

ORIGINAL ARTICLE

Building by Syntax: The Neural Basis of Minimal Linguistic Structures

Emiliano Zaccarella^{1,2}, Lars Meyer¹, Michiru Makuuchi^{1,3} and Angela D. Friederici^{1,2}

¹Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig 04103, Germany, ²Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Berlin 10099, Germany and ³National Rehabilitation Center for Persons with Disabilities, Section of Neuropsychology, Tokorozawa 8555, Japan

Address correspondence to Emiliano Zaccarella. Email: zaccarella@cbs.mpg.de

Abstract

Language comes in utterances in which words are bound together according to a simple rule-based syntactic computation (merge), which creates linguistic hierarchies of potentially infinite length—phrases and sentences. In the current functional magnetic resonance imaging study, we compared prepositional phrases and sentences—both involving merge—to word lists—not involving merge—to explore how this process is implemented in the brain. We found that merge activates the pars opercularis of the left inferior frontal gyrus (IFG; Brodmann Area [BA] 44) and a smaller region in the posterior superior temporal sulcus (pSTS). Within the IFG, sentences engaged a more anterior portion of the area (pars triangularis, BA 45)—compared with phrases—which showed activity peak in BA 44. As prepositional phrases, in contrast to sentences, do not contain verbs, activity in BA 44 may reflect structure-building syntactic processing, while the involvement of BA 45 may reflect the encoding of propositional meaning initiated by the verb. The pSTS appears to work together with the IFG during thematic role assignment not only at the sentential level, but also at the phrasal level. The present results suggest that merge, the process of binding words together into syntactic hierarchies, is primarily supported by BA 44 in the IFG.

Key words: Broca's area, fMRI, merge, phrases, sentences

Introduction

The human capacity to process language is claimed to be based on a low-level computation, which binds words together to form phrases and sentences of increasing length (Berwick et al. 2013). This process—called merge in theoretical linguistics (Chomsky 1993, 1995; Zwart 2011)—is at the base of syntactic complexity and necessarily precedes the comprehension of more complex constructions (Bemis and Pytkkanen 2011). Because of its fundamental nature, the investigation of the neural representation of merge and whether the construction of minimal phrases (*on the ship*) and minimal sentences (*the ship sinks*) differs are central objectives to any comprehensive cognitive

model aiming at understanding the neural mechanisms of human language processing.

Experimental evidence for the neural reality of merge still remains remarkably vague (Grodzinsky and Friederici 2006; Zaccarella and Friederici 2015). Neurolinguistics has traditionally been more interested in understanding how the brain supports complex syntactic processing—that is, sentential embedding, scrambling, and word-order variation—compared with simple processing in which no such complexity occurs (Just et al. 1996; Roder et al. 2002; Santi and Grodzinsky 2007; Shetreet and Friedmann 2014; see also Friederici 2011 for a recent review). Accordingly, in these studies merge cannot be directly observed—either

because it is equally involved during the comprehension of both complex and simple sentences, or because the large brain activity associated with the processing of complex sentences masks the subtle brain activity associated with merge. In either case, prior results only allow to speculate on the neural reality of this basic computation. Contrary to complexity manipulations, recent neurolinguistic studies tried to probe merge directly, by comparing sentence processing to word list processing, in which syntax is subtracted away and no merge applies. Unstructured word lists have been used as control condition for different syntactic constructions, across languages and modalities, using both positron emission tomography (PET; Mazoyer et al. 1993; Bottini et al. 1994; Stowe et al. 1998, 1999) and functional magnetic resonance imaging (fMRI; Friederici, Meyer et al. 2000; Vandenberghe et al. 2002; Humphries et al. 2005, 2006; Snijders et al. 2009). From these studies however, a rather conflicting picture emerges, with different regions believed to play a major role in the merge mechanism, including Broca's area (Brodmann Area [BA] 44 and 45); the anterior portion of the left temporal lobe (BA 38); the posterior portion of the left superior temporal gyrus/sulcus and the middle temporal gyrus (pSTS/STG and MTG; BA 21/22); and the left frontal operculum/anterior insula (FOP/aINS).

In these experiments, the type of syntactic manipulation and the type of word list control condition used could constitute potential reasons explaining the divergent results. As to the type of syntactic manipulation, syntactic conditions used in prior research consisted of very complex structures such as stories (Mazoyer et al. 1993), embedded clauses (Stowe et al. 1998), complex sentential modifications (Stowe et al. 1999; Vandenberghe et al. 2002; Snijders et al. 2009), or long subject-object sentences (Humphries et al. 2005, 2006). Therefore, it remains unclear whether the reported effects isolate merge processing, or rather comprise additional cognitive mechanisms, including working memory, integration across long-distance dependencies, or sentential embedding, which are also found to activate the inferior-frontal and temporal regions (Friederici, Bahlmann, et al. 2006; Santi and Grodzinsky 2007; Makuuchi et al. 2009; Meyer et al. 2012). As for the second aspect, word list conditions often employ both function words (e.g., determiners, prepositions, conjunctions) and content words (e.g., nouns, verbs, adjectives), which may unpredictably enhance rather than decrease the construction of minimal structures (e.g., "but this, in stumble") in the non-syntactic conditions. Content words, for instance, primarily carry lexical-semantic information. Function words, conversely, primarily carry syntactic information, bearing reduced semantic content, and rather facilitate structural assignment during linguistic processing, by anchoring, linking, or sequencing other items. They are, therefore, context dependent and may enhance syntactic processing (Garrett 1975, 1976). Thus, in prior studies, the comparison of sentences against word lists with remaining syntactic chunks may have lead partly to a subtraction of syntactic processes, rather than purifying merge-related brain activation. Interestingly, those studies using word lists with both function words and content words mostly report activation in the temporal cortex, while 1 study that uses content-word-only lists rather reports activation in the inferior frontal region, the left FOP, bordering on BA 44, therefore suggesting merge sensitivity only in the IFG (Friederici, Meyer, et al. 2000).

Neuroanatomical dissociations between content words and function words have been reported frequently within recent neurolinguistic literature (Bradley and Garrett 1983; Friederici 1985; Shapiro and Jensen 1986; Neville et al. 1992; Mohr et al. 1994; Pulvermuller 1995; Osterhout et al. 1997; Small et al. 1998; Brown et al. 1999; Bastiaansen et al. 2005; Wang et al. 2008).

Early clinical studies investigating speech processing in aphasic patients with anterior lesions noted some impairment in both the production and the auditory and written comprehension of functional lexicon (Goodglass et al. 1972; Samuels and Benson 1979; Benson and Geschwind 1985). An fMRI study examining lexical access at the single-word level discovered that while content words activated the anterior IFG (BA 47)—together with the posterior middle temporal cortex in the angular gyrus (BA 39), medial and anterior temporal regions and posterior cingulate—function words elicited activity in the posterior IFG (BA 44/45)—together with the precentral gyrus in motor and premotor cortex (BA 4/6), middle temporal, and supramarginal gyri (Nobre et al. 1997). Another fMRI study interested in differential effects of semantic task (concrete/abstract judgment) and syntactic task (noun/function word judgment) across single content and function words reported a gross subdivision in the IFG with selective activation of the anterior part of Broca's area (pars triangularis; BA 45) during semantic judgment, and selective activation of the more posterior part (pars opercularis (BA 44)/frontal operculum) during syntactic judgment (Friederici, Opitz, et al. 2000). Because, however, these past studies mostly used single-word stimuli, the question of how the 2-word classes participate in the creation of syntactic hierarchies beyond the single-word level still remains a largely unexplored question. This is rather surprising given that some words—prepositions, but also certain types of adverbs, affixes and negation—can switch functional role depending on the surrounding linguistic context in which they occur (Friederici 1982; Bebout 1993; Del Prato and Pyllkanen 2014). Prepositional particles for instance, together with a conventional syntactic role they carry as members of the function class, also bear additional semantic information similar to verbs, because they can assign thematic roles to express certain relations with the following noun (i.e., the spatial relation of the preposition "on" in "I didn't find anything on the ship"). Therefore, prepositions can still provide semantic relational meaning with incoming elements they head, although they may lack proper content semantics. Interestingly, clinical evidence exists which revealed that comprehension accuracy for prepositions in sentential contexts decreased in Broca's aphasics, when correct processing could solely rely upon syntactic knowledge, but not when correct processing could rely on semantic knowledge (Swinney et al. 1980; Friederici 1981). This means that the distinctiveness of prepositions appears to be not just connected to the function of their class membership, but also dependent upon their own functional role within a specific linguistic context in which they combine. Therefore, prepositions in prepositional phrases (PPs) might show a "sentence-like" behavior in those brain regions responsible for thematic role assignment, together with expected increased neural activity in those areas accountable for syntactic merging processing.

