The language skeleton after dissecting meaning:

a functional segregation within Broca’s Area

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Abstract

Broca’s area is proposed as a crucial brain area for linguistic computations. Language processing goes beyond word-level processing, also implying the integration of meaningful information (semantics) with the underlying structural skeleton (syntax). There is an on-going debate about the specialisation of the subregions of Broca’s area—Brodmann areas (BA) 44 and 45—regarding the latter aspects. Here, we tested if syntactic information is specifically processed in BA 44, whereas BA 45 is mainly recruited for semantic processing. We contrasted conditions with sentence structure against conditions with random order in two fMRI experiments. Besides, in order to disentangle these processes, we systematically removed the amount of semantic information available in stimuli. This was achieved in Experiment 1 by replacing meaningful words (content words) by pseudowords. Within real words conditions we found broad activation in the left hemisphere, including the inferior frontal gyrus (BA 44/45/47), the anterior temporal lobe and posterior superior temporal gyrus (pSTG) and sulcus (pSTS). For pseudowords we found a similar activation pattern, still involving BA 45. Among the pseudowords in Experiment 1, we kept those word elements that convey meaning like un- in unhappy or –hood in brotherhood (i.e. derivational morphology). In Experiment 2 we tested whether the activation in BA 45 was due to their presence. We therefore further removed derivational morphology, only leaving word elements that determine syntactic structure (i.e. inflectional morphology, e.g. the verb ending –s in he paints). Now, in the absence of all semantic cues, including derivational morphology, only BA 44 was active. Additional analyses showed a selective responsiveness of this area to syntax-relevant cues. These findings confirm BA 44 as a core area for the processing of pure syntactic information. This furthermore suggests that the brain represents structural and meaningful aspects of language separately.

Keywords

language processing, fMRI, Broca’s area, syntax, morphology, pseudowords
1. Introduction

Language is more than words. It is also the combination of content words (categories that convey meaning, e.g. nouns and verbs) and their derivational forms (e.g. brotherhood derived from brother), which are particularly relevant for sentence meaning, i.e. carry semantic information. No less important are their inflectional forms and function words, which are the elements that convey the relationships between them and hence the global sentence structure, i.e. carry morphosyntactic information. Thus, during language processing, the skeleton of syntactic information interacts with semantics. Early fMRI studies (e.g. Dapretto & Bookheimer, 1999; Sakai et al., 2002) showed a dissociation of these two dimensions, but no consensus has been reached so far, as to which brain areas deal with the processing of the different types of linguistic information. This holds in particular for the involvement of the inferior frontal gyrus (IFG) (e.g. Rogalsky & Hickok, 2011).

Broca's area in the IFG, which consists of the posterior pars opercularis (BA 44) and the more anteriorly located pars triangularis (BA 45) (Amunts et al., 1999), has long been identified as one of the classical language areas. However, the specific function of Broca's area and, in particular, of its subparts remains to be specified. Review articles, meta-analyses (Hagoort & Indefrey, 2014) and models of language processing (Friederici, 2011) suggest that BA 44 is more likely to be involved in the processing of syntax, whereas BA 45 seems to be more highly engaged by the processing of semantics, especially at the sentence level (Hagoort, 2005; Vigneau et al., 2006; Price, 2010; Friederici, 2011). However, results across different languages and paradigms do not allow for a clear specification of the function of Broca's area's subregions.

The relevance of the distinction of these two neighbouring brain areas, BA 44 and BA 45, also lies in the striking difference in their anatomical connectivity with the temporal cortex, which is crucial for sentence comprehension. Whereas BA 44 and the posterior temporal cortex are connected by a dorsal fibre tract via the superior longitudinal
fasciculus (SLF) and the arcuate fasciculus (AF), BA 45 and the superior and middle temporal gyri (STG/MTG) are connected by a ventral fibre tract running via the extreme capsule fibre system (ECFS) (for an overview see Friederici & Gierhan, 2013). Indeed, the tractography-based neuroanatomical parcellation of Broca’s area consistently leads to a subdivision into an anterior and a posterior portion corresponding to BA 45 and 44 respectively (Anwander et al., 2007). Furthermore, while the dorsal pathway has been associated with the processing of complex syntactic structures (Friederici et al., 2006; Wilson et al., 2011), the ventral pathway seems to be consistently involved in semantic comprehension (Saur et al., 2008; Griffiths et al., 2013; Almairac et al., 2014). These findings on brain connectivity are consistent with the aforementioned functional segregation within Broca’s area.

However, not all functional brain imaging studies that focused on syntactic processing report major activation only in BA 44 (as it is the case of Friederici et al., 2006; Newman et al., 2010; Kinno et al., 2008), but report additional activation in BA 45 (Tyler et al., 2008, 2010; Santi & Grodzinsky, 2007, 2010; Fedorenko et al., 2011; Pallier et al., 2011). The reason for this difference may be that these studies differed in the stimulus material or in the specific task demands, but it may also be due to the experimental languages they used. In fact, German studies show a clear activation of BA 44 for various syntactic manipulations (Friederici et al., 2006a; Makuuchi et al., 2009; Obleser et al., 2011), whereas English studies frequently showed the activation of BA 44 and additionally BA 45 (Caplan et al., 2008; Santi & Grodzinsky, 2010; Tyler et al., 2010, but see Newman et al., 2010).

