



Segregating the core computational faculty of human language from working memory

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In contrast to simple structures in animal vocal behavior, hierarchical structures such as center-embedded sentences manifest the core computational faculty of human language. Previous artificial grammar learning studies found that the left pars opercularis (LPO) subserves the processing of hierarchical structures. However, it is not clear whether this area is activated by the structural complexity per se or by the increased memory load entailed in processing hierarchical structures. To dissociate the effect of structural complexity from the effect of memory cost, we conducted a functional magnetic resonance imaging study of German sentence processing with a 2-way factorial design tapping structural complexity (with/without hierarchical structure, i.e., center-embedding of clauses) and working memory load (long/short distance between syntactically dependent elements; i.e., subject nouns and their respective verbs). Functional imaging data revealed that the processes for structure and memory operate separately but co-operatively in the left inferior frontal gyrus; activities in the LPO increased as a function of structural complexity, whereas activities in the left inferior frontal sulcus (LIFS) were modulated by the distance over which the syntactic information had to be transferred. Diffusion tensor imaging showed that these 2 regions were interconnected through white matter fibers. Moreover, functional coupling between the 2 regions was found to increase during the processing of complex, hierarchically structured sentences. These results suggest a neuroanatomical segregation of syntax-related aspects represented in the LPO from memory-related aspects reflected in the LIFS, which are, however, highly interconnected functionally and anatomically.

DTI | fMRI | hierarchical structure

Language appears to be a trait specific to humans—at least in its core computational component, that is, grammar. Defining language as a sequence of symbols, Chomsky (1) proposed a hierarchy of grammars as language production mechanisms with increasing generative powers. The lowest-level grammar is finite state grammar (FSG). FSG can be fully specified by transition probabilities between a finite number of states (e.g., words), being not powerful enough to generate structures of natural human languages. Phrase structure grammar (PSG) has more generative power than FSG. A key difference between FSG and PSG is that only PSG can generate the sequence A^nB^n , where A and B denote symbols and n the number of repetitions. The ability to process the sequence A^nB^n is crucial for the processing of center-embedded sentences, such as “The man the boy the dog bit greeted is my friend.” where subjects (i.e., the man, the boy, and the dog) are A-symbols and the verbs (bit, greeted, and is) are B-symbols. Surprisingly, tests on monkeys (2) and on songbirds (3) showed that whereas songbirds can process A^nB^n sequences, monkeys cannot. However, even if the birds could correctly discriminate A^nB^n sequences from A^nB^m , ($4 > n, m > 0, n \neq m$), it does not necessarily mean that they were able to process the sequences with center-embedded structures as found in human languages. The reason is that human language requires the ability to process *nested* sequences such as $A_3A_2A_1B_1B_2B_3$ where the correct coupling of pairs A_3-B_3, A_2-B_2 and A_1-B_1 is required instead of AAABBB sequences in which no relation between particular As and Bs exists but only the number of the

As and Bs matters. Therefore, the $A_3A_2A_1B_1B_2B_3$ sequence type would be a better representative structure for testing the fundamental property of PSG that is suggested to represent the core computational faculty of human language (4).

If the processing of PSG is fundamental to human language, the questions about how the brain implements this faculty arise. The left pars opercularis (LPO), a posterior part of Broca’s area, was found as a neural correlate of the processing of A^nB^n sequences in human studies by an artificial grammar learning paradigm comprised of visually presented syllables (5, 6). These 2 studies therefore strongly suggest that LPO is a candidate brain area for the processor of PSG (i.e., hierarchical structures). However, as these 2 studies contrasted AAABBB and $A_3A_2A_1B_1B_2B_3$ (i.e., PSG sequences) with AB-ABAB, a FSG sequence, they are not able to answer the question whether LPO activities are exclusively explained by the structural hierarchy or whether and to what extent verbal working memory (VWM) plays a crucial role in the processing of hierarchically structured sequences. In these studies, the distances between the dependent pairs (As and Bs) in PSG sequences were much longer (i.e., 4 symbols between A_3 and B_3) than that in FSG sequences (i.e., A and B were next to each other). To factor out the effect of the memory load required to process the long-distance dependency, FSG sequences with long distance dependencies would make a better contrast for PSG that contains long-distance dependencies by definition.

