an influence of animacy (2c) on word order-related activation within the left pars opercularis has been demonstrated for both English (Chen, West, Waters, & Caplan, 2006) and German (Grewe et al., 2006). These previous findings are problematic for a movement-based account of pars opercularis function because they either involve information types that are not easily amenable to movement-based analyses (e.g. animacy, thematic roles) or because movement-based approaches make incorrect predictions with regard to the fine-grained pattern of activation differences between the different word orders (e.g. pronouns). For a detailed discussion of the problems that these findings pose for movement-based accounts, see Bornkessel et al. (2005) and Grewe et al. (2005, 2006). At the same time, they raise the bar for domain-general explanations, since the differences between the word orders in question (e.g. in terms of acceptability or other behavioral processing measures) are considerably more subtle than for “standard” word order manipulations involving only subjects and objects. Hence, they are not as easily amenable to one of the most straightforward domain-general explanations, namely that the word order variants engendering increased pars opercularis activation are simply less “natural” or “more difficult” in some way.

1.2. The present study

In the present study, we aimed to further corroborate the perspective that word order processing (and its neural bases) require a multi-factorial account. To this end, we examined a type of prominence information that has not been scrutinized from a functional-neuroanatomical perspective to date and investigated whether prominence-based activation modulations in the pars opercularis can also lead to activation differences between subject-initial structures. To this end, we manipulated word order and noun phrase definiteness/specificity (cf. 2d) in German. A more elaborate version of the definiteness/specificity scale (Aissen, 2003) is given in (3). We chose not to manipulate definiteness directly, e.g. by comparing noun phrases with definite and indefinite determiners, because the indefinite determiner ein(e) (‘a’) is also compatible with a numeral reading (‘one’) in German. It could therefore be interpreted as a quantifier (Fodor & Sag, 1982), thereby leading to a confound during word order processing (cf. the results of the rating study in Haupt et al., 2008, for a first indication of such an influence). Specificity is also difficult to manipulate directly in German as it is not morphologically expressed (in contrast to languages such as Turkish, e.g. Comrie, 1989). For the prominence manipulation, we thus drew upon a subpart of the definiteness scale, which, following Croft (2003), can be termed the “referentiality scale” (cf. 4). Note that, rather than representing a theoretical claim about the nature of referentiality, this scale expresses a cross-linguistic generalization about different noun phrase types and their participation in a range of morphosyntactic phenomena (see Croft, 2003, Chapter 5, for details).

(3) Definiteness scale (Aissen, 2003, p. 437)

personal pronoun > proper name > definite NP > indefinite specific NP > non-specific NP

In accordance with the scale in (4), the present study contrasted sentences in which an argument that was higher in referentiality (a proper name) preceded an argument that was lower in referentiality (a bare plural common noun) in terms of linear order or vice versa. Proper names are higher in referentiality than common nouns—and thereby more prominent—because they are usually uniquely identifiable, whereas common nouns denote sets of entities. Crucially, note that the purpose of the present study was not to examine the neural representation of referentiality per se (e.g. by examining whether proper names and bare plurals engender activation in different neural regions) but rather to investigate how the referentiality scale influences the processing of argument order.

Whereas, prima facie, one might question whether the referentiality distinction between proper names and common nouns also holds when a sentence is presented out of context, previous psycholinguistic studies have demonstrated robust differences between proper names and common nouns even in isolated sentences (Gordon, Hendrick, & Johnson, 2001; Gordon, Hendrick, & Levine, 2002; Lee et al., 2007). In particular, these previous experiments suggest that similarity-based interference between co-arguments is reduced when one argument is a proper name and the other is a common noun, thereby attesting to distinct representations for the two noun phrase types and to the robustness of the referentiality contrast. By using names and bare plurals we were thus able to manipulate argument prominence on the definiteness/specificity scale (3), while avoiding the potential confounding influence of a quantificational reading that might result from the use of indefinite determiners. The critical sentence types resulting from this manipulation are shown in Table 1.

The experimental conditions in Table 1 instantiate a 2 x 2 design involving the factors subject-object ORDER (subject-initial, A/B vs. object-initial, C/D) and REFERentiality (proper name precedes plural nominal, A/C vs. plural nominal precedes proper name, B/D). As a result of the referentiality manipulation (i.e. the use of proper names and bare plurals as motivated above), the critical sentences were locally ambiguous between a subject- and an object-initial reading, with disambiguation effected via the number agreement information of the clause-final verb. Previous findings suggest that this should not affect activation in the left pars opercularis: for sentences structures similar to those under

(4) Referentiality scale (Croft, 2003, p. 130)

pronoun < proper name < common noun

Whereas bare plurals may lead to an ambiguity between a non-specific and a specific (generic) reading (Carlson, 1977), it suffices for the purposes of the present manipulation that, even under a specific reading, they are still outranked by proper names on the definiteness/referentiality scales.
We thus predicted that the voxels within the pars opercularis that are activated by the ORDER contrast (object-initial – subject-initial) should also show increased activation for the REferentiality contrast (bare-plural-initial – proper-name-initial). Furthermore, if the linearization hypothesis is correct, differences in argument prominence (cf. 2) should not only serve to attenuate activation increases for object-initial sentences, but should also lead to activation differences between subject-initial conditions. This prediction was also tested in the present study.