One possible account for this distinction is that German and English strongly differ in the linguistic features that are crucial for sentence processing, and in particular the processing of sentence structure. In German, word order is relatively free, with sentence building blocks (called constituents) being able to occupy different positions in the sentence and the verb being the only fixed element. This flexibility in word order is
counterbalanced by the rich morphosyntactic information—word elements that convey the relations established between constituents (inflectional morphology), e.g. express “who did what to whom” in form of case marking (Haider, 2010). In turn, English speakers mainly rely upon word order to identify the syntactic roles of constituents, since morphosyntactic information is comparatively scarce (Thompson, 1978). We therefore postulate that whereas the activation of BA 44 happens in response to pure syntactic information (in particular, morphosyntactic inflections and function words), the activation of BA 45 is present mainly as a result of parallel sentence-level semantic processing based on the meaning of words and their derivational morphology (like un-in unhappy or -hood in brotherhood). EEG studies could indeed show that semantic processing (in the form of N400) could be blocked by syntactic violations revealed by an ELAN (Friederici et al., 1999; Hahne & Jescheniak, 2001). These findings would explain why we would only find parallel semantic processing in stimuli with sentence structure. Furthermore, these additional semantic computations should be most salient in the absence of rich morphosyntactic information as it is the case of English when compared to German.

In order to test whether the differential activation in BA 44 and BA 45 reported in the literature is a function of the language type (English or German) and/or the function of the respective information type available in the stimulus material, we designed a close replication of the English study of Tyler et al. (2010) using German as the experimental language. In the English study—an fMRI adaption from a well-established behavioural word monitoring paradigm (Marslen-Wilson & Tyler, 1980)—subjects were presented with three conditions: first, a normal prose (NP) condition; second, a nonsense sentence condition—anomalous prose (AP)—in which all content words of a normal sentence were replaced by semantically implausible words of the same lexical category; third, a condition consisting of the same word material of AP sentences in a permutated order that disrupted syntactic structure—random word order (RWO). The authors of this
fMRI study reported a widespread activation for syntax based on a contrast between AP and RWO. This activation pattern, however, could result from the additional recruitment of semantic processes, since semantic information was widely available in these conditions. In the present study we therefore progressively removed the semantic information of sentences in order to find the central hub for pure syntactic processing in language. Our study hence included additional conditions with pseudowords, words that respect the phonological rules of a language but are devoid of word meaning. The conditions of this study not only comprised those tested by Tyler et al. (2010), but also their pseudoword counterparts respectively called Jabberwocky Prose (JP) and Jabberwocky in Random Order (JRO). Two fMRI experiments were conducted in order to disentangle different aspects of semantics by systematically removing meaning from the stimuli, first in the form of content words and then of derivational morphemes.

2. Material and Methods

2.1. Participants

Twenty-three participants (11 females, 26.3 ± 3.3 years of age, M ± SD) took part in fMRI Experiment 1. 32 participants (16 females, 27.3 ± 3.2 years of age, M ± SD) were recruited for fMRI Experiment 2. All participants in both experiments were right-handed, as assessed by an abridged version of the Edinburgh Inventory (Oldfield, 1971), and were native speakers of German. They had normal or corrected to normal vision, and did not report any history of neurological, psychiatric, or hearing disorder. All subjects were naïve as to the purpose of the study. Participants received financial compensation of 16 € for each of the fMRI experiments. The local ethics committee of the University of Leipzig approved all procedures.

2.2. Stimuli

2.2.1. General description

Experiment 1 systematically varied semantic information encoded by content words (for an overview of stimulus properties see Inline Supplementary Table 1). We first
replaced content words in a normal sentence—NP—by words of the same lexical category, destroying the overall sentence meaning—AP—as already done in the aforementioned study. In the second step, these were replaced by pseudowords, words that respect the phonological rules of a language but are devoid of word meaning, hence originating JP. The word order of both AP and JP was then scrambled in such a way that no overall sentence structure could arise, originating respectively RWO and JRO. In all experimental conditions we kept function words (words that rather help forming sentence structure like determiners or relative pronouns). In this first experiment, we maintained both inflectional and derivational morphology in the pseudoword conditions, although derivational morphology actually also carries meaning.

Insert Supplementary Table 1 here

In Experiment 2 we further removed semantic information from the pseudoword conditions of the first experiment, now renamed as JP1 and JRO1 (for an overview of stimulus properties see Inline Supplementary Table 2). We further deleted the derivational morphology from these conditions resulting in JP2 and JRO2. In JP3, moreover, inflectional morphology was also removed. For a detailed description of stimulus construction, see the following sections.