Dissociating syntactic computation from non-syntactic VWM during sentence processing is of particular importance at the level of cognitive theorizing and at the functional neuroanatomical level since the 2 processes have not been segregated neuroanatomically. At the psycholinguistic level, there are 2 opposing views concerning the relation of syntactic computation, which has been called syntactic VWM by some researchers (7, 8), and non-syntactic VWM, with one position assuming a single VWM system for all verbal-related processes (9) and the other position suggesting a separate VWM system supporting sentence comprehension (10, 11). At the level of functional neuroanatomy, both syntactic computation (5, 6, 8, 12–17) and non-syntactic VWM (18) have been localized in the left prefrontal cortex. However, thus far there is no clear evidence for their segregation. Studies focusing on the relationship between syntactic computation and non-syntactic VWM have pointed toward an interaction of these 2 processes. An interaction between syntactic computation and non-syntactic VWM has been demonstrated at a behavioral level (9, 19) and a neurophysiological level using event-related brain potential measures (20, 21) as well as functional magnetic

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resonance imaging (fMRI) (13). However, all of these studies used a group comparison approach comparing individuals with different memory spans during reading (i.e., high versus low reading span). Such an approach can only provide indirect evidence for the interplay between syntactic computation and VWM as it is not clear what the nature of VWM as measured by reading span is. Thus, a dissociation of the 2 processes at the neuroanatomical level would be of major interest, both in terms of resolving the conflict between cognitive theories and understanding the functional neuroanatomy of language processing.

In the present study, we addressed the following key questions using fMRI and diffusion tensor imaging (DTI). First, can LPO activities for PSG against FSG be reproduced independent of WM load (i.e., when the distance between the paired dependent items is controlled)? Second, can core syntactic computations be neuroanatomically dissociated from non-syntactic VWM during sentence processing within the left inferior frontal gyrus (LIFG)? Here, core syntactic computations are operationalized as processing of the structural hierarchy of a sentence, whereas non-syntactic VWM is defined as maintenance cost of the verbal information for a certain period irrespective of the syntactic structure of the sentence. Third, if neuroanatomically dissociable, do syntactic computations and non-syntactic VWM interact during sentence processing?

These questions were investigated using a natural language, namely German. Using structures analogous to PSG sequences used in earlier studies with an artificial grammar paradigm (6), the present study tested sentences with nested subject relative clauses (hereafter hierarchical conditions) (Fig. 1). In these sentences, subject-verb pairs (S_3-V_3 , S_2-V_2 , S_1-V_1) in the complement clause corresponded to A_3-B_3, A_2-B_2 and A_1-B_1 of the $A_3A_2A_1B_1B_2B_3$ sequence, respectively (Fig. 1A, Condition A). The main subject (“Maria”) and the auxiliary verb (“hatte”) in the complement clause were separated with eight words, by which we measured distance (Fig. 1B, Condition A). Similar to the FSG conditions in artificial grammar studies (5, 6), the present study constructed linearly-structured sentences (hereafter linear conditions) in which A and B represented the dependent subject-verb pairs, and C other elements that allowed us to control the distance between A-B pairs (Fig. 1A, Conditions C and D). We hypothesized that non-syntactic VWM operationalized by the factor distance between subjects and verbs (long in conditions A and C vs. short in conditions B and D, Fig. 1) can be distinguished from syntactic computation operationalized as processing load caused by structural complexity (hierarchy in Conditions A and B vs. linear in Conditions C and D, Fig. 1). This 2×2 factorial design permitted us to dissociate the effects of syntactic STRUCTURE (hierarchy vs. linear) from non-syntactic VWM captured in the factor DISTANCE (long vs. short distance between related elements). Following the analysis of variance (ANOVA) of the functional data, we examined effective connectivity and anatomical connectivity between the detected functional regions in LIFG by psychophysiological interaction (PPI) analysis and by probabilistic fiber tracking from DTI data, respectively.