Based on the above considerations, in the current fMRI study, we want to assess how the merge mechanism is implemented in the human brain, in a way that we could 1) remove syntax-related activity in the word list control conditions; 2) reduce complexity confounds arising in previous studies in the syntactic conditions; 3) investigate functional differentiations and similarities during the creation of minimal prepositional and sentential hierarchies. To this end, we 1) used noun-only word lists to discourage syntactic processing in the control conditions; we 2) drastically reduced the length of the stimulus items to a very fundamental 3-word level; and 3) created 2 types of syntactic contexts: simple phrasal contexts, namely a PP consisting of a preposition, together with a determiner phrase (DP), and simple sentential contexts, consisting of a verb together with the same DP.

We were first interested in localizing the main effect of merge—in which both phrases and sentences were analyzed together and contrasted with word lists of equal syllabic length. Based on previous studies, we hypothesized main activity increase for both constructions in the IFG, as the core region associated with hierarchical computation (Friederici, Bahlmann, et al. 2006; Makuchi et al. 2009). We also expected activity modulation in the pSTS—which is thought to support thematic role assignment at the sentential level (Bornkessel et al. 2005; Friederici et al. 2009; den Ouden et al. 2012)—although we had to leave open the question of whether this region's sensitivity to thematic assignment would have generalized to PPs as well. Second—expecting the IFG to be the locus of hierarchical processing—we wanted to perform a closer inspection in Broca's region, to see whether at a finer grained level, dissociable anatomical trajectories between phrases and sentences exist in the area. We followed the hypothesis that BA 44 is the area that more strongly responds to pure structure-building syntactic processing, and therefore may be more active during prepositional processing, while BA 45 rather supports verb-level sentential integration (Friederici, Opitz, et al. 2000; Friederici 2011; Zhu et al. 2013).

Materials and Methods

Participants

Eighteen native German speakers were included in the analysis (11 female; mean age 25.5 years, standard deviation [SD] 2.03 years; all native German speakers). All of them were right handed according to the Edinburgh Inventory (Oldfield 1971) and had normal or corrected-to-normal vision. Six additional participants were scanned but excluded from further analysis because of reduced performance (see below). Three other subjects were removed early on due to a lack of sustained wakefulness during the experiment. Prior to scanning, participants gave written informed consent. No participant declared to have implanted metal objects such as aneurysm clips or a pacemaker. Each subject received monetary compensation (15 EUR) for participating in the study. All procedures were approved by the local ethics committee (University of Leipzig).

Stimuli

The experimental paradigm was intended to assess neural activity related to the merge operation generated during the processing of syntactic structures, compared with noun lists of equal syllabic length. The experiment was organized in a factorial design with 2 independent variables. The first variable was MERGE (M), with 2 corresponding levels: syntax (+M) and word list (−M). The second variable was hierarchy TYPE, involving 2 levels: PHRASE (PH) and SENTENCE (SE), with equal numbers of words in the corresponding lists conditions (Fig. 1). The PH(+M) context consisted of a PP of 3 syllables, in which a preposition (P) was followed by a DP ($PP = P_{auf/on} + DP_{das Schiff/the ship}$). The SE (+M) context had a 3-syllable sentence (S) in which a full DP was followed by a V ($S = DP_{das Schiff/the ship} + V_{sinkt/sinks}$). For the noun phrases (NPs) forming the DPs, we selected 48 monosyllabic nouns from the CELEX database (Baayen et al. 1995). We only used feminine and neuter nouns, which do not distinguish nominative and accusative case at the determiner level between phrasal hierarchies and sentential hierarchies. Specifically, we selected 24 feminine nouns (mean CELEX lemma frequency = 24.12; SD = 27.62), and 24 neuter nouns (mean CELEX frequency = 24.41; SD = 26.97). In condition PH(+M), 6 monosyllabic

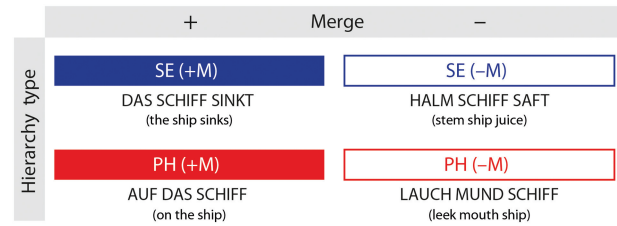


Figure 1. Experimental design: 2 × 2 design with the factors MERGE (+Merge and −Merge) and Hierarchy TYPE (Phrase vs. Sentence).

prepositions (+ACC) were employed (i.e., “an, für, durch, auf, vor, and in”). In condition SE(+M), 48 monosyllabic verbs were selected and used to generate simple meaningful sentences in agreement with the 48 determiner-noun combinations described above. In the word list conditions SE(−M) and PH(−M), the 48 nouns were placed in the exact same position as in the (+M) conditions, while the remaining words were replaced by 192 monosyllabic nouns. The final stimulus set consisted of 192 items (i.e., 48 items, 4 conditions each) and 12 fillers. Fillers ensured that participants paid attention to each individual word within each item, such that prior to the final word across items, participants could not predict whether the stimulus belonged to the syntactic condition, the corresponding word list condition, or to a third filler condition—named rubbish condition—in which all nonbordering letters within the last word were replaced with “X” strings (KXXXXT, instead of KRAUT/cabbage). For example, at PH level, after the first word had appeared (i.e., AUF/on), one of the 3 possible sequences could have followed: 1) [DAS/the] → [SCHIFF/ship] = auf das Schiff, PH(+M); 2) [BIS/until] → [ZU/to] = auf bis zu, word list filler; 3) [DAS] → [KXXXXT] = auf das KxxT, rubbish filler. None of the fillers was used in the experimental conditions.