### 2. Materials and methods

#### 2.1. Participants

Thirty monolingually raised, right-handed native speakers of German (16 females; mean age: 25.0 years; age range: 21–32 years) participated in the fMRI study after giving written informed consent. Two further participants were excluded from the final data analysis on account of movement artifacts and/or problems in performing the task.

#### 2.2. Materials

Thirty-six sets of the four critical sentence conditions (see Table 1) were constructed on the basis of lexical triplets consisting of a proper name, a bare plural noun, and a verb assigning accusative object case. Each sentence was combined with a matrix clause of the form shown in Table 1 (matrix clauses were always identical for one lexical set). An additional 36 sets of the four critical conditions were constructed by replacing the verb in each of the first 36 sets with a verb assigning dative object case. This variation (CASE) was implemented as a between-participants factor in order to control for possible influences of different kinds of object case on word order processing (see Bornkessel, McElree, Schlesewsky, & Friederici, 2004, for ERP data showing such differences). Note that all verbs allowed generic and indefinite readings for bare plural subjects and objects, hence ruling out a subject-object asymmetry based on differences in ambiguity. The complete experimental materials thus consisted of 144 sentences with accusative verbs (36 per condition) and 144 sentences with dative verbs (36 per condition). These were subsequently subdivided into four lists of 72 sentences each, with two lists containing only sentences with accusative verbs and two lists containing only sentences with dative verbs. Each list contained 18 sentences from each of the four conditions in Table 1 and two sentences from each lexical set. List presentation was counterbalanced across participants. Each participant read the materials from a single list once and was thereby either confronted with critical sentences containing accusative verbs or with critical sentences containing dative verbs.

Each list of 72 critical sentences was pseudo-randomly combined with 72 filler sentences, 42 of which were ungrammatical (to balance responses for the acceptability judgment task; see below). Thirty-six null events (empty trials) were also included in each list in order to improve the statistical evaluation of the data (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). The pseudo-randomization ensured that not more than two sentences from a single condition were presented in a row, that at least twenty trials intervened between the repetition of lexical materials and that critical sentences, null events and fillers were distributed equally among the two functional runs (see below). The filler sentences were identical in all versions of the experiment and were of a similar structure to the critical sentences (including a matrix clause of the type exemplified in Table 1 and a subordinate clause introduced by the complementizer dass). Furthermore, the filler sentences included varying orders and noun phrases of varying referentiality so that they would be initially indistinguishable from the critical experimental sentences. Ungrammatical fillers included violations of case marking or agreement.

#### 2.3. Procedure

Participants read the sentences via LCD goggles (Visuastim, Magnetic Resonance Technology, Northridge, CA). To control for reading strategies, sentences were presented in a segmented manner, with a presentation time of 600 ms for the matrix clause, 500 ms for each of the arguments in the embedded clause and 400 ms for the complementizer dass and the clause-final verb. The inter-stimulus interval (ISI) was always 100 ms. Trials began with the presentation of an asterisk (300 ms plus 200 ms ISI) and ended with a 500 ms pause, after which a question mark signaled to participants that they should judge the acceptability of the preceding sentence. In the instructions, it was emphasized that participants should not judge whether the sentences described a plausible event, but rather whether the chosen way of expressing this event is possible in German or not. Participants were also instructed to rely on their intuitions rather than on rules of “good style” that they might remember from school (where “subject-first” is often enforced as a prescriptive stylistic rule). The rationale for using a judgment task was twofold: (a) it ensured comparability with a number of previous studies on word order and argument prominence in German (Grewe et al., 2005, 2006, 2007); (b) it served to avoid possible activations that have been shown to occur in response to a probe sentence in a comprehension task (Caplan, Chen, & Waters, 2008). The participants performed the judgment

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**Table 1**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common matrix</td>
<td>Gernst hat jeder gehört, ...</td>
</tr>
<tr>
<td>clause</td>
<td>&quot;Yesterday, everyone heard...</td>
</tr>
<tr>
<td>A. SO-REF</td>
<td>dass [Reinhold</td>
</tr>
<tr>
<td></td>
<td>... that ReinholdSG authorsPL laughs-at ACCPL/applaudsDATPL.</td>
</tr>
<tr>
<td></td>
<td>... that Reinhold laughs at/applauds Reinhold.</td>
</tr>
<tr>
<td>B. SO-NREF</td>
<td>dass [Autorinnen</td>
</tr>
<tr>
<td></td>
<td>... that authorsSG ReinholdSG laugh-at ACCPL/applaudsDATPL.</td>
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<tr>
<td></td>
<td>... that authors laugh at/applaud Reinhold.</td>
</tr>
<tr>
<td>C. OS-REF</td>
<td>dass [Reinhold</td>
</tr>
<tr>
<td></td>
<td>... that ReinholdSG authorsPL laugh-at ACCPL/applaudsDATPL.</td>
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<td>... that authors laugh at/applaud Reinhold.</td>
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<tr>
<td>D. OS-NREF</td>
<td>dass [Autorinnen</td>
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<tr>
<td></td>
<td>... that authorsSG ReinholdSG laugh-at ACCPL/applaudsDATPL.</td>
</tr>
<tr>
<td></td>
<td>... that Reinhold laughs at/applauds authors.</td>
</tr>
</tbody>
</table>
task by pressing one of two push-buttons with their right index and middle fingers (maximal response time: 2300 ms). After the response, the screen remained blank for the remainder of the trial. The assignment of fingers to acceptable and unacceptable was counterbalanced 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 5 (Miezin et al., 2000). All trials (180 per participant) had a length of 8 s, thus resulting in a total measurement time of 24 min, which was separated into two functional runs.