Results

Behavioral Data. In 20% of the trials, comprehension questions were given 100 ms after the sentence presentation, and the participants were requested to judge whether the given short sentences matched the preceding sentences or not, and to indicate this by pressing the response buttons as soon as possible. The mean accuracy rates for the comprehension questions were above chance for all conditions (Condition A $77.8\% \pm 3.24\%$ SE; Condition B $74.1\% \pm 3.81\%$; Condition C $77.8\% \pm 3.59\%$; Condition D $82.1\% \pm 3.72\%$). The mean reaction times (RTs) were as follows: Condition A 1727 ms \pm

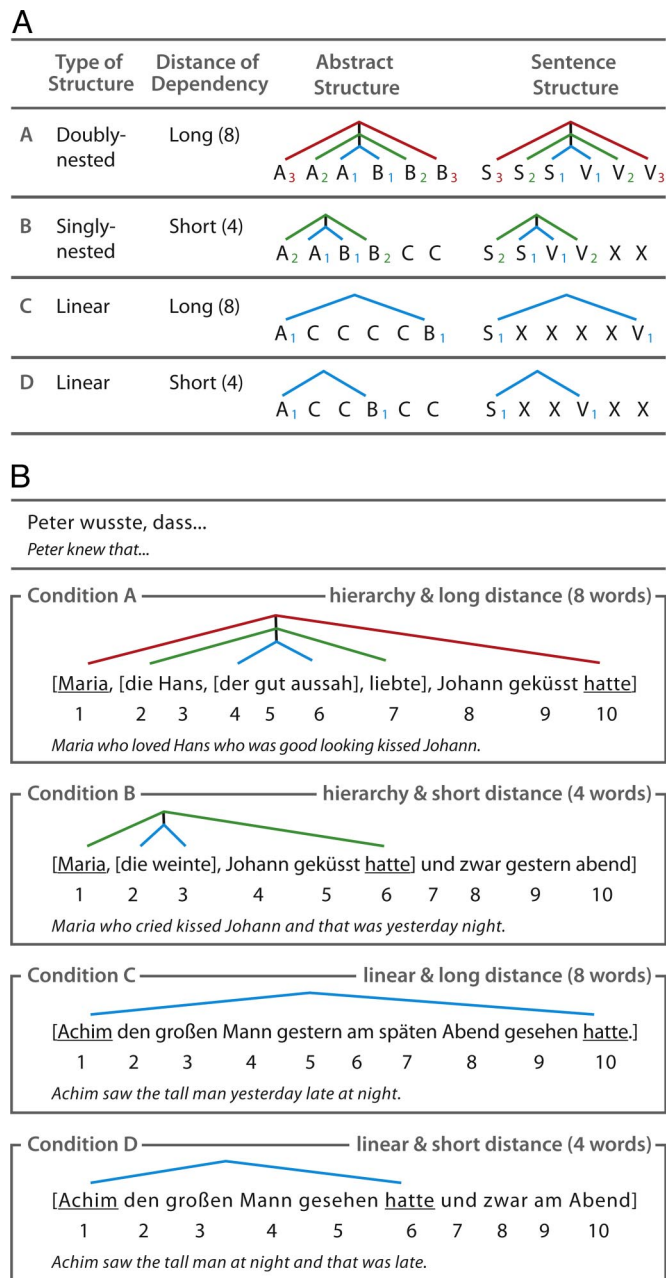


Fig. 1. Conditions. (A) Structures. Conditions A and B had hierarchical structures and C and D had linear structures. Abstract structures were represented with A–C, where A and B denote dependent pairs. Pairings are indicated by subscript and by colors. Sentence structures were created by replacing A with S (subject), B with V (verb), and C with X (other sentential elements). (B) Sentence examples. Sentences in all conditions always started with “Peter wusste, dass” (Peter knew that). Only the complement clauses of four conditions were shown. Complement clauses were constructed with ten words. Distance was defined by the number of words between the main subject and the verb, that is, 8 words (long) or 4 words (short). The main subjects and the verbs are underlined.

70.1 ms SE; Condition B 1825 ms \pm 48.0 ms; Condition C 1785 ms \pm 70.0 ms; Condition D 1787 ms \pm 71.2 ms. Within-subject ANOVAs with factors STRUCTURE (hierarchical/linear) and DISTANCE (long/short) revealed no significant main effect or interactions for either accuracy rate [$F(1, 17) = 1.54$ ns, 0.00 ns, and 1.74, ns for factors STRUCTURE, DISTANCE, and interaction] or RT [$F(1, 17) = 0.07$ ns, 1.60 ns, 1.71 ns].