Insert Supplementary Table 2 here

2.2.2. Stimuli of Experiment 1

The first condition—NP—consisted of normal sentences in German following three different sentence structure templates. In a second condition—AP, all content words of NP were replaced in the same paradigm by words of the same category that, however, did not allow for a coherent interpretation of the resulting sentence. In order to generate the so-called jabberwocky conditions—JP, JRO—function words from the AP condition remained unaltered in order to keep sentence structure, whereas the content words were replaced by pseudowords. For pseudoword generation, consonants in real words were replaced by other consonants with the same manner of articulation (e.g. the
stop consonant /p/ could be replaced for instance by another stop consonant such as /b/ or /t/). Vowels were changed so that the resulting word was not a close neighbour to an existing word, hence eliciting unwanted associations. Inflectional and derivational morphemes were left unchanged if possible. In order to obey to the phonetic rules of German, an inventory of syllable onsets and endings was taken into account (Ruske & Schotola, 1978) in stimulus generation. As content-free function words, we utilized pronouns—personal (e.g. “she”), possessive (e.g. “her”), demonstrative (e.g. “this”) and relative (e.g. which); articles (e.g. “the“); and prepositions in collocations (obligatory prepositions), according to the findings of Friederici (1985). The random order conditions (RWO, JRO) were generated by permuting the words from the previous conditions in order to eliminate sentence structure, therefore not allowing for legal local transitions or sentence fragments. Examples of the stimuli used the original language are provided in the Inline Supplementary Table 3. The pseudowords were then verified in German dictionaries and compared with corpus information of CELEX (Baayen et al., 1993). All stimuli were analysed by three independent German native speakers to rule out similarities to existing words and ensure plausibility and naturalistic perception of the stimuli.

Insert Supplementary Table 3 here

2.2.3. Stimuli of Experiment 2

Here we additionally varied the presence of derivational morphology. Simple words—or word stems—can be modified by other elements called bound morphemes. Inflectional morphemes adapt the word to its grammatical context, while derivational morphemes transform words into others with a different but related meaning and often change their category. The verb “to like” in the third person singular (e.g. with the subject “he”) receives an additional –s, which is an inflectional morpheme, establishing a relation between the subject and the verb (i.e. “he likes”). If we add the derivational morpheme dis- to this verb, we will change its meaning to “dislike”. If we instead add the suffix –
able, we originate a different word category, an adjective, while also changing the meaning. Thus, derivational morphemes are said to carry meaning whereas inflectional morphemes hardly have any semantic content. Illustrative examples of the stimuli in English are provided in Table 1 for a better understanding of derivational and inflectional morphology in our experiments.

Insert Table 1 here

Conditions JP1 and JRO1 were generated similarly to JP and JRO from Experiment 1. The additional conditions (JP2, JP3 and JRO2) in the second experiment were generated from the conditions JP1 and JRO1. Derivational morphemes of JP1 and JRO1 were replaced by content-free letter sequences using the phonological rules of the first experiment originated respectively JP2 and JRO2. The identification of word category (nouns, verbs or adjectives) was done according to the most frequent word endings of these categories, instead of using derivational morphemes for this purpose. JP3 was created by removing inflectional morphology, only leaving word stems, and replacing determiners with monosyllabic pseudowords. Examples of the stimuli used the original language are provided in the Inline Supplementary Table 4. Once again, stimuli were analysed by three independent German native speakers.

Insert Supplementary Table 4 here

2.2.4. Procedure for Stimuli

All sentences were spoken by a trained female German speaker, who was instructed to apply the prosodic structure of the template sentence to all conditions. This ensured the presence of intonational phrase boundaries across all stimuli at the same sequence length in syllables and a naturalistic pronunciation even in the case of pseudoword lists. The stimuli were recorded in a soundproof chamber with a Sennheiser® MKH 40 condenser microphone and a Roland® CD-2 digital sound recorder, with 16bit resolution and 44.1kHz sampling rate. The recordings were cut in Adobe® Audition™ CS5.5 and normalized in Praat 5.3 (Boersma and Weenink, 2001) according to the root
mean square amplitude of all files. All sentences were spoken maintaining the prosody of the original template (NP in Experiment 1 and JP1 in Experiment 2). An individual pseudo-randomized list of stimuli was generated for each subject. The list consisted of 300 stimulus sentences (60 per condition) in Experiment 1 and 250 sentences (50 per condition) in Experiment 2.

The task consisted in the recognising of a target word presented before each sentence at a late position in that sentence (according to Marslen-Wilson & Tyler, 1980). Since it was not possible to use real words as content word targets for the jabberwocky conditions, 50% of the stimuli had a function word as the target word. The other 50% of the stimuli had a content word or a matched pseudoword as the target word. Besides, in order to diminish the predictability of detection of the target word at a late sentence position and therefore enforce the processing of the whole stimulus, 20% of the stimuli constituted a filler condition with an early target word. Target words were word stems (without affixes) and were controlled for phonotactics (local transition probabilities and legal syllable onsets and codas), for corpus frequency in real words and for length in syllables and duration (ANOVA across conditions, p>0.05 in both experiments). Stimulus length did not differ across conditions either (p>0.05).

Stimuli were drawn from a stimulus pool that had previously been piloted behaviourally. Sentences whose accuracy and reaction time of detection of the target word were outside of the range mean ± 2 standard deviations were excluded. The final stimulus pool was drawn in a counterbalanced way out of the remaining sentences.