Procedure

Prior to scanning, participants performed a short practice session of the actual experiment on a desktop computer located outside of the scanner room. None of the stimuli used in the practice session was used during the experimental session. Stimuli were presented visually using the software package Presentation® (Neurobehavioral Systems, Inc., Albany, CA, USA) with a Sanyo PLC-XP50L LCD XGA (Sanyo Electric Co., Ltd., Moriguchi, Japan; pixels = 1024 × 768 × 3; refresh rate = 100 Hz) mirror-projection system mounted on the head coil. A mono-spaced font in white letters on a gray background was used (capitalized letters; 45 pt). An experimental trial started with a white fixation cross at the center of the screen; after a random jitter of either 0 or 1000 ms after acquisition of the previous volume, the words of a visual stimulus appeared in sequence, lasting 300 ms each. Mean stimulus onset asynchrony was 8.6 s. Total trial duration was adjusted to 900 ms (Fig. 2). As soon as the fixation cross reappeared, right after the last word within the trial had been shown, participants were requested to indicate via button press whether the preceding stimulus was a phrase/sentence, a word list, or rubbish (Friederici, Meyer, et al. 2000). A triple-choice button box was used. Participants were requested to use the right index finger, the right middle finger, or the right ring finger to accomplish the task. Each participant received an individual, pseudo-randomized stimulus list. Given the easiness of the stimulus material, we followed indications from previous electroencephalography studies, which suggested that structure-building syntactic processes are quite automatic in adults and only require very limited neural resources to be implemented (Hahne and Friederici 1999;

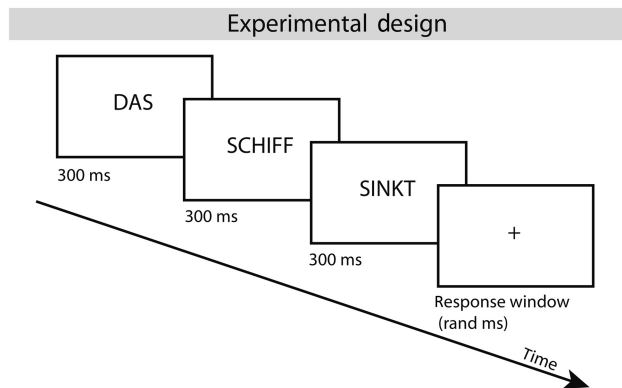


Figure 2. Timing of visual presentation: for each trial, participants judged whether the stimulus was a possible phrase, a list, or a rubbish-stimulus containing “X” letters.

Hahne et al. 2002). Therefore, subjects performing below 75% accuracy in any of the experimental conditions were considered to be bad performers and excluded from further analysis, as done in other functional studies interested in the same type of process (Snijders et al. 2009; Westerlund et al. 2015). Stimuli were presented in 12 mini blocks 24 items from the same TYPE level (i.e., 12 PH(+M) and 12 PH(−M), respectively), 6 fillers, and 8 null events. Each functional dataset collection lasted approximately 48 min.

Behavioral Data Acquisition

We acquired single-trial responses and reaction times.

Image Acquisition

Functional images were acquired with a whole-body 3 Tesla Bruker Medspec 3000. The functional data were acquired using a T_2^* -weighted gradient-echo echo-planar-imaging (EPI) sequence, with the following parameters: TR = 2.0 s, TE = 30 ms, flip angle = 90° , FOV = 19.2×19.2 cm², in-plane resolution = 3×3 mm²; data matrix = 64×64 ; slice thickness = 3 mm; interslice gap = 1 mm; number of slices = 30 (axial slices, parallel to AC-PC line/whole-brain coverage, ascending direction), number of volumes = 1270 volumes. T_1 -weighted 3D MP-RAGE (magnetization-prepared rapid gradient echo) images (Mugler and Brookeman 1990) TI = 650 ms; TR = 1300 ms; $\alpha = 10^\circ$; FOV = 256×240 mm) were previously acquired with a nonselective inversion pulse to be used for preprocessing of the functional data.

Behavioral Data Analysis

From the single-trial responses and reaction times for the 4 conditions for each participant, we calculated accuracy rates and mean reaction times. A 2×2 analysis of variance (ANOVA) with factors MERGE and TYPE was used to test condition effects on both accuracy rates and mean reaction times. All analyses employed MATLAB® (The MathWorks, Inc., Natick, MA, USA) and SPSS (PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc.).

Preprocessing of the Imaging Data

Functional imaging data were pre-processed using the SPM 8 software package (Wellcome Imaging Department, University College, London, UK, freely available at <http://fil.ion.ucl.ac.uk/spm>). Subject-specific functional volumes were co-registered

with corresponding structural T_1 -weighted images. Functional time series were realigned to the first image to correct for motion artifacts and resliced for timing correction. A gray matter segmentation-based procedure was used for normalization to the standard MR template included in the SPM software package. A Gaussian filter of 8 mm FWHM was used to smooth the functional data. A high-pass filter of 128 s was used to attenuate slow global signal changes.

Whole-Brain Imaging Data Analysis

We performed a 2-stage random-effects analysis to ensure result generalizability over the population level (Penny and Holmes 2003). The first 5 volumes from each dataset were excluded to allow for magnetic saturation effects to establish. Subject-specific general linear models were assessed using the hemodynamic response function from the SPM software (Friston et al. 1995). Error trials and filler trials were modeled as distinct conditions, and the 6 movement parameters per volume were treated as regressors of no interest. Contrast estimates for the experimental conditions were obtained from a first-level t-contrast against the global mean and then passed into a second-level 2×2 ANOVA, where we assessed the MERGE \times TYPE interaction, as well as the main effects of MERGE and TYPE. Significance level was set to a family-wise-error-corrected $P < 0.05$. Local maxima were reported using the Montreal Neurological Institute (MNI) coordinate convention. Anatomical landmarks were identified using the SPM Anatomy Toolbox (Eickhoff et al. 2005).

Distribution Assessment in Broca's Region

In a second phase, we restricted our functional analysis to Broca's area alone. This increased statistical power, enabling us to gain further information on the different linguistic nature of phrases and sentences used in the experiment, and possibly, the associated functional subdivision between BA 44 and BA 45 (Friederici, Opitz, et al. 2000; Zhu et al. 2013). The cytoarchitectonically defined LIFG from the Jülich Anatomy Toolbox for SPM was used as independent search space to remove selection bias during second-level analysis (Kriegeskorte et al. 2009; Vul and Kanwisher 2010). The population map of BA 44 and BA 45 of the left hemisphere was truncated at 50%, with the mask created by combining the 2 volumes. For this analysis, we performed t-test comparisons, with phrasal stimuli and sentential stimuli directly compared with their corresponding word list conditions: [PH(+M) > PH(−M)] and [SE(+M) > SE(−M)]. We assessed the corresponding anatomical position relative to BAs 44 and 45 of the Jülich Atlas. To assess whether the 2 subregions within Broca's were differently engaged by phrases and sentences, we extracted for each participant the MNI coordinate of the maximum individual activation peak voxel for each the significant phrasal and sentential contrast (see Results) within the Broca's area mask. To assess the spatial difference between the resulting 2 individual sets of MNI coordinates, we then calculated the individual Euclidean distance between each participant's 2 coordinate sets. On the resulting values, we ran a 1-sample t-test, hypothesizing that if the vector was significantly different from 0, then the 2 structures yielded spatially distinct subregions within Broca's area.

Results

Behavioral Results

Analysis of the behavioral data showed neither significant main effects nor a significant interaction for neither accuracy rates

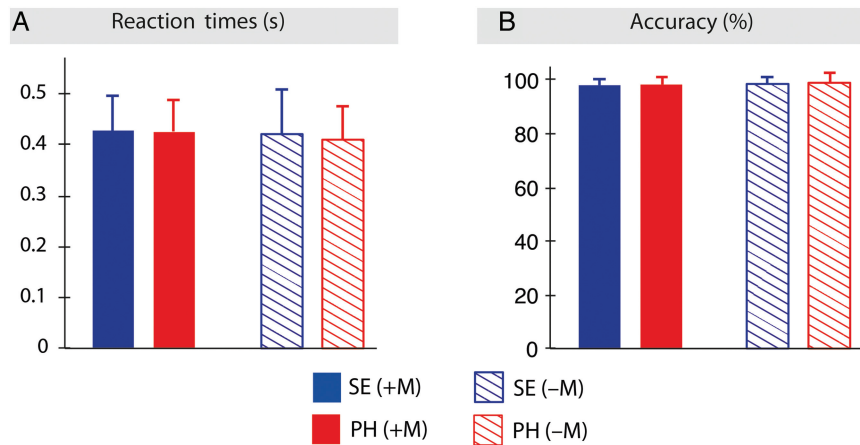


Figure 3. Behavioral results: 2×2 repeated measures ANOVA (factor MERGE and factor H-TYPE). A, RESPONSE TIMES: no significant effect found. B, ACCURACY: no significant effect found. Error bars show SD.