Participants completed a short practice session before entering the scanner.

2.4. fMRI data acquisition

The experiment was carried out on a 3T scanner (Medspec 30/100, Bruker, Ettlingen). Twenty axial slices (19.2 cm FOV, 64 by 64 matrix, 4 mm thickness, 1 mm spacing), parallel to the AC-PC plane and covering the whole brain were acquired using a single shot, gradient recalled EPI sequence (TR 2000 ms, TE 30 ms, 90° flip angle). Two functional runs of 360 time points were collected, with each time point sampling over the 20 slices. Prior to the functional runs, 20 anatomical T1-weighted MDEFT (Norris, 2000; Ugurbil et al., 1993) images (data matrix 256 × 256, TR 1.3 s, TE 10 ms) and 20 T1-weighted EPI images with the same geometrical parameters as the functional data were acquired.

2.5. fMRI data analysis

The fMRI data were analyzed using the LIPSIA software package (Lohmann et al., 2001). Functional data were corrected for motion using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation based on the Nyquist-Shannon-Theorem was applied. A temporal highpass filter with a cutoff frequency of 1/112 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm FWHM was applied.

To align the functional data slices onto a 3D stereotactic coordinate reference system, a rigid linear registration with 6° of freedom (three rotational, three translational) was performed. 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 set (acquired for each subject 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 & Tournoux, 1988). The same rotational and translational parameters were normalized, i.e., transformed to a standard size via linear scaling. The resulting parameters were used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. This normalization process was improved by a subsequent non-linear normalization (Thirion, 1998), which serves to adjust structural-anatomical differences between different brains by using a procedure known as “demon matching”. Here, an anatomical 3D data set is deformed such 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 (constructed by a gamma density function, Glover, 1999). The response delay was set to 6 s and the undershoot delay to 16 s. The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of 4 s. FWHM dispersion to deal with the temporal autocorrelation (Worsley & Friston, 1995). 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 (Holmes & Friston, 1998). Subsequently, t values were transformed into Z scores. To protect against false positive activations, only regions with a Z score greater than 3.1 (p < 0.001 uncorrected) and with a volume greater than 288 mm³ (eight measured voxels) were considered (Braver & Bongiolatti, 2002; Forman et al., 1995).

3. Results

3.1. Behavioral data

The behavioral task revealed the following mean acceptability rates/standard deviations: SO-REF (95.65%/5.56); SO-NREF (94.17%/11.23); OS-REF (79.44%/22.70); OS-NREF (43.33%/37.61). A repeated measures ANOVA revealed significant main effects of (subject/object) ORDER (F(1, 28) = 63.41; p < .0001) and REFERentiality (F(1, 28) = 27.95; p < .0001) as well as a significant interaction ORDER × REF (F(1, 28) = 17.59; p < .001). Resolving this interaction by ORDER showed a significant effect of REF for object-initial (F(1, 28) = 23.16; p < .0001) but not for subject-initial sentences (p > .26).

A closer examination of the individual participant data showed that the mean acceptability rating for the OS-NREF condition (43.33%) resulted from a relatively high variability of judgments across participants. Thus, as visualized in Fig. 1, several participants showed a very high mean acceptability rating for this condition, while others reliably judged it as unacceptable. This pattern of inter-individual variability did not, however, generalize to the OS-REF condition, i.e. it was not the result of certain participants accepting and certain participants rejecting object-initial structures in general (see Fig. 1). Rather, the data pattern speaks in favor of an acceptability continuum, in which the addition of a further influencing factor (e.g. a violation of the referentiality principle) may lead to a reversal of a participant’s judgment behavior. Note that this data pattern is by no means unprecedented in the domain of word order variations in German: a range of studies has demonstrated that speakers’ intuitions in this domain are graded rather than absolute (e.g. Keller, 2000; Peichmann, Uszkoreit, Engelkamp, & Zerbst, 1994; Schlesewsky, Bornkessel, & McElree, 2006). Furthermore, as shown by Keller (2000), different word order constraints can act in a cumulative manner. Thus, it is not surprising that referentiality has a stronger effect in the object-initial sentences. Finally, a recent ERP study using an identical experimental manipulation (Haupt et al., 2008, Experiment 2) revealed a very similar pattern of acceptability judgments, but showed by means of a comprehension task that the low acceptability of the OS-NREF sentences does not preclude a correct understanding of the sentences. Taken together, these previous results indicate that the acceptability pattern observed here is by no means atypical and that it should not be taken to indicate that participants did not understand the sentences (for a dissociation between acceptability and comprehensibility in German word order variations, see also Friederici et al., 2006). Nevertheless, in order to determine the influence of individual judgment patterns on our results, we conducted parametric analyses of our fMRI data using the behavioral data as predictors (see below).

Turning now to the analysis of the reaction times, this yielded the following mean values/standard deviations: SO-REF (595 ms/168); SO-NREF (653 ms/194); OS-REF (822 ms/253); OS-NREF
(817 ms/293). A repeated measures ANOVA again revealed a significant main effect of ORDER ($F(1, 28) = 65.46; p < .0001$) and a significant interaction of ORDER and REF ($F(1, 28) = 5.42; p < .05$). Planned comparisons for each of the two levels of ORDER showed a significant effect of REF for subject-initial ($F(1, 28) = 18.96; p < .001$) but not for object-initial structures ($F < 1$).