2.3. Experimental procedure

Stimuli were presented using the software package Presentation® (Neurobehavioural Systems, Inc., Albany, CA, USA). Auditory stimuli were presented using air-conduction headphones (Resonance Technology, Inc., Northridge, CA, USA). Visual stimuli were presented on a Sanyo PLC-XP50L LCD XGA mirror-projection system with a refresh rate
of 100Hz (Sanyo Electric Co., Ltd., Moriguchi, Japan), mounted onto the headcoil. A sans-serif font in white letters against a grey background (font size 32p) was used.

Insert Figure 1 here

The experimental trials are depicted schematically by Figure 1. Each trial started with a random jitter of either 0 or 1000ms. It was followed by the visual presentation of the target word that stayed on screen for the whole trial. Simultaneously, the target word was presented auditorily (mean length=0.52s, SD=0.05s in Experiment 1; mean length=0.54s, SD=0.13s in Experiment 2). After 1000ms, the auditory stimulus started—the actual sentence (mean length=5.5s, SD=0.30s in Experiment 1; mean length=5.0s, SD=0.42s in Experiment 2). To keep the number of acquired volumes constant across trials, all trials lasted for 8 seconds, with a silent period between stimulus and trial end. The subject was required to press a button upon recognition of the target word within the sentence as fast as possible. All sentences contained the presented target word. All trials were included in the analysis.

2.4. MR acquisition parameters

Functional image acquisition was performed with a 3 Tesla Siemens TIM TRIO scanner (Siemens Healthcare, Erlangen, Germany) and a 12-channel headcoil at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. A T2*-weighted gradient-echo echo-planar-imaging (EPI) sequence was run (data matrix 64 × 64, TR=2.0s, continuous scanning, TE=30ms, flip angle=78°, bandwidth 116kHz, FOV=19.2cm, in-plane resolution 3mm×3mm, slice thickness 3mm, interslice gap 0.75mm, 32 horizontal slices parallel to AC–PC line with whole-brain coverage) with a functional scan time of 52 minutes in Experiment 1 (1550 volumes) and 43 minutes in Experiment 2 (1280 volumes). All participants had previously acquired T1-weighted images used for registration to the MNI template and subsequent normalisation of the T2*-weighted images.

2.5. fMRI data analysis
Preprocessing and statistical analysis were performed with SPM8 (Ashburner & Friston, 2005; available at www.fil.ion.ucl.ac.uk, Wellcome Institute of Cognitive Neurology, London, UK), under MATLAB (Mathworks, Inc., Sherborn, MA, USA). All EPI images were realigned to the first EPI image (excluding the 4 initial lead-in images) to correct for head motion, corrected for distortions in the magnetic field, and then spatially normalized to a standard MNI (Montreal Neurological Institute) EPI template with DARTEL (Ashburner, 2007). Statistical modeling was done according to the general linear model (GLM) (Friston et al., 1995) as implemented in SPM8. For all experimental conditions, sentence durations were convolved with canonical hemodynamic response function (HRF) and the onset of each sentence was taken as trial onset of the trial in the SPM analysis model. The realignment parameters were not included in the GLM. Both baseline contrasts and the contrasts of interest were computed at the first level analysis. The second level analysis was conducted with a flexible factorial design (commonly known in SPM as random effects) on the corresponding contrast images. A within-subject ANOVA was computed at the second level as a within-subject flexible factorial design also over the contrast images of the relevant conditions against baseline in the first level. Activations were thresholded at p<0.001 uncorrected at the voxel level, and significant clusters were reported only when they survived p<0.05, cluster-level corrected for multiple comparisons unless stated otherwise. Activation peak coordinates are reported in MNI space and labelling is done according to the SPM Anatomy toolbox including the Jülich cytoarchitectonic probability maps (Eickhoff et al., 2007).

3. Results

3.1. Behavioural data

In Experiment 1, the mean accuracy rate was 97.9% (SD=4.2%) and in Experiment 2, it was 95.1% (SD=6.3). In Experiment 1, only one participant performed under mean-2SD and was excluded from further analysis. In Experiment 2, a total of 5 participants with
accuracy rate under the same threshold of mean-2SD were excluded. In spite of the very high accuracy rates in the monitoring task, it was possible to observe significant differences in reaction times and accuracies across stimulus conditions. In Experiment 1, we performed a 2x2 within-subject design ANOVA with the factors syntax (sentence structure present or absent) and semantics (real words or pseudowords), including the conditions AP, RWO, JP and JRO. Condition NP was not included in the overall factorial analysis of Experiment 1 since it differed from the other conditions in an additional factor. This analysis showed significant main effects for reaction times (syntax: F(1,21)=7.46, p=0.012; semantics: F(1,21)=18.70, p<0.001) and accuracy rates (syntax: F(1,21)=9.30, p=0.006; semantics: F(1,21)=3.17, p=0.090) and significant interaction only for accuracy (F=7.25, p=0.014). See the left side of Figure 2 for a graphical display of the behavioural results and the factorial design of Experiment 1. We performed an analogous ANOVA in Experiment 2, now with the factors syntax (sentence structure present or absent) and morphology (derivational morphemes or inflectional morphemes only) including conditions JP1, JRO1, JP2 and JRO2. Condition JP3 was not included in the overall factorial analysis of Experiment 2 since it differed from the other conditions in an additional factor. This analysis showed a significant main effect in accuracy for both syntax (F(1,26)=4.45, p=0.045) and morphology (F(1,26)=6.77, p=0.015), but no significant interaction. Regarding reaction times, only a significant main effect of syntax (F(1,26)=6.65, p=0.016) was present, but not of morphology or interaction (p>0.05). See the right side of Figure 2 for a graphical display of the behavioural results and the factorial design of Experiment 2.