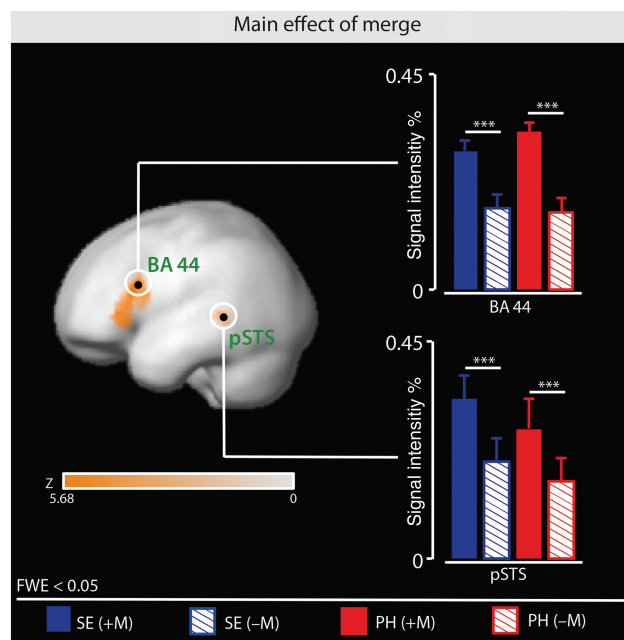


Figure 4. Main effect of merge: whole-brain analysis for the main effect of merge (FWE-corrected; $P < 0.05$), with signal intensity (percentage) at local maxima. BA 44, Brodmann area 44; pSTS, posterior superior temporal sulcus. Mean signal extraction from local maxima was done using Marsbar 0.41 for SPM (<http://marsbar.sourceforge.net>). *** $P < 0.001$; corrected for multiple comparisons.

($P = 0.544$ [MERGE]; $P = 0.944$ [TYPE]; $P = 0.393$ [MERGE \times TYPE]; Fig. 3A) nor reaction times ($P = 0.291$ [MERGE]; $P = 0.496$ [TYPE]; $P = 0.637$ [MERGE \times TYPE]; Fig. 3B)—that is, participants performed at ceiling and equally fast across conditions. Five subjects were excluded, because they performed below 75% accuracy in any of the conditions (the overall performance was about 1 SD from group mean for 2 subjects, 1.5 SD for 1 subject, and about 2 SD for the remaining 2 subjects). One additional subject was further excluded because of excessively slow reaction time, which was about 2.5 SD from the group mean.

Whole-Brain Imaging Data Results

Analysis of functional data revealed a main effect of MERGE with in the left inferior frontal gyrus, with the peak in BA 44 (MNI peak

Table 1 Functional results from the whole-brain analysis and the small volume correction (SVC) analysis in Broca's area (BA 44/45)

Anatomical area	MNI coordinate			K _E (voxels)	Z _E
	X	Y	X		
Whole-brain analysis					
Merge effect					
Left BA44/pars opercularis	-51	11	16	190	5.68
Left pSTS	-57	-43	1	34	5.08
Broca's area					
Phrases					
BA44/pars opercularis	-51	11	19	165	5.48
Sentences					
BA45/pars triangularis	-54	26	10	82	4.10

Note: Voxel dimension is 3 mm^3 . All values are FWE-corrected at $P < 0.05$.

coordinate $x = -51$, $y = 11$, $z = 16$; $Z = 5.68$; $K_E = 190$ voxels; Fig. 4 and Table 1). A smaller cluster was found in the pSTS (peak coordinate $x = -57$, $y = -43$, $z = 1$; $Z = 5.08$; $K_E = 34$ voxels; Fig. 4 and Table 1). The main effect of TYPE, as well as the MERGE \times TYPE interaction, did not yield any significant clusters that survived the statistical thresholds.

Distribution Assessment in Broca's Region

In the hypothesis-driven analysis inside Broca's area, we found that main peak activity for phrases was located in BA 44 (peak coordinate $x = -51$, $y = 11$, $z = 19$; $Z = 5.48$; $K_E = 165$ voxels; Fig. 5 and Table 1), while the main peak activity for sentences was located in BA 45 (peak coordinate $x = -54$, $y = 26$, $z = 10$; $Z = 4.10$; $K_E = 82$ voxels; Fig. 5 and Table 1). For the sentential constructions, we additionally found activation in BA 44 at $x = -48$, $y = 17$, $z = 22$ ($Z = 4.09$) and at $x = -51$, $y = 11$, $z = 13$ ($Z = 4.06$). The spatial distance between the subject-based phrasal and the sentential peak was significant ($t_{(17)} = 8.53$; $P < 0.001$ [test value = 0]).

Discussion

The present fMRI study set out to identify the brain regions involved in basic syntactic structure building—the merge operation (Chomsky 1995)—during natural language processing. In our paradigm, participants were asked to read 3-word phrases,

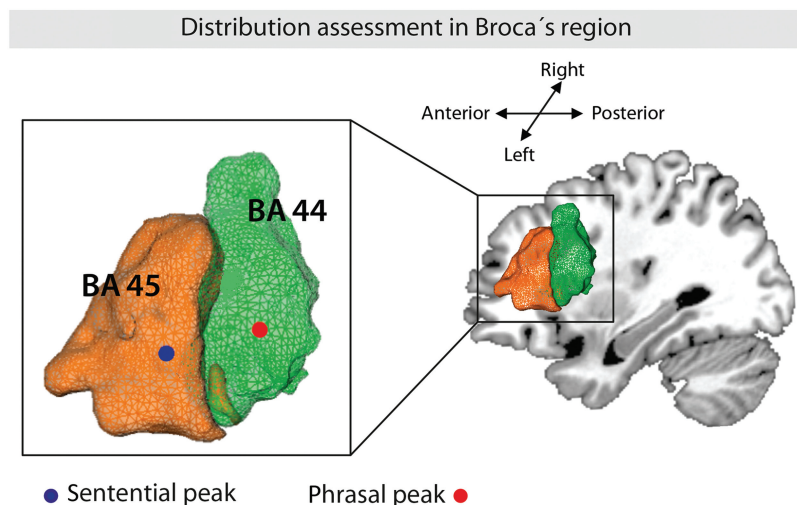


Figure 5. Small volume correction (SVC) analysis in Broca's area: main peak for sentential effect (blue: "das Schiff sinkt" > "Halm Schiff Saft"); main peak for phrasal effect (red: "auf das Schiff" > "Lauch Mund Schiff"). FWE-corrected; $P < 0.05$. The cytoarchitectonically defined left IFG from the SPM anatomy toolbox for SPM was used as mask for the volume-of-interest analysis. The population map of Area 44 and Area 45 of the left hemisphere was truncated at 50%, with the mask created by combining the 2 volumes together. BA 45, Brodmann area 45; BA 44, Brodmann area 44.

sentences, and corresponding unstructured word lists of equal length. A main effect of merge was found in the group-level statistics in the IFG with peak in in the left pars opercularis/BA 44 and to a small extent in the pSTS. A closer inspection in Broca's region revealed that minimally hierarchical 3-word phrases—in which a full noun phrase was combined with a PP—showed peak activity in BA 44. Conversely, minimal 3-word sentences—in which a full noun phrase was combined with a verbal phrase—activated the most inferior part of the IFG, in BA 45.

The involvement of Broca's area (BA 44) for the main effect of syntax we report here is in line with results from numerous neuroimaging studies investigating syntactic processing (Stromswold et al. 1996; Friederici 2002; Bornkessel et al. 2005; Hagoort 2005, 2008; Grodzinsky and Santi 2008; Makuuchi et al. 2009, 2013; Perani et al. 2011). Within this literature, however, there is a tendency to link the involvement of the IFG—and in particular BA 44—to the concept of syntactic complexity at the sentential level. Complexity has been defined either in terms of non-canonical reordering in German or in Japanese, for example (Roder et al. 2002; Friederici, Fiebach, et al. 2006), or, alternatively, in terms of hierarchical sentential embedding in natural language (Makuuchi et al. 2009) and artificial grammar studies (Bahlmann et al. 2008).