### 3.2. fMRI data: order and referentiality

In a first step, we calculated the contrast between object- and subject-initial sentences in order to isolate the network involved in the processing of non-canonical structures and to thereby enable us to examine the referentiality effect within this network. The results of this contrast are shown in Figs. 2 and 3 and Table 2.

As predicted, the present study revealed increased activation for object- vs. subject-initial sentences in the pars opercularis of the left IFG, with activations extending into the adjacent deep frontal operculum/anterior insula and the inferior frontal junction area (IFJ). Further activations were observed in the right deep frontal operculum, left intraparietal sulcus (IPS) and in the head of the left caudate nucleus. This network is very similar to previous findings for word order permutations in the medial portion of the German clause (e.g. Bornkessel et al., 2005; Friederici et al., 2006; Grewe et al., 2005; Röder et al., 2002).

In a second step, we calculated the main effect of referentiality (i.e. the contrast bare-plural-initial order, NREF – proper-name-initial order, REF). As shown in Fig. 4 and Table 3, sentences in which the less prominent bare plural argument preceded the more prominent proper name yielded increased activation in the left inferior frontal junction area, extending into pars opercularis of the inferior frontal gyrus, and in the left intraparietal sulcus. By contrast, increased activation for sentences with a proper name preceding a
bare plural was observable in the posterior cingulate gyrus and the frontomedian wall (BA 10). An additional conjunction analysis between the ORDER and REF contrasts showed common activation only in left inferior frontal regions, namely in the left IFG (pars opercularis) and left IFJ (maximum: /C0 41 9 30).

Finally, we examined the possible main effect of case by comparing the activation across all four critical sentence conditions in the two participant groups (ACC vs. DAT). This analysis revealed no significant differences.

As the primary aim of this study was not to examine effects of referentiality per se, but to investigate the impact of this linearization factor within the network that is sensitive to word order permutations (i.e. object-before-subject orders), we conducted a region of interest analysis for each of the regions identified using the order contrast (see Table 2). For each of these regions, we extracted the time course of the underlying BOLD signal. The percent signal change (relative to the mean signal intensity) for the voxel with the highest z-value (in the group contrast) and the 26 adjacent voxels was averaged for each condition and participant.4 The time course of the null events was subtracted from the time courses for the critical sentence conditions (Burock, Buckner, Woldorff, Rosen, & Dale, 1998).

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

### Table 2

<table>
<thead>
<tr>
<th>Region</th>
<th>Talairach coordinates</th>
<th>Max. z-value</th>
<th>Volume (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ORDER contrast (OS vs. SO)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. inferior frontal gyrus (IFG), pars opercularis</td>
<td>–53 11 5</td>
<td>4.35</td>
<td></td>
</tr>
<tr>
<td>L. deep frontal operculum/anterior insula</td>
<td>–34 23 5</td>
<td>4.73</td>
<td>11,966</td>
</tr>
<tr>
<td>L. inferior frontal junction area (IFJ)</td>
<td>–40 5 32</td>
<td>4.77</td>
<td></td>
</tr>
<tr>
<td>R. deep frontal operculum/anterior insula</td>
<td>31 20 6</td>
<td>4.49</td>
<td>1693</td>
</tr>
<tr>
<td>L. pre-SMA</td>
<td>–7 23 41</td>
<td>4.89</td>
<td>4300</td>
</tr>
<tr>
<td>L. intraparietal sulcus (IPS)</td>
<td>–32 –58</td>
<td>4.22</td>
<td>915</td>
</tr>
<tr>
<td></td>
<td>41</td>
<td></td>
<td>41</td>
</tr>
<tr>
<td>L. caudate nucleus</td>
<td>–14 1 18</td>
<td>3.78</td>
<td>309</td>
</tr>
</tbody>
</table>

As is evident from Table 4, three regions within the overall network sensitive to linear order also proved sensitive to

---

4 ROIs were defined as the activation maximum and the 26 voxels adjacent to it in accordance with the procedure adopted in previous studies examining word order and linearization parameters (Bornkessel et al., 2005; Grewe et al., 2005, 2006, 2007).
In order to examine the nature of the activations observed for order and referentiality more closely, we performed a series of additional analyses in which we used the individual behavioral data acquired in the scanner as parametric predictors. This analysis was motivated: (a) by the inter-individual variability in the accessibility of the object-initial structures (see above), and (b) by the conjecture formulated in Grewe et al. (2005) that the activation of the deep frontal operculum/anterior insula in the context of word order variations may arise from the relative ease or difficulty of performing an acceptability judgment task. For the pars opercularis, by contrast, the linearization hypothesis would not predict that the activation is simply due to a correlation with behavioral parameters. The parametric analyses tested these hypotheses by examining for which brain regions the activation patterns in the present study could be predicted on the basis of behavioral parameters alone.