Insert Figure 2 here

3.2. fMRI data

The results of Experiment 1 are summarized in Table 2. The syntactic contrast within the real-word conditions (AP>RWO) yielded activation in the frontal lobe in BA 44, BA 45 and in the temporal lobe in the anterior STG and MTG and in the posterior STG
extending into the angular gyrus (Figure 3a). The activation of the typical frontotemporal language network was similar to the analogous contrast in the English study conducted by Tyler et al. (2010). Regarding the syntactic contrast in the pseudoword conditions (JP>JRO), we expected the activation of BA 44 alone, but we found additional activation in BA 45 and in the posterior superior temporal gyrus/sulcus (Figure 3b). For the interested reader, we provide the sagittal and axial slices of the SPMs with the respective statistical values in the Inline Supplementary Figure 1.

Similarly to the behavioural analysis, we performed an additional 2x2 within subject whole brain ANOVA with the factors syntax and semantics (See left Figure 2 for factorial design). The syntactic main effect was significant in the IFG (peaks at [-52, 27, 12] and [-42 20 21], corresponding to BA 45 and BA 44 respectively), the anterior temporal cortex (peak at [-52, 12, -18]), and in the posterior temporal cortex (peak at [-57, -42, 3]), whereas the semantic main effect was significant in the bilateral anterior temporal cortex (left peak at [-52, 0, -21] and right peak at [60, -4, -17]) and in the posterior temporal cortex (peak at [-52, -54, 16]). There was a significant interaction in the posterior temporal cortex/angular gyrus (peak at [-39, -64, 18]) and in the anterior temporal cortex (peak at [-48, 12, -23]). Inline Supplementary Figure 2 depicts an additional ROI analysis in both temporal interaction peaks. The percent signal change reveals that the interaction results from the larger difference in activation between conditions with and without syntactic structures within real word stimuli than within pseudoword stimuli.
In order to test whether the activation in BA 45 and in the posterior STG was due to the presence of the semantic dimension carried by the derivational morphemes in the pseudoword conditions in the first experiment, we conducted Experiment 2.

Here, the respective pseudoword conditions were presented with and without derivational morphemes. The results of Experiment 2 are summarized in Table 3. We applied a small volume correction for the contrast JP2>JRO2, which is justified by our clear *a priori* hypothesis of activation in BA 44 for syntactic information. This hypothesis issues from the literature about the functional specialisation of subareas of the IFG as well as from the first experiment. The respective ROI for small volume correction has 12616mm$^3$. Again, for JP1>JRO1 both subregions of Broca's area (BA 44 and BA 45) were activated during sentence processing when semantic information carried by derivational morphology was present (Figure 4a). However, once all semantic information—content words and derivational morphology—was deleted, leaving only pure syntactic information (provided by function words, inflectional morphology and word order) as in JP2>JRO2, only BA 44 was significantly activated (Figure 4b).

Additional contrasts with JP3 did not hold significant activations. For the interested reader, we provide the sagittal and axial slices of the SPMs with the respective statistical values in the Inline Supplementary Figure 3.

Similarly to Experiment 1, we performed a supplementary 2x2 within subject whole brain ANOVA, here with the factors syntax and derivational morphology (See right Figure 2 for factorial design). The main effect syntax showed activation in Broca's area (p<0.05 FWE corrected), but there was neither a significant main effect for morphology nor a significant interaction between factors.

We performed additional comparisons on Experiment 1 regarding the selective processing of function and content words in a task with syntactic demands (Figure 5a and 5b). We expected that function words would engage brain areas involved in pure
syntactic processing more than content words, which contribute more to semantic processing and rather involve brain areas recruited with lexical access. Indeed we found activation in BA 44 for the contrast function words>content words (peak coordinates in MNI space [-48, 5, 16]; p<0.05 FWE corrected) in the frontal operculum and anterior insula (peak coordinates in MNI space [-30, 23, 1]; p<0.05 FWE corrected), and in the supramarginal gyrus and posterior STG (peak coordinates in MNI space [-56, -36, 24]; p<0.05 FWE corrected). For the reverse contrast—content words>function words—we found three clusters at a threshold of p<0.001 uncorrected and cluster extent above 400 voxels (displayed in Figure 5b). Activation was found in the anterior temporal lobe (peak at [-54, -6, -15]), inferior posterior temporal lobe (peak at [-40, -42, -15]) and in the fusiform gyrus (peak at [-16, -85, -9]). Previous studies (e.g. Fedorenko et al., 2011) claimed that no brain area was more sensitive to syntactic information than to lexical information, therefore we also tested whether part of Broca’s area responds more to the jabberwocky condition (JP) than to the scrambled real words (RWO). Again we found an activation peak in BA 44 at the coordinates [-40, 18, 21] (p<0.001 uncorrected, p<0.05 small volume corrected). For the interested reader, we provide the sagittal and axial slices of the SPMs with the respective statistical values in the Inline Supplementary Figure 4.