The present data confirm the general notion of BA 44 being activated as a function of structural hierarchy, but they clearly go beyond this view by proposing that BA 44's sensitivity to structure is already evident when processing a minimal hierarchy, that is, during a minimal merge operation. By following the view that merge is the computational algorithm forming more complex hierarchical structures in language, we propose that BA 44 is found active whenever syntactic structures are formed, be they simple or more complex. Both simple and more complex constructions share the essential merging process in language, which corresponds to increased neural activity in BA 44. This functional specialization, however, does not entail that merge in language is the only process recruiting BA 44. A recent functional subparcellation of this area (Clos et al. 2013) suggests that BA 44 also supports the processing of phonological and musical structures and the imagination of action sequences, although localized at partly different subregions. The present

results demonstrate that within the language network merge is neurally implemented in BA 44 (Berwick et al. 2013).

In the light of the present findings, 1 potential source of criticism to the proposal that BA 44 activates as a reflection of merge seems to come from the observation that in our design, lists of content words have been compared with stimuli including content words as well as function words like determiners and prepositions. Therefore, the main effect observed in BA 44 could have been driven by the function words themselves. Hemodynamic evidence in the literature however suggests that the merge effect in BA 44 we report here cannot be simply associated to the absence of function words in the control conditions. This evidence comes from a study that used function word only to create word list control conditions (e.g., "this and off to that which why"), and which still reported activity in the IFG (BA 44) for the contrast syntactic processing versus word list processing (Maguire and Frith 2004).

Once the relative spatial distribution of phrasal structures and sentential structures is separately investigated, a fine-grained functional specification in subregions of Broca's area is observable, with phrases yielding more activity in the posterior frontal region—that is, BA 44 and sentences involve the more anterior region—BA 45. Although both phrases and sentences involve merge processes, the relatively stronger involvement of semantic processes in sentences is higher, leading to higher BA 45 activation. This is in line with a study that found BA 44 for sentence structure when semantic information was stripped away, but an involvement of BA 45 when semantic information was present (Goucha and Friederici 2015). Neuroanatomically, it has long been known that the IFG is a heterogeneous region, with cytoarchitectonically distinct cortical patches. Structural subdivisions within Broca's distinguishing between the more posterior BA 44 and the more anterior BA 45 exist, based on the cellular organization of corresponding regional tissues (Brodmann 1909), and cell density profiles on postmortem brains (Amunts et al. 1999, 2010), which found Layer IV density differences between the dysgranular BA 44 and the granular BA 45. This structural differentiation goes well in hand with the large body of experimental evidence strongly supporting the view that different

subsystems within the IFG exist (Friederici 2002; Hagoort 2005; Grodzinsky and Friederici 2006; Rogalsky and Hickok 2011). The activity we observed for sentential constructions in the present study is in line with the proposal that the more anterior part of the IFG is recruited within the specific processes of the semantic system (Bookheimer 2002; Friederici 2002, 2011), being selectively involved in different aspects of linguistic comprehension, including—as in the current study—the encoding of propositional meaning. The semantic sensitivity of the anterior IFG has been discussed by different reviews dedicated to lexical-semantic access (Fiez 1997; Gabrieli et al. 1998) and reported in several experimental studies focusing on semantic encoding, which included either concreteness judgment or semantic priming (Demb et al. 1995; Poldrack et al. 1999; Friederici, Opitz, et al. 2000; Wagner et al. 2000). Beyond single-word semantics, functional evidence shows that the anterior IFG actively participates at sentential level during propositional evaluation (Zhu et al. 2013). In a plausibility judgment study, neural activity in the anterior IFG was found to increase when participants were requested to assess whether a certain sentence expressed a propositional concept that could have been imagined in the real world (Caplan et al. 2008). Seemingly, BA 45 was found active during sentential semantic integration, when pairs of sentences had to be contrasted against each other to evaluate whether both expressed the same event (Newman et al. 2010), or when subjects read sentences and judged whether or not they were semantically acceptable (Zhu et al. 2009). Given the nature of our stimulus items, we propose that increased activity in BA 45 results from the encoding of propositional meaning expressed by the verb in the sentence. The same does not hold true for phrasal constructions, in which propositional mapping is not established, as no verb is available. In this respect, we argue that the engagement of BA 44 during the construction of basic PPs most probably reflects syntactic processing in this area, given the grammatical nature of prepositional items.

In addition to engaging the left IFG, our results also indicate that the processing of both phrases and sentences involves the left posterior STS. Previous findings consistently reported posterior superior temporal cortex to come into play when lexical-semantic information is available (Stowe et al. 1998; Bornkessel et al. 2005; Friederici et al. 2009), and more specifically, when thematic assignment at the sentential level is more difficult to process (Roder et al. 2002; Ben-Shachar et al. 2003; Constable et al. 2004; Bornkessel et al. 2005; Friederici et al. 2009). In this respect, it has been proposed that the left posterior STS works in an interactive relation with the inferior frontal cortex to act as an integration region mapping lexical/thematic information to syntactic argument hierarchies (Bornkessel et al. 2005; den Ouden, et al. 2012). Compared with previous studies, however, the present manipulation allowed us to show that pSTS activation, as expected for sentence processing, is visible also when PPs are processed. Therefore, we obtained a positive answer to the question of whether the pSTS's sensitivity to thematic assignment would have been further generalizable to prepositional constructions. The status of a PP is seen as special within the grammatical system, as prepositions can assign thematic roles (Carnie 2007) to the noun phrases contained within the PP (e.g., “the ship” in “on the ship” here), depending on the specific function they serve (e.g., “locative” role). Intriguingly, this aspect was already noted in early patient studies, which revealed opposite performance patterns in Broca's aphasics and Wernicke's aphasics during sentential processing with correct or incorrect prepositions. While indeed patients with infero-frontal lesion and reduced syntactic ability could still make use of semantic knowledge

to establish thematic dependencies between preposition and noun, patients with lesion in the posterior superior temporal lobe and spared syntactic knowledge had severe lexical problems in selecting the appropriate preposition for the correctly assigned syntactic category (Friederici 1982; Friederici et al. 1982; Bennis et al. 1983). Therefore, if resorting to the posterior STS is necessary to the extraction of linguistic meaning, and if this is true even during the processing of PPs, our tentative hypothesis is that the region supports semantic inference of thematic assignment already beyond sentential level, nonetheless confirming the highly integrative nature of the region, within and outside the linguistic system (Scott and Johnsrude 2003; Friederici 2011).