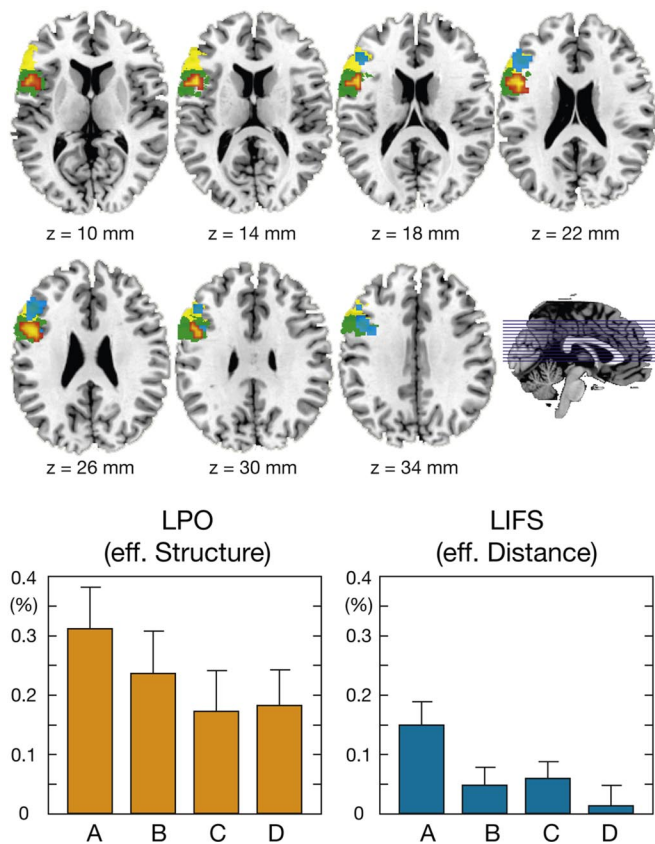


Fig. 2. ANOVA results. Red-orange, main effect of STRUCTURE; Blue, main effect of DISTANCE; Green, area 44; Yellow, area 45. The search volume was confined to LIFG VOI and SPM{T}s are thresholded at $P < 0.05$ (corrected for LIFG VOI). The left hemisphere is on the left side. The activated clusters revealed by ANOVA served as VOIs from which mean signals were extracted using Marsbar 0.41 (available at <http://marsbar.sourceforge.net>). The unit of signal intensity is percentage. Error bars denote standard errors.

Imaging Data. ANOVA. A within-subject ANOVA was performed in each voxel within the volume of interest, namely the left inferior frontal gyrus. A main effect of STRUCTURE and a main effect of DISTANCE were detected. We created statistical parametric maps with t contrasts (SPM{T}) instead of F contrasts (Fig. 2). The main effect of STRUCTURE was identified with the contrast of $A + B > C + D$ as a cluster that occupied the lateral convexity of the LPO [peak $(-45\ 6\ 24)$, $P = 0.004$, $Z = 3.53$, cluster size = 85]. The main effect of DISTANCE was revealed with the contrast of $A + C > B + D$ in the left inferior frontal sulcus (LIFS) as two separate clusters [peak $(-45\ 27\ 27)$, $P = 0.028$, $Z = 3.81$, cluster size = 46; peak $(-45\ 9\ 36)$, $P = 0.040$, $Z = 3.64$, cluster size = 40]. No interaction was detected. All of the reverse contrasts (i.e., $A + B < C + D$, $A + C < B + D$, and $A - B < C - D$) did not show any significant activation with the given threshold.