4. Discussion

The two experiments show that Broca’s area (BA 44 and BA 45, extending anteriorly to BA 47) is activated as a whole during sentence processing as long as syntactic and semantic information is available. Once all semantic information is deleted and only
pure syntactic information is left—provided by function words, inflectional morphology and word order—only BA 44 is activated. This finding provides evidence for a functional segregation of Broca’s area into BA 44 and BA 45 with a functional specificity of BA 44 for syntax.

The present data support the view that BA 44 subserves syntactic processes. Moreover, the additional contrasts between function and content words highlight how different word elements contribute to different processing streams in function of their role in a sentence. Whereas content words mainly recruit the middle and inferior temporal cortex, most likely due to lexical access, function words trigger again the activation of BA 44, which is in agreement with their fundamental role in establishing sentence structure.

To our knowledge, this is the first study that systematically manipulated both derivational and inflectional morphology at a sentence level, hence simultaneously investigating its interaction not only with lexical access but also with syntactic processing. Indeed, previous studies have shown that Broca’s area is involved in the processing of both derivational and inflectional morphology at the word level (Bozic & Marslen-Wilson, 2010; Whiting et al., 2013). In particular, several studies showed that morphosyntactic information activate BA 44, be it word category (Heim et al., 2003), gender (Heim et al., 2006) or regular verb inflection (Marslen-Wilson & Tyler, 2007; Fonteneau et al., 2011). However, the question of how this information interacts with sentence processing has been mainly left unanswered. Here we show that these sources of linguistic information are integrated in either semantic or syntactic processing according to the cues they carry. Although we removed these two linguistic cues in step-wise, a parametric variation of the semantic content in stimuli, analogous to previous syntax studies (Pallier et al., 2011; Ohta et al., 2013), might show a gradient of activation within the IFG.
Although the more dorsal part of the posterior region of the IFG has also been implied in phonological processing (e.g. Poeppel et al., 2012), there is no strong reason to believe that the activation we found in BA 44 is due to phonological processes involved in the processing of pseudowords, since the pseudoword conditions that were contrasted were recorded with normal sentence prosody and were controlled for phonological variables. These conditions strictly obeyed to the phonotactic rules of German and followed the most frequent syllable onsets and endings of German words. Furthermore, the very good performance in the behavioural task indicate that participants were able to identify word boundaries effortlessly, hence being able to process the corresponding sentence structures, even if devoid of meaning. Other accounts of low-level linguistic processing in Broca's area include short-term phonological memory (Rogalsky & Hickok, 2011). Our task design, however, took this possible confound in consideration, since the target word was presented continuously during the trial. Indeed, previous studies (Embick et al., 2000; Suzuki et al., 2003) had already shown the relevance of the IFG in syntactic processing compared with low-level phonological processing. One could additionally argue that these ventrolateral prefrontal regions specifically engage in the processing of pseudowords (Heim et al., 2005, Zhuang et al., 2012). However, both sentence material and target words were maintained constant across conditions with and without sentence structure, which makes this interpretation unlikely. However, both sentence material and target words were maintained constant across conditions with and without sentence structure, which makes this interpretation unlikely.

Although previous studies have already dealt with the distinction between syntax and semantics, they were not able to show any brain with a preference to structural information over content. Several of these studies (e.g. Fedorenko et al., 2012), however, did not keep enough cues in the pseudoword stimuli to allow participants to perceive the underlying sentence structure. Our extensive use of function words (as prepositions), inflectional morphology (as verb endings and case marking) and word endings corresponding to a specific word class (e.g. –ation for nouns or –ise for verbs) provided participants with the necessary cues to establish syntactic structure. We also
tried to overcome some of the shortcomings of studies pinpointing the anterior temporal lobe (ATL) as the central area for linguistic combinatorial processes (Stowe et al., 1998; Vanderberghe et al., 2002; Humphries et al., 2006). These studies often included sentence fragments and even entire constituents in their conditions with random word order. Besides, some of these stimuli were scrambled short sentences from which the original order was easily retraceable. We can therefore argue that the IFG engaged in repair mechanisms in those conditions with random order, no longer showing a contrast in activation with simple sentences. Indeed, Stowe et al. (1998) showed that the IFG was only more active for complex sentences than for scrambled sentences, which goes in line with this hypothesis. The ATL would rather play a role in conceptual semantic combinatorial processes, therefore being only present in real word conditions. In contrast, we could observe how BA 44 was especially sensitive to pure structural information in the jabberwocky condition compared the lexical information present in scrambled real words.

It was considered that the different patterns in brain activation for English and German speakers reported in the literature could be related to the different types of information available in the stimulus material with richer morphosyntactic information in German than in English. However, here we show different activation patterns even within German: activation of BA 44 only when derivational morphology is absent and additional activation of BA 45 as when derivational morphology is present. These findings are clear evidence for a fine-grained functional selectivity of the subregions of the IFG as long as the stimulus material is well controlled for the semantic and syntactic aspects of linguistic information. Whereas BA 44 is responsible for processing pure syntactic information, BA 45 is involved from the moment semantic processes come into play.