To estimate the influence of all possible aspects of the judgment task, we conducted parametric analyses (Büchel, Wise, Mummery, Poline, & Friston, 1996) using each participant's mean acceptability rating, mean reaction time and standard deviation of acceptability for each of the four critical conditions as predictor values (in separate models). Each of these analyses used a regressor consisting of the behavioral parameter of interest per participant per condition, e.g. for the acceptability, the mean acceptability for each participant and for each of the four critical conditions (see Volz, Schubotz, & von Cramon, 2003, for a similar application in a non-linguistic context). These parametric analyses should therefore identify brain regions correlating with the demands of the behavioral task, as measured by individual performance. While increased reaction times may, in principle, reflect either increased difficulty in understanding the sentence or in performing the judgment task, we also chose the individual standard deviation (of acceptability) per condition as we reasoned that this value would provide a good measure of how confident participants were in judging a particular sentence condition as acceptable or unacceptable. As noted above, it is well-known that speakers' judgments about their native language are often not categorical, but that they may rather also display a certain degree of "gradience" (for comprehensive discussions of this phenomenon, see for example Fanselow, Féry, Vogel, & Schlesewsky, 2006; Featherston, 2007, and the commentaries on this article) and word order permutations of the type examined here are particularly prone to such gradient judgment behavior. Thus, the standard deviation of the individual acceptability ratings per condition should provide a good estimate of how certain individual participants were in judging a particular sentence type as either acceptable or unacceptable. Furthermore,

### Table 4

Summary of the global statistical analysis for the averaged percent signal change for the voxel with the maximal activation and the 26 adjacent voxels in the regions identified via the ORDER contrast (cf. Table 2). Each cell gives the significance level for an effect (n.s. = not significant; m = p < .07; + = p < .05; ++ = p < .01; +++ = p < .001) and the F-value for significant effects. In all cases, the degrees of freedom were df1 = 1, df2 = 28. Abbreviations used: ACC = verb subcategorizing for an accusative object; DAT = verb subcategorizing for a dative object; SG = singular; PL = plural.

<table>
<thead>
<tr>
<th>Region</th>
<th>ORDER</th>
<th>REF</th>
<th>CASE</th>
<th>REF x ORDER</th>
<th>CASE x ORDER</th>
<th>CASE x REF</th>
<th>CASE x REF x ORDER</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. IFG, pars opercularis</td>
<td>+++ (25.71)</td>
<td>+ (6.26)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L. deep frontal operculum/anterior insula</td>
<td>+++ (18.68)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L. IFJ</td>
<td>+++ (18.57)</td>
<td>++ (10.95)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>R. deep frontal operculum/anterior insula</td>
<td>+++ (17.40)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>+ (5.16)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L. pre-SMA</td>
<td>+++ (33.15)</td>
<td>m. (4.15)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L. IPS</td>
<td>+++ (14.39)</td>
<td>++ (8.30)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>+ (4.56)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L. caudate nucleus</td>
<td>+++ (20.77)</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</tbody>
</table>
Fig. 5. Averaged BOLD timecourses for the regions of interest defined via the word order contrast (see Table 2). Abbreviations: SO = subject-before-object; OS = object-before-subject; REF = adhering to the referentiality principle; NREF = violating the referentiality principle.
because of the gradient acceptability of the structures under consideration, there were essentially no right or wrong answers in the judgment task. Therefore, reaction times for all trials entered the parametric analysis (i.e. not just “acceptable” responses). The results of the parametric analyses are shown in Fig. 6 and summarized in Table 5.

![Fig. 6. Results of the parametric analyses using individual behavioral data. The figure shows averaged brain activations (z > 3.09) correlating with individual standard deviations of acceptability ratings (panel A), with individual mean reaction times (panel B) and with individual mean acceptability ratings (panel C).](image)

<table>
<thead>
<tr>
<th>Region</th>
<th>Talairach coordinates</th>
<th>Max. z-value</th>
<th>Volume (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acceptability R. post-central sulcus</td>
<td>43 -27 27</td>
<td>3.84</td>
<td>378</td>
</tr>
<tr>
<td>Reaction time</td>
<td>L. deep frontal operculum</td>
<td>-38 18 3</td>
<td>4.45</td>
</tr>
<tr>
<td>Standard deviation (acceptability)</td>
<td>L. deep frontal operculum</td>
<td>-38 27 3</td>
<td>3.98</td>
</tr>
<tr>
<td></td>
<td>R. deep frontal operculum</td>
<td>28 24 3</td>
<td>3.61</td>
</tr>
</tbody>
</table>

5 Note that, in the sense used here, “pars opercularis” refers exclusively to the lateral convexity of the opercular part of the inferior frontal gyrus.

4. Discussion

The present findings provide the first demonstration that sentence-level linearization principles can engender activation differences between subject-initial sentences in the pars opercularis of the left IFG as part of a (mainly) left-lateralized fronto-parietal-basal ganglia network. In the following, we discuss the consequences of this finding for a characterization of the processing mechanisms underlying linear order in language.