The strong involvement of the left inferior frontal (and posterior temporal) cortex we report in our study casts doubts on the role of other regions—the anterior temporal lobe (ATL), FOP/aINS—which have been suggested to play for the merge mechanism in previous works. The present data appear to disagree with those experiments putting the left ATL in focus (Stowe et al. 1998, 1999; Vandenberghe et al. 2002; Humphries et al. 2005, 2006; Xu et al. 2005; Rogalsky and Hickok 2009). Because in those studies the ATL was found activated for sentences relative to word lists, some authors raised the possibility that the ATL may be the key region for syntactic structure building under merge (Rogalsky and Hickok 2009). In our functional analysis however, ATL failed to show up as active for the contrast between syntax and word lists. One possible reason for this opposite pattern is that, contrary to our stimuli, studies reporting ATL activation mostly compared long sentences to word lists containing remaining syntactic chunks, which removed syntactic effect from the data and rather boosted semantic processing in the anterior temporal region (Mazoyer et al. 1993; Stowe et al. 1998, 1999; Humphries et al. 2006). In this sense, we follow the view that the ATL may reflect combinatorial semantic—rather than syntactic—operations between words, to create complex coherent meanings from more basic ones (Barsalou 1982; Humphries et al. 2007; Baron et al. 2010; Baron and Osherson 2011). A semantic role for the ATL would more easily explain activation in the region found in Vandenberghe et al. (2002), which reported sentence versus word list differences in the ATL, only when the sentences were semantically coherent. This would also be in line with a fMRI study investigating the functional relationship between neural activity and size of linguistic structures, which found an effect of size in ATL only when lexico-semantic information was available, but not when semantics was removed by replacing content words with pseudo-words (Pallier et al. 2011). Recent magnetoencephalographic studies looking at compositionality effects at a very basic 2-word level also proposed the ATL to be crucial for basic combinatorics in the semantic rather than in the syntactic domain (Bemis and Pyllkanen 2013; Del Prado and Pyllkanen 2014). Finally, data from a clinical investigation showed that both in patients suffering from semantic variant primary progressive aphasia (semantic PPA)—with severe bilateral atrophy of the ATL—and in normal control subjects, the left inferior frontal and posterior temporal regions were the only 2 areas being functionally modulated by syntactic processing, while ATL was not consistently modulated (Wilson et al. 2014). The semantic nature of the ATL is finally stressed in distributed-plus-hub models of cortical semantic networks, which consider the ATL to be a shared amodal conceptual hub, where distributed conceptual representations coming from different modality-specific systems are bound together and processed by a common set of neurons and synapses (Patterson et al. 2007; Lambon Ralph et al. 2010). Our study also did not find consistent involvement of the FOP/adINS at stringent thresholds.

The FOP/adINS may thus rather be thought to support word-accumulation processing in which the categorical information of the word is first accessed according to its lexical status (Friederici Opitz et al. 2000) and then shortly maintained on hold before further processing takes place (Grasby et al. 1994). A low functional specialization for syntax in the FOP/adINS finds support in another hemodynamic study in which the region, in contrast to BA 44, was not able to discriminate between grammar types, since it was only able to detect an error in the order of syllables, regardless of the structure of the sequence in which the error occurred (Friederici, Bahlmann, et al. 2006).

Finally, coming back to merge, research on the cognitive basis of merge has stimulated a growing discussion in the literature in the last decade, which especially focused on the issue whether merge should be seen as a purely language-specific computation or as a rather basic process common to other cognitive mechanisms (Fitch and Hauser 2004; Grodzinsky and Friederici 2006; Bolhuis et al. 2014). Recursive processes have been assumed to possibly also apply to non-language domains such as music and mathematics (Hauser et al. 2002). Here we argue that merge as defined for language can be localized within the language temporo-frontal network in BA 44. At the theoretical level, it has been proposed that merge in language is specific in the property that words have to create constituents that inherit the lexical feature of word category from their constituent words (Murphy 2015); that is, information in a single, dominant word (e.g., determiner) exhibits a hierarchical influence onto the remainder of the syntactic constituent (e.g., DP). From a neurobiological point of view, BA 44 now appears to be a multifunctional area subserving different cognitive mechanisms (Clos et al. 2013); syntactic processes in the narrow sense may only engage a subportion of this region. Future investigations on merge may want to use highly detailed parcellation maps to allow for a finer grained structure-to-function cortical mapping.

Conclusion

The syntactic merging mechanism creating phrases and sentences activates the IFG with highest activity in BA44 and a smaller region in the posterior STS. A finer grained investigation into the neural behavior of phrases and sentences in Broca's revealed an activity shift for sentences towards the ventral portion of the IFG (BA 45), while phrases rather boosted activity in BA 44. As sentences in contrast to PPs contain verbs, the involvement of BA 45 reflects the encoding of propositional meaning. Conversely, the involvement of BA44 for phrases marks pure syntactic processing in the area. The posterior STS may support thematic assignment already beyond sentential level, since it is equally active for both structures. The most general finding of the present study is that merge as the basic syntactic operation of binding words syntactically is primarily performed in BA 44 in the IFG.

Funding

This work was supported by a grant from the European Research Council (ERC-2010-AdG 20100407 awarded to A.D.F.) and by the School of Mind and Brain (E.Z).

Notes

The authors thank Mandy Jochemko, Anke Kummer, and Simone Wipper for MRI data acquisition, Isabell Wartenburger for her comments during the manuscript preparation, and Katja Barnickel for her help during the construction the stimulus material. *Conflict of Interest:* None declared.

References

- Amunts K, Lenzen M, Friederici AD, Schleicher A, Morosan P, Palomero-Gallagher N, Zilles K. 2010. Broca's region: novel organizational principles and multiple receptor mapping. *PLoS Biol.* 8:e1000489.
- Amunts K, Schleicher A, Burgel U, Mohlberg H, Uylings HB, Zilles K. 1999. Broca's region revisited: cytoarchitecture and intersubject variability. *J Comp Neurol.* 412:319–341.
- Baayen RH, Piepenbrock R, Gulikers L. 1995. The CELEX lexical database. Philadelphia, PA: Linguistics Data Consortium, University of Pennsylvania.
- Bahlmann J, Schubotz RI, Friederici AD. 2008. Hierarchical artificial grammar processing engages Broca's area. *Neuroimage.* 42:525–534.
- Baron SG, Osherson D. 2011. Evidence for conceptual combination in the left anterior temporal lobe. *Neuroimage.* 55:1847–1852.
- Baron SG, Thompson-Schill SL, Weber M, Osherson D. 2010. An early stage of conceptual combination: Superimposition of constituent concepts in left anterolateral temporal lobe. *Cogn Neurosci.* 1:44–51.
- Barsalou LW. 1982. Context-independent and context-dependent information in concepts. *Mem Cognit.* 10:82–93.
- Bastiaansen MC, van der Linden M, Ter Keurs M, Dijkstra T, Hagoort P. 2005. Theta responses are involved in lexical-semantic retrieval during language processing. *J Cogn Neurosci.* 17:530–541.
- Bebout L. 1993. Processing of negative morphemes in aphasia: an example of the complexities of the closed class/open class concept. *Clin Linguist Phon.* 7:161–172.
- Bemis DK, Pyllkanen L. 2013. Flexible composition: MEG evidence for the deployment of basic combinatorial linguistic mechanisms in response to task demands. *PLoS ONE.* 8:e73949.
- Bemis DK, Pyllkanen L. 2011. Simple composition: a magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *J Neurosci.* 31:2801–2814.
- Bennis H, Prins R, Vermeulen J. 1983. Lexical-semantic versus syntactic disorders in aphasia: the processing of prepositions. *Publikaties van het Instituut voor Algemene Taalwetenschap* 40. Amsterdam, The Netherlands: University of Amsterdam.
- Ben-Shachar M, Hendler T, Kahn I, Ben-Bashat D, Grodzinsky Y. 2003. The neural reality of syntactic transformations: evidence from functional magnetic resonance imaging. *Psychol Sci.* 14:433–440.
- Benson DF, Geschwind MD. 1985. Aphasia and related disorders: a clinical approach. In: Mesulam MM, editor. *Principles of behavioral neurology*. Philadelphia (PA): F. A. Davis Company. p. 193–238.
- Berwick RC, Friederici AD, Chomsky N, Bolhuis JJ. 2013. Evolution, brain, and the nature of language. *Trends Cogn Sci.* 17:89–98.
- Bolhuis JJ, Tattersall I, Chomsky N, Berwick RC. 2014. How could language have evolved? *PLoS Biol.* 12:e1001934.
- Bookheimer S. 2002. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu Rev Neurosci.* 25:151–188.
- Bornkessel I, Zysset S, Friederici AD, von Cramon DY, Schlesewsky M. 2005. Who did what to whom? The neural basis of argument hierarchies during language comprehension. *Neuroimage.* 26:221–233.
- Bottini G, Corcoran R, Sterzi R, Paulesu E, Schenone P, Scarpa P, Frackowiak RS, Frith CD. 1994. The role of the right hemisphere in the interpretation of figurative aspects of language.