PPI analysis. We hypothesized that the LPO and LIFS interact to process hierarchically structured sentences since the LIFS can be considered to assist syntactic computation at the LPO by supporting increased demand for memory during sentence processing. To test this hypothesis, we examined the change in the effective connectivity of LPO between hierarchical and linear conditions (i.e., the contrast of “ $A + B > C + D$ ”) using PPI analysis (22). PPI analyses with the seed regions in the LIFS were not performed because LIFS activation was not consistent among participants. The PPI analysis revealed a cluster in the LIFS that enjoyed significantly higher coupling with the LPO

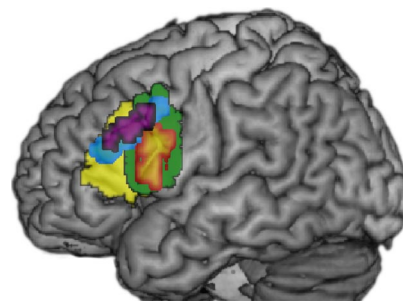


Fig. 3. Results of PPI analysis. The results of PPI and ANOVA projected onto the surface of the left hemisphere of the brain. Violet, significant cluster for PPI analysis; Red-orange, main effect of STRUCTURE; Blue, main effect of DISTANCE; Green, area 44; Yellow, area 45. The search volume was confined to LIFG VOI and SPM{T}s are thresholded at $P < 0.05$ (corrected for LIFG VOI). The seed region for PPI analysis was centered at the maxima in the LPO cluster that had the main effect of STRUCTURE (the red-orange cluster). PPI analysis detected the regions that showed an increase in effective connectivity with the seed region during the hierarchical conditions relative to the linear conditions. See *SI Methods* for details of analysis.

during the processing of hierarchically structured sentences than during that of linearly structured sentences ($P < 0.028$ corrected for LIFG VOI, Fig. 3). This cluster lay in the middle of the 2 LIFS clusters revealed by the main effect of DISTANCE with the most significant PPI ($z = 3.07$) at the coordinate of $(-51, 21, 33)$. Fifty percent of the PPI-LIFS cluster overlapped the LIFS cluster revealed by the main effect of DISTANCE.

Anatomical connectivity. The LPO and 3 LIFS clusters were all found to be interconnected in more than 50% of participants (Fig. 4 and Fig. S1). In this section, we call the 2 LIFS clusters identified for the main effect of DISTANCE (located at the anterior and posterior portion of LIFS) LIFSa, and LIFSp, and the cluster revealed by PPI analysis (located at the middle portion of LIFS) LIFSm, respectively. The connections from the LPO to the LIFSm and from the LPO to the LIFSa were detected in 22.2% and 33.3% of participants, respectively, but the reverse directions showed higher ratios (55.6% for both). As shown above, the computed connectivity values are directly influenced by the fiber tracking direction, resulting in asymmetric estimates. This is caused by variable estimation errors in both tracking directions, which lead to different underestimations of the connectivity value. The higher value is less influenced by these

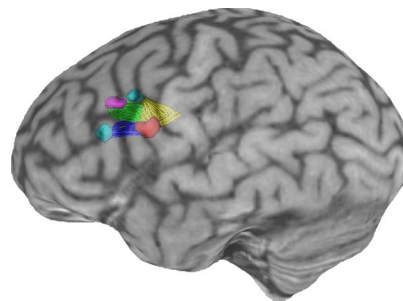


Fig. 4. Anatomical connections. Deterministic fiber tracking in 1 participant’s DTI data are shown with the transparent surface brain. Anatomical connections between the LPO (revealed by the main effect of STRUCTURE, red) and LIFSm (revealed by PPI analysis, violet), LIFSa, and LIFSp (by the main effect of DISTANCE, blue) are depicted from the left view. The fibers are colored differently. We have measured connectivity in each participant’s DTI with probabilistic fiber tracking method, but here we used a deterministic tracking method to create more easily seen fibers. Deterministic fiber tracking was performed using in-house software. See Fig. S3 for different views and the connections between LIFSm and LIFSa and LIFSm and LIFSp.