4.1. Referentiality as a linearization parameter

The finding of referentiality-based activation differences in a network responsive to the linearization of arguments is significant in several respects. Firstly, referentiality cannot be considered an entirely syntactic parameter. Rather, linearization effects due to this information type are closely tied to the interface between syntax, semantics and pragmatics, as they are essentially a subcase of the more general preference to order old (or known) information before new information (e.g. Choi, 1999; Lenerz, 1977). The present findings thus lend further support to a “supra-syntactic” account of the functional neuroanatomy of word order processing (see also Grewe et al., 2006). A second and related point concerns the observation of referentiality-based activation differences in the pars opercularis between two subject-initial sentence structures. As outlined in the introduction, a crucial prediction of the linearization hypothesis was that order-based activation differences in this region are, in principle, independent of the relative positioning of subject and object. The finding of activation differences between subject-initial structures thus provides strong converging support for this claim. Crucially, as the two critical subject-initial conditions did not differ in acceptability (see Haupt et al., 2008, for converging acceptability data which attest to the reliability of this observation), the activation increase for the SO-NREF condition cannot be attributed to lower acceptability or a decrease in “naturalness”. Furthermore, the present results demonstrate that word-order-based activation differences cannot generally be reduced to a dependency between the first (“permuted”) element encountered and a second element on which it is dependent (as sketched out for object-before-subject orders in the introduction): increased processing cost for a violation of the referentiality principle cannot arise until the relative referentiality status of both arguments has been evaluated. This can only take place once the second argument has been reached, since an initial argument that is low on the referentiality scale is fully compatible with either an intransitive
showing a sensitivity to both subject-object order and referentiality (Rosen, & Gabrieli, 2002). We therefore suggest that the network are well-known for their involvement in cognitive control. Notably, should require the recruitment of a larger network of regions that appears highly plausible that precisely this type of mechanism during language comprehension (e.g. Friederici & Alter, 2004), it reanalysis is typically described as a late and controlled process (sis processes in order for the correct reading to be computed. As we will outline in the following, we believe that a more precise consideration of which (combinations of) regions were observed in which studies can help to shed further light on the factors involved in modulating subparts of the overall “linearization network”.

4.2. A network for linear order?

While our prediction – as based on the linearization hypothesis – focused mainly on the left pars opercularis, the complete neural network for the processing of linear order in language of course also encompasses a number of further regions. In the present study, the ORDER manipulation engendered activation in a greater network of regions comprising bilateral deep frontal opercular cortices, left basal ganglia (caudate nucleus), left pre-SMA, left inferior frontal junction area (IFJ) and left intraparietal sulcus (IPS). While all of these regions have been observed in one or more previous studies examining clause-medial word variations in German (Bornkessel et al., 2005; Friederici et al., 2006; Grewe et al., 2005, 2006, 2007; Röder et al., 2002), individual studies typically only yielded activation in a subset of the overall network observed here. As we will outline in the following, we believe that a more precise consideration of which (combinations of) regions were observed in which studies can help to shed further light on the factors involved in modulating subparts of the overall “linearization network”.

4.2.1. Frontoparietal (IFJ-IPS) network

With regard to the present study, recall that – in addition to the left pars opercularis – only the left IFJ and left IPS regions also proved sensitive to the referentiality manipulation. The only other study on word order variations in similar sentence structures that observed a left-lateralized network consisting of the pars opercularis, IFJ and IPS was reported by Bornkessel et al. (2005). The main commonality between this experiment and the present study was that both employed ambiguous sentence structures, in which the order of subject and object was only disambiguated at the end of the critical embedded sentences. By contrast, all other experiments on word order permutations in comparable sentence structures in German used only unambiguously case marked sentences in which the word order was clear from the very beginning (Friederici et al., 2006; Grewe et al., 2005, 2006, 2007; Röder et al., 2002). As local ambiguities between a subject- and an object-first reading are preliminarily resolved towards a subject-first order (Frazier & Flores d’Arcais, 1989), initially ambiguous object-initial sentences of the type used here and in Bornkessel et al. (2005) require reanalysis processes in order for the correct reading to be computed. As reanalysis is typically described as a late and controlled process during language comprehension (e.g. Friederici & Alter, 2004), it appears highly plausible that precisely this type of mechanism should require the recruitment of a larger network of regions that are well-known for their involvement in cognitive control. Notably, the association between a subnetwork involving the IFJ/IPS and cognitive control has been established in a range of experiments (e.g. Brass & von Cramon, 2002, 2004; Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002).6 We therefore suggest that the network showing a sensitivity to both subject-object order and referentiality in the present experiment (left pars opercularis, IFJ and IPS) subserves the processing of linear order under conditions giving rise to increased demands on cognitive control. An account along these lines might also explain the involvement of the caudate nucleus, which has also been implicated in language processing under “controlled” circumstances (Friederici, 2006). However, this region did not show an effect of referentiality.

4.2.2. Pre-SMA and deep frontal operculum/anterior insula

When activations in the pre-SMA and deep frontal operculum/anterior insula are observed in studies examining word order variations in German, these tend to co-occur (Friederici et al., 2006; Grewe et al., 2005). In particular, the likelihood for an involvement of these regions appears to increase with the use of gradient stimuli (i.e. word order permutations that give rise to significantly degraded acceptability ratings) and an acceptability judgment task. On the basis of this observation and following a proposal advanced in Grewe et al. (2005), we assume that this subnetwork may be particularly involved in the evaluation of linguistic structures under conditions of increased uncertainty. Such an assumption is highly compatible with the results of studies investigating the functional neuroanatomy of decision-making in the presence of uncertainty (e.g. Volz et al., 2003).

The results of our parametric analyses provide converging support for this “decision-based” account: of the regions that proved sensitive to our critical manipulation (order and referentiality), only the deep frontal operculum covaried with any of the behavioral predictors. Specifically, individual standard deviations of acceptability predicted the bilateral activation of fronto-opercular cortices, while individual reaction times predicted the activation pattern of the left deep frontal operculum. While we do not wish to speculate with respect to a possible functional significance of the lateralization differences observed for the two predictors, their joint contribution to the fronto-opercular activation observed here suggests that a participant’s confidence in judging a particular condition to be acceptable or unacceptable may be the key factor underlying this activation. Whereas reaction time differences per se could be attributed to a number of factors (including individual differences between “slow responders” and “fast responders”, for example), higher individual per-condition standard deviations for acceptability are clearly indicative of a higher variability in judgment behavior – as would be expected under conditions of judgment uncertainty. This, in turn, is compatible with longer reaction times. In view of these two sources of converging evidence, it appears plausible to associate increased activation in the frontal operculum that arises in studies using a linguistic judgment task (e.g. Grewe et al., 2005) with increased judgment uncertainty. Interestingly, the “output” of this evaluation process, namely the final acceptability value per participant and condition, predicts neither the fronto-opercular activation nor activation in any of the regions within the greater language network. This observation underscores the point raised above that confidence in performing the judgment task need not decrease with a decrease in acceptability, i.e. participants can be very confident in rejecting certain sentence structures. These observations are thus in line with Grewe et al.’s (2005) finding that the acceptability of a critical sentence condition correlates neither with the activation pattern of the frontal operculum nor with that of the pars opercularis.