Our study has implications for cross-linguistic comparisons in general. We pinpoint the crucial role of BA 44 for the processing of pure syntactic structures in German as a
highly inflected language. Other languages, like English, that may rely on additional semantic information for the computation of syntactic structures leading to a recruitment of additional brain areas, especially BA 45. Indeed, such differences are considered in the field of neurotypology (see Bornkessel-Schlesewsky et al. (2011) for a review), where it has been pointed out that different linguistic cues are prioritised differently across different languages. So far, however, such cross-linguistic comparisons have not been conducted systematically in fMRI studies. The available monolingual studies investigating the syntactic phenomenon of movement point in this direction since BA 44 seems to be engaged primarily for languages with case marking, like German (Friederici et al., 2006b; Makuuchi et al., 2012) or Hebrew (Ben-Shachar et al., 2004), whereas the additional activation of BA 45 is often found in English, where these morphosyntactic cues are not available (Santi & Grodzinsky, 2010). Under the assumption that the language network attunes to the properties of a particular language and its relevant cues during language acquisition, we could expect subtle differences in the connectivity between the linguistically relevant brain areas across languages, both in terms of functional and anatomical connectivity. The patterns of functional and structural language network in the brain should also be a function of those language-specific syntactic and semantic cues and their contribution to different streams of processing. The brain as such, however, clearly differentiates between semantic and syntactic aspects, which suggests a universal segregation of these distinct representations in the human brain. Systematic cross-linguistic studies are therefore necessary in order to disentangle universal language representations from those which are typological in their nature.

4.1. Conclusions

The present study rather highlights the parallel use of different information types during language processing, that is semantics and syntax. The experimental paradigm applied here involved an implicit task, which allows us to make claims about the
automatic processing of natural language. The data suggest that whenever syntactic structure is maintained, parallel syntactic and semantic processes take place, as we see activations in areas typically involved in semantic processing when we compare stimuli with sentence structure with random sequences. But crucially we were able to observe that the language processing network got more focused on a single core area as semantic information was progressively eliminated. When only syntactic information is left, we observe the isolated activation of BA 44. These data indicate that BA 44 is the core area of syntax processing. These findings furthermore suggest that there is a dimension to the representations of linguistic structure that is independent from meaning.

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References


Bornkessel-Schlesewsky, I., Kretzschmar, F., Tune, S., Wang, L., Genç, S., Philipp, M., ... &


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Figure captions

All figures are to be printed in colour.

**Figure 1. Trial structure with stimulus example in German.** The target word is shown on the screen and played simultaneously at the onset of the trial. One second after the onset of the target word, the sentence is played and the participant is instructed to press the button upon recognition of the target word. In this example the participant presses the button after hearing the word "IDEE" (in English "idea") during the sentence. The target word is kept on the screen during the whole trial.

**Figure 2. Behavioural analysis of Experiment 1 and 2 and corresponding factorial designs.** The accuracies as percentage of correct answers over all trials (mean plotted as bars with error bars corresponding to 2x standard error of the mean) and reaction times for late trials in milliseconds (mean plotted as dotted line). Factorial design shows the manipulated factors in both experiments and the corresponding levels (as + for present and − for absent). For abbreviations and properties of conditions see Table 1.
Figure 3. Significant brain activations for Experiment 1. A Contrast AP>RWO – Significant activation clusters – Broca’s area (purple), anterior temporal cortex (yellow) and posterior Superior Temporal Gyrus/Sulcus (pSTG/STS) (green) (p<0.05 FWE corrected); B Contrast JP>JRO – Significant activation clusters – BA 44 (red), BA 45 (blue) and pSTG/STS (green) (p<0.05 FWE corrected), detail perspective with Jülich maximum probability maps for BA 45 (green) and BA 44 (orange). For abbreviations and properties of conditions see Table 1 and Inline Supplementary Table 1.

Figure 4. Significant brain activations for Experiment 2. A Contrast JP1>JRO1 – Activation clusters in the language network – BA 45 (blue) (p<0.001 uncorrected), BA 44 (red) and pSTG/STS (green) (p<0.001); B Contrast JP2>JRO2 – Activation clusters in Broca’s area – BA 44 (red) (p<0.05 FWE corrected, small volume correction), detail perspective with Jülich maximum probability maps for BA 45 (green) and BA 44 (orange). For abbreviations and properties of conditions see Table 1 and Inline Supplementary Table 2.