- A positron emission tomography activation study. *Brain*. 117:1241–1253.
- Bradley DC, Garrett MF. 1983. Hemisphere differences in the recognition of closed and open class words. *Neuropsychologia*. 21:155–159.
- Brodman K. 1909. *Vergleichende Lokalisationslehre der Großhirnrinde*. Leipzig: Barth JA.
- Brown CM, Hagoort P, ter Keurs M. 1999. Electrophysiological signatures of visual lexical processing: open- and closed-class words. *J Cogn Neurosci*. 11:261–281.
- Caplan D, Chen E, Waters G. 2008. Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex*. 44:257–275.
- Carnie A. 2007. *A generative introduction*. Malden (MA): Blackwell Publishing.
- Chomsky N. 1993. A minimalist program for linguistic theory. In: Hale KL, Keyser SJ, editors. *The view from Building 20: essays in linguistics in honor of Sylvain Bromberger*. Cambridge: MIT Press. p. 1–52.
- Chomsky N. 1995. *The minimalist program*. Cambridge: MIT Press.
- Clos M, Amunts K, Laird AR, Fox PT, Eickhoff SB. 2013. Tackling the multifunctional nature of Broca's region meta-analytically: Co-activation-based parcellation of area 44. *Neuroimage*. 83:174–188.
- Constable RT, Pugh KR, Berroya E, Mencl WE, Westerveld M, Ni W, Shankweiler D. 2004. Sentence complexity and input modality effects in sentence comprehension: an fMRI study. *Neuroimage*. 22:11–21.
- Del Prato P, Pyllkanen L. 2014. MEG evidence for conceptual combination but not numeral quantification in the left anterior temporal lobe during language production. *Front Psychol*. 5:524.
- Demb JB, Desmond JE, Wagner AD, Vaidya CJ, Glover GH, Gabrieli JD. 1995. Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *J Neurosci*. 15:5870–5878.
- den Ouden DB, Saur D, Mader W, Schelter B, Lukic S, Wali E, Timmer J, Thompson CK. 2012. Network modulation during complex syntactic processing. *Neuroimage*. 59:815–823.
- Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K. 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*. 25:1325–1335.
- Fiez JA. 1997. Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum Brain Mapp*. 5:79–83.
- Fitch WT, Hauser MD. 2004. Computational constraints on syntactic processing in a nonhuman primate. *Science*. 303:377–380.
- Friederici AD. 1985. Levels of processing and vocabulary types: evidence from on-line comprehension in normals and agrammatics. *Cognition*. 19:133–166.
- Friederici AD. 1981. Production and comprehension of prepositions in aphasia. *Neuropsychologia*. 19:191–199.
- Friederici AD. 1982. Syntactic and semantic processes in aphasic deficits: the availability of prepositions. *Brain Lang*. 15:249–258.
- Friederici AD. 2011. The brain basis of language processing: from structure to function. *Physiol Rev*. 91:1357–1392.
- Friederici AD. 2002. Towards a neural basis of auditory sentence processing. *Trends Cogn Sci*. 6:78–84.
- Friederici AD, Bahlmann J, Heim S, Schubotz RI, Anwander A. 2006. The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proc Natl Acad Sci USA*. 103:2458–2463.
- Friederici AD, Fiebach CJ, Schlesewsky M, Bornkessel ID, von Cramon DY. 2006. Processing linguistic complexity and grammaticality in the left frontal cortex. *Cereb Cortex*. 16:1709–1717.
- Friederici AD, Makuuchi M, Bahlmann J. 2009. The role of the posterior superior temporal cortex in sentence comprehension. *Neuroreport*. 20:563–568.
- Friederici AD, Meyer M, von Cramon DY. 2000. Auditory language comprehension: an event-related fMRI study on the processing of syntactic and lexical information. *Brain Lang*. 75:289–300.
- Friederici AD, Opitz B, von Cramon DY. 2000. Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cereb Cortex*. 10:698–705.
- Friederici AD, Schonle PW, Garrett MF. 1982. Syntactically and semantically based computations: processing of prepositions in agrammatism. *Cortex*. 18:525–534.
- Friston KJ, Holmes AP, Worsley J-P, Frith CD, Frackowiak RS. 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp*. 2:189–210.
- Gabrieli JD, Poldrack RA, Desmond JE. 1998. The role of left prefrontal cortex in language and memory. *Proc Natl Acad Sci USA*. 95:906–913.
- Garrett MF. 1976. Syntactic processes in sentence comprehension. In: Wales RJ, Walker E, editors. *New approaches to language mechanisms*. Amsterdam: North Holland. p. 231–256.
- Garrett MF. 1975. The analysis of sentence production. In: Bower G, editor. *The psychology of learning and motivation: advances in research and theory*. New York: Academic Press. p. 137–177.
- Goodglass H, Gleason JB, Bernholtz NA, Hyde MR. 1972. Some linguistic structures in the speech of a Broca's aphasic. *Cortex*. 8:191–212.
- Goucha T, Friederici AD. 2015. The language skeleton after dissecting meaning: a functional segregation within Broca's Area. *Neuroimage*. 114:294–302.
- Grasby PM, Frith CD, Friston KJ, Simpson J, Fletcher PC, Frackowiak RS, Dolan RJ. 1994. A graded task approach to the functional mapping of brain areas implicated in auditory-verbal memory. *Brain*. 117:1271–1282.
- Grodzinsky Y, Friederici AD. 2006. Neuroimaging of syntax and syntactic processing. *Curr Opin Neurobiol*. 16:240–246.
- Grodzinsky Y, Santi A. 2008. The battle for Broca's region. *Trends Cogn Sci*. 12:474–480.
- Hagoort P. 2005. On Broca, brain, and binding: a new framework. *Trends Cogn Sci*. 9:416–423.
- Hagoort P. 2008. The fractionation of spoken language understanding by measuring electrical and magnetic brain signals. *Philos Trans R Soc Lond B Biol Sci*. 363:1055–1069.
- Hahne A, Friederici AD. 1999. Electrophysiological evidence for two steps in syntactic analysis. Early automatic and late controlled processes. *J Cogn Neurosci*. 11:194–205.
- Hahne A, Schroger E, Friederici AD. 2002. Segregating early physical and syntactic processes in auditory sentence comprehension. *Neuroreport*. 13:305–309.
- Hauser MD, Chomsky N, Fitch WT. 2002. The faculty of language: what is it, who has it, and how did it evolve? *Science*. 298:1569–1579.
- Humphries C, Binder JR, Medler DA, Liebenthal E. 2006. Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *J Cogn Neurosci*. 18:665–679.
- Humphries C, Binder JR, Medler DA, Liebenthal E. 2007. Time course of semantic processes during sentence comprehension: an fMRI study. *Neuroimage*. 36:924–932.