estimation errors and is a better representation of the connection strength. Therefore, we took the higher value of the 2 (from regions X to Y or from Y to X) to represent the connectivity between the 2 regions. With this rule, the connection between the LPO and the LIFSm (i.e., the cluster revealed by PPI analysis as having increased effective connectivity during the processing of hierarchical structures) was confirmed in 55.6% of participants. To evaluate the anatomical connectivity between the 2 regions more quantitatively, we calculated connectivity indices. The index was defined by counting the number of connected voxels in a target VOI and dividing it by the size of the target VOI. One-sample *t*-tests on the connectivity index of LPO-LIFSm confirmed that it was significantly larger than 0 ($P = 0.0052$). Thus, we take this as evidence that the LPO and LIFSm were interconnected not only functionally (as found by PPI analysis) but also anatomically. Other connections among the 4 regions were more consistent across the individual data. The connection LIFSa-LIFSm was found in all participants (100%), LPO-LIFSp in 94.4%, and LIFSm-LIFSp and LIFSp-LIFSa in 88.9%. One-sample *t*-tests on the connectivity indices show that all of the connections were significantly larger than 0 ($P < 0.05$, Bonferroni correction for 6 comparisons, $P = 0.0052, 0.0024, 1.9E-06, 1.3E-16, 8.8E-05, \text{ and } 1.9E-05$ for the connections of LPO-LIFSm, LPO-LIFSa, LPO-LIFSp, LIFSa-LIFSm, LIFSm-LIFSp, and LIFSp-LIFSa, respectively).

Discussion

Functional Neuroanatomical Segregation of Syntactic Computation from Non-syntactic VWM. The present study found 2 distinct regions in the LIFG to vary as a function of the structural hierarchy of a sentence and the distance of dependent elements in a sentence, respectively. The significance of the functional segregation of processing of hierarchical structures and VWM in LIFG is 2-fold: first, it is most relevant to the recent debate on the neural underpinning of processing structural hierarchies (5, 6, 23), and second, it throws light on the controversy over the involvement of specific (6, 10, 11, 24, 25) versus general (9, 26, 27) VWM operative in language processing.

With respect to hierarchical processing, the present study complements the previous artificial grammar studies (5, 6). First, the present study serves as empirical evidence that the previous artificial grammar findings of LPO involvement in the processing of hierarchically structured sequences can be generalized to natural language. AGL paradigms have the advantage of purifying the syntactic computation by factoring out semantics from sequence processing, but its relevance to natural language has lacked empirical support until now. By testing a similar hierarchical structure in German, the present study demonstrates that LPO activation during the processing of hierarchically structured sequences in previous artificial grammar studies also holds for the processing of similar structures in a natural language. Second, the obligatory paired dependency of grammatical subjects and verbs in center-embedded clauses requires the reader to keep track of each subject-verb dependency to assign the thematic roles adequately, thus ensuring the processing of the nested dependency. Some researchers have cast doubt on the appropriateness of AⁿBⁿ sequences used in artificial grammar studies as stimuli to examine the ability to process PSG language, since judgment of the grammaticality of AⁿBⁿ sequences might be managed merely by counting the number of As and Bs without processing the hierarchical, nested structure (28, 29).

The present study clearly demonstrates that the syntactic computations involved in the processing of syntactically complex sentences is neuroanatomically separate from the non-syntactic VWM, thus favoring the view that syntactic processes are independent of general VWM (10, 11, 24, 25). VWM has

long been thought to be involved in sentence processing on the grounds that processing difficulty is well modeled by the memory cost (9, 11, 30). Specifically, this hypothesis can explain why center-embedded sentences are difficult to process (30). However, there is considerable debate about the psycholinguistic and neuroanatomical details of this hypothesis (8–11, 13, 16, 24–27, 30–36). Linking the subject nouns to the corresponding verbs in the processing of center-embedding sentences can be truly demanding, because of possible interferences between the multiple nouns (S_1, S_2, S_3 in Fig. 1) and verbs (V_1, V_2, V_3 in Fig. 1) (33–35). The present data indicate that the cost of keeping track of multiple relations between nouns and verbs in multiply center-embedded structures cannot be accounted for by the distance between dependent items alone; rather it is due to the hierarchical structure, where syntactic computation is indispensable.

The activation in the LIFS extending into the dorsal bank of the left pars triangularis is revealed by the main effect of DISTANCE in the present study. There is considerable variation in the anatomical details, but the entire left pars triangularis has been reported to react to the processing of sentences [for a review, see (37)]. The present data suggest that only the most dorsal part of the left pars triangularis is recruited for the processing of sentences with high demands on memory. Further research is needed to elucidate the essential role of the pars triangularis in sentence processing.