A possible conclusion from these findings appears to be that the deep frontal operculum – as well as the pre-SMA, with which it

6 An account along these lines can also derive the sensitivity of the frontoparietal (IFJ-IPS) network to further information types important to linearization (the thematic hierarchy in Bornkessel et al., 2005; and referentiality in the present study). While these information types do not impact upon the initial subject-preference for locally ambiguous sentences (cf. Haupt et al., 2008, and Kroetzschmar, Bornkessel-Schlesewsky, Staab, Boehm, & Schlesewsky, submitted for publication, for ERP and eye-tracking evidence in this regard), they can aid the reanalysis process by serving as additional cues for the object-initial order (see Bornkessel et al., 2004, for a detailed description). They are therefore relevant for determining the overall “cost” of reanalysis and, thereby, the degree of cognitive control required.
appears to act in concert – provide an interface between linguistic properties and more general task or decision-related mechanisms. This assumption is corroborated both by the high correlation between fronto-opercular activation and behavioral parameters and by the lower degree of sensitivity of the frontal operculum/pre-SMA to the critical linguistic manipulation employed here: in contrast to the pars opercularis, these regions did not show an effect of referentiality. It is also supported by findings in the literature of task-demand-related activations within the frontal operculum/ anterior insula, which have been reported, for example, for increased interference cost (Wager et al., 2005) or (for the right anterior insula) as correlating with valence in explicit and implicit evaluative judgments (Cunningham, Raye, & Johnson, 2004).

4.2.3. The pars opercularis of the left IFG

When all available studies of (clause-medial) word order variations in German are considered, the pars opercularis of the left IFG stands out as the only region that is consistently activated, independently of the task or the modality of presentation (visual or auditory) employed. Furthermore, and perhaps even more importantly for present purposes, only the left pars opercularis has proven sensitive to all of the linearization parameters hitherto examined: subject > indirect object > direct object (Friederici et al., 2006; Röder et al., 2002); pronoun > non-pronominal argument (Grewe et al., 2005); animate > inanimate (Grewe et al., 2006); higher thematic role > lower thematic role (Bornkessel et al., 2005); and higher referentiality > lower referentiality in the present study. It is this sensitivity to all critical word order-related factors (see Lenerz, 1977; and Müller, 1999, for theoretical discussion) in combination with the independence from the experimental environment (task, modality) that leads us to view the pars opercularis as the neural region that is at the core of linearization-related processes during sentence comprehension. While activation in this region is, of course, typically observed as part of a larger network in any given study, the overall makeup of the network – with the exception of the pars opercularis – appears largely determined by the particular experimental setting in which the critical sentences are presented.

4.3. Linearization: consequences for pars opercularis function

As outlined above, the left pars opercularis shows a sensitivity to all parameters known to influence argument linearization in German. Importantly, the set of information types involved (the thematic roles, animacy, definiteness/specificity, pronouns vs. non-pronominals) is not arbitrary: as noted briefly in the introduction, they have been identified as a major source of cross-linguistic similarities and differences with respect to a wide range of morphosyntactic phenomena (e.g. Comrie, 1989; Croft, 2003). Most generally, these factors serve to change the (conceptual) “prominence” status of an argument (Actors are more prominent than Undergoers, animate entities are more prominent than inanimate entities etc.), with conceptual prominence ideally corresponding to morphosyntactic prominence. For example, a prominent argument is more likely to be realized as a subject rather than an object (cf. Aissen, 1999, and the references cited therein). In addition, and more importantly for present purposes, prominent arguments preferentially precede their coarguments in terms of linear order (Tomlin, 1986). The pars opercularis of the left IFG thus appears to play a crucial role in basic – and universal – processes of linearization in language.

The empirical observations in the domain of linearization yield a number of important consequences with respect to the function of the pars opercularis in the processing of linear order in language. In particular, the overall data pattern poses a challenge to prominent language-specific (syntactic) and domain-general approaches to the function of this cortical region.