- Humphries C, Love T, Swinney D, Hickok G. 2005. Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Hum Brain Mapp.* 26:128–138.
- Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR. 1996. Brain activation modulated by sentence comprehension. *Science.* 274:114–116.
- Kriegeskorte N, Simmons WK, Bellgowan PS, Baker CI. 2009. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat Neurosci.* 12:535–540.
- Lambon Ralph MA, Sage K, Jones RW, Mayberry EJ. 2010. Coherent concepts are computed in the anterior temporal lobes. *Proc Natl Acad Sci USA.* 107:2717–2722.
- Maguire EA, Frith CD. 2004. The brain network associated with acquiring semantic knowledge. *Neuroimage.* 22:171–178.
- Makuuchi M, Bahlmann J, Anwender A, Friederici AD. 2009. Segregating the core computational faculty of human language from working memory. *Proc Natl Acad Sci USA.* 106:8362–8367.
- Makuuchi M, Grodzinsky Y, Amunts K, Santi A, Friederici AD. 2013. Processing noncanonical sentences in Broca's region: reflections of movement distance and type. *Cereb Cortex.* 23:694–702.
- Mazoyer B, Tzourio N, Frak V, Syrota A, Murayama N, Levrier O, Salamon G, Dehaene S, Cohen L, Mehler J. 1993. The cortical representation of speech. *J Cogn Neurosci.* 5:467–479.
- Meyer L, Obleser J, Anwender A, Friederici AD. 2012. Linking ordering in Broca's area to storage in left temporo-parietal regions: the case of sentence processing. *Neuroimage.* 62:1987–1998.
- Mohr B, Pulvermüller F, Zaidel E. 1994. Lexical decision after left, right and bilateral presentation of function words, content words and non-words: evidence for interhemispheric interaction. *Neuropsychologia.* 32:105–124.
- Mugler JP III, Brookeman JR. 1990. Three-dimensional magnetization-prepared rapid gradient-echo imaging (3D MP RAGE). *Magn Reson Med.* 15:152–157.
- Murphy E. 2015. Labels, cognomes, and cyclic computation: an ethological perspective. *Front Psychol.* 6:715.
- Neville HJ, Mills DL, Lawson DS. 1992. Fractionating language: different neural subsystems with different sensitive periods. *Cereb Cortex.* 2:244–258.
- Newman SD, Ikuta T, Burns T Jr. 2010. The effect of semantic relatedness on syntactic analysis: an fMRI study. *Brain Lang.* 113:51–58.
- Nobre AC, Price CJ, Turner R, Friston KJ. 1997. Selective processing of nouns and function words in the human brain. *Neuroimage.* 5:S53.
- Oldfield RC. 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia.* 9:97–113.
- Osterhout L, Bersick M, McKinnon R. 1997. Brain potentials elicited by words: word length and frequency predict the latency of an early negativity. *Biol Psychol.* 46:143–168.
- Pallier C, Devauchelle AD, Dehaene S. 2011. Cortical representation of the constituent structure of sentences. *Proc Natl Acad Sci USA.* 108:2522–2527.
- Patterson K, Nestor PJ, Rogers TT. 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci.* 8:976–987.
- Penny WD, Holmes AP. 2003. Random effect analysis. In: *Franckowiak RSJ, Friston KJ, Fritch CD, Dolan R, Price CJ, Zeki S, Ashburner J, Penny WD, editors. Human brain function.* San Diego: Academic Press. p. 843–850.
- Perani D, Saccuman MC, Scifo P, Anwender A, Spada D, Baldoli C, Poloniato A, Lohmann G, Friederici AD. 2011. Neural language networks at birth. *Proc Natl Acad Sci USA.* 108:16056–16061.
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JD. 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage.* 10:15–35.
- Pulvermüller F. 1995. Agrammatism: behavioral description and neurobiological explanation. *J Cogn Neurosci.* 7:165–181.
- Roder B, Stock O, Neville H, Bien S, Rosler F. 2002. Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: a functional magnetic resonance imaging study. *Neuroimage.* 15:1003–1014.
- Rogalsky C, Hickok G. 2009. Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex. *Cereb Cortex.* 19:786–796.
- Rogalsky C, Hickok G. 2011. The role of Broca's area in sentence comprehension. *J Cogn Neurosci.* 23:1664–1680.
- Samuels JA, Benson DF. 1979. Some aspects of language comprehension in anterior aphasia. *Brain Lang.* 8:275–286.
- Santi A, Grodzinsky Y. 2007. Working memory and syntax interact in Broca's area. *Neuroimage.* 37:8–17.
- Scott SK, Johnsrude IS. 2003. The neuroanatomical and functional organization of speech perception. *Trends Neurosci.* 26:100–107.
- Shapiro LP, Jensen LR. 1986. Processing open and closed class-headed nonwords: left hemisphere support for separate vocabularies. *Brain Lang.* 28:318–327.
- Shetreet E, Friedmann N. 2014. The processing of different syntactic structures: fMRI investigation of the linguistic distinction between Wh-movement and verb movement. *J Neurolinguistics.* 27:1–17.
- Small SL, Flores DK, Noll DC. 1998. Different neural circuits subserved reading before and after therapy for acquired dyslexia. *Brain Lang.* 62:298–308.
- Snijders TM, Vosse T, Kempen G, Van Berkum JJ, Petersson KM, Hagoort P. 2009. Retrieval and unification of syntactic structure in sentence comprehension: an FMRI study using word-category ambiguity. *Cereb Cortex.* 19:1493–1503.
- Stowe LA, Broere CA, Paans AM, Wijers AA, Mulder G, Vaalburg W, Zwarts F. 1998. Localizing components of a complex task: sentence processing and working memory. *Neuroreport.* 9:2995–2999.
- Stowe LA, Paans AM, Wijers AA, Zwarts F, Mulder G, Vaalburg W. 1999. Sentence comprehension and word repetition: a positron emission tomography investigation. *Psychophysiology.* 36:786–801.
- Stromswold K, Caplan D, Alpert N, Rauch S. 1996. Localization of syntactic comprehension by positron emission tomography. *Brain Lang.* 52:452–473.
- Swinney DA, Zurif EB, Cutler A. 1980. Effects of sentential stress and word class upon comprehension in Broca's aphasics. *Brain Lang.* 10:132–144.
- Vandenberghe R, Nobre AC, Price CJ. 2002. The response of left temporal cortex to sentences. *J Cogn Neurosci.* 14:550–560.
- Vul E, Kanwisher N. 2010. Begging the question: the non-independence error in fMRI data analysis. In: *Hanson SJ, Bunzl M, editors. Foundational issues in human brain mapping.* Cambridge: MIT Press. p. 71–91.
- Wagner AD, Koutstaal W, Maril A, Schacter DL, Buckner RL. 2000. Task-specific repetition priming in left inferior prefrontal cortex. *Cereb Cortex.* 10:1176–1184.
- Wang Y, Xiang J, Kotecha R, Vannest J, Liu Y, Rose D, Schapiro M, Degrauw T. 2008. Spatial and frequency differences of neuro-magnetic activities between the perception of open- and closed-class words. *Brain Topogr.* 21:75–85.

- Westerlund M, Kastner I, Al Kaabi M, Pytkkanen L. 2015. The LATL as locus of composition: MEG evidence from English and Arabic. *Brain Lang.* 141:124–134.
- Wilson SM, DeMarco AT, Henry ML, Gesierich B, Babiak M, Mandelli ML, Miller BL, Gorno-Tempini ML. 2014. What role does the anterior temporal lobe play in sentence-level processing? Neural correlates of syntactic processing in semantic variant primary progressive aphasia. *J Cogn Neurosci.* 26:970–985.
- Xu J, Kemeny S, Park G, Frattali C, Braun A. 2005. Language in context: emergent features of word, sentence, and narrative comprehension. *Neuroimage.* 25:1002–1015.
- Zaccarella E, Friederici AD. 2015. Syntax in the brain. In: Toga AW, editor. *Brain mapping: an encyclopedic reference.* New York: Elsevier. p. 461–468.
- Zhu Z, Feng G, Zhang JX, Li G, Li H, Wang S. 2013. The role of the left prefrontal cortex in sentence-level semantic integration. *Neuroimage.* 76:325–331.
- Zhu Z, Zhang JX, Wang S, Xiao Z, Huang J, Chen HC. 2009. Involvement of left inferior frontal gyrus in sentence-level semantic integration. *Neuroimage.* 47:756–763.
- Zwart J-W. 2011. Structure and order: asymmetric merge. In: Boeckx C, editor. *The Oxford handbook of linguistic minimalism.* Oxford: Oxford University Press. p. 96–118.