Functional Coupling and Structural Connectivity Between the LPO and LIFS.

The present study demonstrated that the LPO and LIFS are functionally distinct brain regions, but are functionally coupled and neuroanatomically interconnected. The PPI analysis, applied for the first time with data from a sentence processing paradigm, revealed a significant increase in coupling between the LPO and LIFS in hierarchical conditions relative to linear conditions. These results suggest that the 2 functionally distinct subregions in the LIFG work in tandem for the processing of center-embedded sentences that have both hierarchical structures and long distance dependency. DTI data provide supporting evidence of the anatomical connection between the LPO and LIFS. It should be noted that PPI results and DTI data complement each other: PPI analysis reveals which regions have increased connectivity in a given task/context regardless of the anatomical connectivity, whereas DTI data can provide information about the anatomical connections between regions.

Functional and neuroanatomical connections were shown, but the functional relationship between the LPO and LIFS is yet to be clarified. Our speculation is as follows. Syntactic computation may have a capacity limit on the distance over which information has to be held and also on the number of items of the same word category (26, 33–35). To cope with this limitation, the syntactic computational unit may require additional memory resources provided by the LIFS to deal with the partial products of parsing of doubly embedded sentences. Indeed, a recent voxel-based morphometry study found that gray-matter volume reduction in the LIFS correlates with a deterioration in the comprehension of center-embedded sentences (38).

In conclusion, functional and structural data provide direct evidence for functional segregation of the core syntactic computation and non-syntactic VWM, with the former being located in the LPO and the latter being located in the LIFS, but, moreover, for a functional and structural connection between these brain regions.

Methods

Participants. Eighteen young, right-handed, healthy subjects were examined (9 females). All of the participants were native German speakers. Handedness

was assessed with the Edinburgh Inventory (39) (females: mean 96.7, range 80–100, males: mean 97.7, range 89–100). The mean age was 24.6 years old, and the range was 21–27 years old for females and 23.9 and for males (range 21–30). All had no history of neurological disorders. Because of the high cognitive demand of the processing of the doubly center-embedded sentences, we recruited participants who had a high reading span (> 4.5, mean 4.7 for both females and males) measured by a German version of the Daneman and Carpenter reading span test (19). The experimental procedures were approved by the Research Ethics Committees of the University of Leipzig. Written informed consents were given by all subjects.

Experimental Design. Stimuli. The experiment comprised of four conditions derived from a 2×2 factorial design with factors STRUCTURE (hierarchical/linear) and DISTANCE (long/short) (Fig. 1). The sentences always started with the same lead-in phrase [i.e., “Peter wusste, dass (Peter knew that)”]. This was followed by complement clauses that were constructed with 10 words for every condition. All of the grammatical subjects that appeared in the complement clauses were humans. Conditions A and B had hierarchical structures that could be derived from and accepted by PSG but not FSG. In contrast, the complement clauses in Conditions C and D had linear structures, for which FSG sufficed. The distance was defined as the number of the words placed between the main subject and the verb of the complement clause. Conditions A and C were with a long distance, with 8 words between the main subject and the verb, and Conditions B and D had a short distance (4 words).

In Condition A, the complement clauses were in a doubly center-embedded construction with two nested subject relative clauses. The main subject and the verb were placed at the most outward positions with 8 words between them. In condition B, the complement clauses were in a singly nested construction with a subject relative clause. The main subject and the verb were positioned at the first and sixth position from the beginning of the complement clause, thus leaving 4 words between them, and another 4 words following the main verb. In Conditions C and D, the complement clauses had only 1 subject and 1 verb without any relativized construction. We introduced a filler condition that consisted of sentences with 2 verbs and 4 commas without any hierarchical structure (e.g., “Peter wusste, dass Antje telefonierte und gesunde, reichhaltige, vegetarische, salzige, heiÙe Suppe kochte.” Peter knew that Antje phoned and cooked healthy, rich, vegetarian, salty hot soup.) Condition A had 4 commas, which might be salient compared to other conditions (2 commas in condition B and no commas in C and D). The filler condition was intended to preventing the frequent commas from signaling the doubly nested construction, thereby foiling the participants’ special cognitive strategy to process the construction.