Figure 5. Additional contrasts in Experiment 1. A Whole brain analysis contrast with higher BOLD response to conditions with function word target than content words (p<0.001 uncorrected; p<0.05 FWE corrected in anterior insula and p<0.05 small volume corrected in BA 44); B Reverse contrast in whole brain analysis—higher BOLD response to conditions with content word target than function words (p<0.001 uncorrected); C Contrast JP>RWO (p<0.001 uncorrected, p<0.05 small volume corrected in BA 44). Labelling according to Jülich probability maps. For abbreviations and properties of conditions see Table 1 and Inline Supplementary Table 1.
### Tables

#### Table 1

<table>
<thead>
<tr>
<th>Conditions</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP</td>
<td>The complexity of the regulations had shocked the unhappy kingdom.</td>
</tr>
<tr>
<td>AP</td>
<td>The vicinity of the constipations had ironed the uncanny wisdom.</td>
</tr>
<tr>
<td>JP1 (JP)</td>
<td>The pandexity of the larisations had zopped the unheggy wogdom.</td>
</tr>
<tr>
<td>JP2</td>
<td>The pandesteek of the larisardens had zopped the enhegged fordem.</td>
</tr>
<tr>
<td>JP3</td>
<td>Thue pandesteek of thue larisarden feg zopp thue enheg fordem.</td>
</tr>
<tr>
<td>RWO</td>
<td>Vicinity the of had constipations wisdom the ironed uncanny the.</td>
</tr>
<tr>
<td>JRO1 (JRO)</td>
<td>Pandexcity the of had larisations wogdom the zopped unheggy the.</td>
</tr>
<tr>
<td>JRO2</td>
<td>Pandesteek the of had larisardens fordem the zopped enhegged the.</td>
</tr>
</tbody>
</table>

Table 1. English examples of stimuli (adaptations to the German stimuli used in the experiments) with illustration of *derivation morphology* and *inflectional morphology*: NP = Normal Prose, AP = Anomalous Prose, JP1 (JP in Experiment 1) = Jabberwocky Prose with derivational morphology, JP2 = Jabberwocky without derivational morphology, JP3 = Jabberwocky without derivational or inflectional morphology, RWO = Random Word Order, JRO1 (JRO in Experiment 1) = Jabberwocky in Random Order with derivational morphology, JRO2 = Jabberwocky in Random Order without derivational morphology.
Table 2

<table>
<thead>
<tr>
<th>Contrasts</th>
<th>Brain region</th>
<th>Coordinates at local maxima</th>
<th>Cluster size</th>
<th>t-value</th>
<th>Statistical significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>AP-RWO</td>
<td>Broca’s Area BA 44</td>
<td>[-42, 20, 22]</td>
<td>4180</td>
<td>7.47</td>
<td>p&lt;0.001; p&lt;0.001 FWE corrected</td>
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<tr>
<td></td>
<td>BA 45</td>
<td>[-50, 24, 9]</td>
<td>7.53</td>
<td></td>
<td>p&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>BA 47</td>
<td>[-45, 29, -15]</td>
<td>7.79</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>aSTG/MTG</td>
<td>[-48, 15, -21]</td>
<td>9.66</td>
<td></td>
<td>p&lt;0.001; p&lt;0.001 FWE corrected</td>
</tr>
<tr>
<td></td>
<td>pSTG/pSTS</td>
<td>[-45, -55, 16]</td>
<td>1502</td>
<td>6.53</td>
<td>p&lt;0.001; p&lt;0.001 FWE corrected</td>
</tr>
<tr>
<td>JP-JRO</td>
<td>Broca’s Area BA 44</td>
<td>[-45, 20, 21]</td>
<td>299</td>
<td>5.15</td>
<td>p&lt;0.001; p=0.003 FWE corrected</td>
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<td></td>
<td>BA 45</td>
<td>[-54, 35, 6]</td>
<td>4.76</td>
<td></td>
<td>p&lt;0.001; p=0.038 FWE corrected</td>
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<tr>
<td></td>
<td>pSTS</td>
<td>[-58, -39, 1]</td>
<td>198</td>
<td>4.69</td>
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</table>

Table 2. Results of Whole Brain Analysis of fMRI data. All coordinates are in MNI space; assignment to BA 44/45 was done according to the Jülich probability maps from the SPM Anatomy toolbox (Eickhoff et al., 2007). For abbreviations of contrasts see Table 1.
Table 3.

Results of Whole Brain Analysis of fMRI data and Small Volume Correction in Broca’s Area (all coordinates are in MNI space; assignment to BA 44/45 was done according to Jülich probability maps). For abbreviations of contrasts see Table 1.

<table>
<thead>
<tr>
<th>Contrasts</th>
<th>Cortical activations</th>
<th>Statistical significance</th>
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<tr>
<td><strong>JP1-JRO1</strong></td>
<td><strong>Brain region</strong></td>
<td><strong>Coordinates at local maxima</strong></td>
</tr>
<tr>
<td>Broca’s Area</td>
<td><strong>BA 44</strong></td>
<td>[-50, 12, 16]</td>
</tr>
<tr>
<td></td>
<td><strong>BA 45</strong></td>
<td>[-54, 29, 12]</td>
</tr>
<tr>
<td></td>
<td>pSTG/pSTS</td>
<td>[-50, -37, -3]</td>
</tr>
<tr>
<td><strong>JP2-JRO2</strong></td>
<td><strong>Brain region</strong></td>
<td><strong>Coordinates at local maxima</strong></td>
</tr>
<tr>
<td>Broca’s Area</td>
<td><strong>BA 44</strong></td>
<td>[-51, 8, 15]</td>
</tr>
</tbody>
</table>