Challenges for a syntactic (movement-based) account (cf. Grodzinsky & Santi, 2008) have already been documented in previous related work (e.g. Bornkessel et al., 2005; Grewe et al., 2006, 2007) and were briefly outlined in the introduction. The present findings serve to further corroborate this perspective. Importantly, existing movement-based accounts of referentiality effects (e.g. Diesing, 1992) assume an influence of referentiality on the surface structure of a sentence, but not on the base positions of the arguments (i.e. the subject is assumed to be generated in a higher structural position than the object independently of referentiality). Specifically, it is assumed that referential arguments (including proper names) must move out of the verb phrase domain in order to be interpretable (cf. Carlson, 2003). Consequently, both REF conditions should require a single movement operation (of the referential argument, whether it is subject or object), whereas both NREF conditions should require two movement operations (the second argument, i.e. the proper name, must have moved since it is referential, and, consequently, the first argument must also have undergone movement in order to ensure its linear precedence). Hence, a movement-based account would only predict a main effect of referentiality and therefore cannot derive the pattern of pars opercularis activation observed here (see also Uszkoreit, 1986).\footnote{Note that similar considerations serve to exclude an explanation of our findings in terms of semantic differences with regard to the interpretation of bare plural NPs in different structural positions. According to Diesing’s (1992) account, the bare plurals should be ambigious between an indefinite and a generic reading in the REF conditions (since they could either be within the VP domain or outside of it). By contrast, they should unambiguously require a generic reading in the NREF conditions, because, here, they precede the proper name, which must be outside the VP domain. (But see Frey, 2001, for problems with a one-to-one mapping between the interpretation of bare plurals and their position within the German middlefield.)}

Turning now to prominent domain-general approaches, working memory-based accounts encounter difficulties when the linearization parameter in question does not induce an inherent dependency between two arguments. A dependency between the arguments (e.g. of an initial object upon a following subject) may clearly lead to increased working memory load because the first argument must be maintained until the second is encountered. However, increased pars opercularis activation is observable even when no such dependency applies (e.g. in the case of arguments that differ in terms of referentiality: see also Grewe et al., 2006, for similar findings involving animacy). Note that possible notions of working memory related to differences in informational load (Almor, 1999) do not apply here, since no reactivation of antecedents was required in the critical sentences.

A second possibility is that the involvement of the pars opercularis in the processing of word order variations stems from the increased involvement of cognitive control mechanisms in these structures (Thompson-Schill et al., 2005). This hypothesis was applied specifically to sentence processing by Novick, Trueswell, & Thompson-Schill (2005), who argue that Broca’s region engages in the resolution of conflicts among competing stimulus representations and is involved in reanalysis processes. On the one hand, this proposal appears partially compatible with the linear order phenomena discussed here: pars opercularis activation increases when there is an incompatibility between the different types of prominence information. However, the proposal that the degree of conflict should be higher in ambiguous structures appears problematic, as Bornkessel et al. (2005) found very similar interactions between subject-object order and thematic information for locally ambiguous and unambiguous structures. Thus, while main effects of ambiguity have been observed in the left pars opercularis and the adjacent pars triangularis, BA 45 (Bornkessel et al., 2005; Fiebach, Vos, & Friederici, 2004; Stowe, Paans, Wijers, & Zwarts, 2007).
2004; see also Rodd, Davis, & Johnsrude, 2005, for findings on lexical/semantic ambiguity), the need for reanalysis does not increase the activation of this region beyond the level observed for the comparable (dispreferred) unambiguous structure. Rather, we have argued above that the degree of cognitive control required in word order processing modulates the overall neural network within which pars opercularis activation can be observed.

Finally, as the linearization principles at issue here are verb-independent, they also pose a challenge for “action understanding”-based approaches to Broca’s area function (Rizzolatti & Arbib, 1998; for a more recent review see Rizzolatti, Fogassi, & Gallese, 2002). Here, it is proposed that filler-slot associations between arguments and predicates, which may be used to represent motor commands, can also serve to model language. More specifically, Broca’s area is viewed as representing “verb phrases” and constraints on the noun phrases that can fill the slots, but not details of the noun phrases themselves (Rizzolatti & Arbib, 1998, p. 192). It is, however, not at all clear how representations of this type could serve to model linearization principles of the type animate-before-inanimate, definite-before- indefinite and pronoun-before-non-pronominal, which depend entirely on the properties of the arguments themselves.

To summarize, existing domain-general models of pars opercularis function cannot easily account for the high sensitivity of this cortical region to linguistic linearization principles. In this respect, these models turn out to be surprisingly similar to what is arguably the most specific language-internal approach, namely the syntactic movement-based account. Importantly, we do not mean to suggest that linearization effects are principally incompatible with domain-general mechanisms, but only that – to the best of our knowledge – there are currently no such models that can derive the fine-grained data patterns in the domain of word order processing. In this context, we would like to stress once more that the phenomena under consideration here are by no means “exotic”: as flexible argument order is very common cross-linguistically (Steele, 1978), the mechanisms examined here are fundamental to the human ability to comprehend language. Thus, in order for the full explanatory potential of non-linguistically-oriented models of pars opercularis function to become clear, we suggest that it would be fruitful for these models to focus less on the rather restricted range of constructions that is available in languages of the English type (which can also be accounted for in a movement-based approach) and more on the rich possibilities that are available cross-linguistically (which cannot).

5. Conclusion

The present study was the first to show word order-related activation differences between subject-initial sentences in the pars opercularis of the left IFG. Specifically, activation in this region increased when an argument that was lower in referentiality preceded an argument that was higher in referentiality—a finding which cannot be explained on the basis of acceptability differences between the critical sentence types. Together with previous findings, this result suggests that the word order-related processing mechanisms subserved by the pars opercularis: (a) apply independently of any inherent dependency between two arguments, (b) are verb-independent and (c) do not necessarily require increased degrees of cognitive control. Furthermore, we have argued that the overall neural network involved in the processing of linear order in language is determined by a number of factors. While a frontoparietal (IF/P) subnetwork comes into play when additional cognitive control is required, fronto-opercular/anterior insular cortices and the pre-SMA support the processing of gradient stimuli and linguistic judgments.

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