Stimuli Presentation. The stimuli presentation was programmed with Presentation 10.3 software (Neurobehavioral Systems, Inc.) on a Windows PC. Stimuli were projected through an LCD projector (PLC-XP50L, SANYO) onto the back of a screen. Subjects viewed the images on the screen above their heads through a mirror attached to the head-coil. A stabilization cushion was laid under and to the sides of the head to reduce head motion.

Procedure. An event-related design was adopted and the sentences in the 5 conditions (4 main conditions and 1 filler condition) were presented in pseudorandom order. In a trial, a fixed phrase “Peter wusste, dass” (Peter knew that) and 10 words were visually presented one by one with a duration of 500 ms for each word and inter-word-interval of 100 ms, so that 1 sentence was presented with 11 frames in 6.5 s. The beginnings of the presentation of the first phrase “Peter wusste, dass” were jittered against the scanning with 0 and 800 ms. Mean sentence onset asynchrony was 11.2 s. Forty-six distinct sentences per condition were given, resulting in a total of 230 trials that were performed in 2 sessions lasting a total of approximately 40 min. In 20% of the trials, short sentences to measure the participants’ comprehension followed 100 ms after the completion of the final word of the sentence and remained on the screen for 3 s in each condition (including the Condition F). Half of the short sentences restated part of the content of the sentence presented previously. Sentences were constructed with 1 subject and the predicate of the correct combination. The other half were similarly made with 1 subject and a predicate, but with sentential elements that did not correspond, resulting in the sentence having a different meaning than the one previously shown. For example, we swapped the subject and the object,

replaced an adverbial, and recombined a subject and a predicate. The questions were delivered in a pseudorandom manner to foil the participants’ anticipation, thus ensuring they had to understand all of the sentences presented. The participants were requested to judge whether the short sentence expressed the same content or not and to report it as soon as possible by pressing MRI-compatible response buttons using the index and the middle finger of either hand. Half of the participants used their left hand to press the buttons, and the other half used the right.

Image Acquisition. See *SI Methods*.

Analysis. Behavioral Data. Mean reaction times (RTs) and accuracy rates were calculated for each condition of each subject and were analyzed using a 2-way within-subject ANOVAs with factors STRUCTURE and DISTANCE.

Imaging data. Preprocessing of structural and functional MRI data. The first 5 volumes of each fMRI session were discarded to eliminate magnetic saturation effects, resulting in a total of 806 volumes per session that were used. The data analysis was carried out using SPM5 (available at <http://www.fil.ion.ucl.ac.uk/spm/>) on a PC workstation. Structural images were corrected for signal intensity bias due to the magnetic field inhomogeneity using the bias correction tool in SPM5. As a preprocessing step, the EPI images were realigned to the first image and then the difference in the slice acquisition time was corrected. EPI images were coregistered to the subjects’ T1 then to 3D high resolution structural images. Normalizing an individual structural image to the SPM5 T1 brain template was processed in 2 steps: 1) estimation of the normalization parameters and 2) writing the normalized images with the parameters. This parameter transformed the structural images and all of the EPI volumes into a common stereotaxic space to allow multisubject analyses. The EPI images were resampled into $3 \times 3 \times 3$ mm³ voxels and the structural images into $1 \times 1 \times 1$ mm³ voxels with the seventh degree B-spline interpolation.

Within-subject ANOVA. At the first level, individual analyses were performed. All of the functional volumes were smoothed with a 6-mm full width at half-maximum isotropic Gaussian kernel before the statistical calculation to improve the signal-to-noise ratio and to compensate for the anatomical variability among individual brains. Each subject’s hemodynamic responses induced by the trials were modeled with a box-car function with the duration of 6.5 s or 9.5 s (trials with comprehension task) and convolved with a hemodynamic function that reaches the peak 6 s after the stimuli onset. The functional data during the trial with comprehension question were modeled as distinct conditions and were not mixed with the main conditions. The global mean intensity of each session was normalized to 100. Confounds by global signal changes were removed by applying a high pass filter with a cut-off cycle of 128 s. Signal increase relative to the baseline in each condition of each participant was estimated according to the general linear model. The resulting individual contrast images were submitted to the second level (group) analysis, the 2-way within-subject ANOVA with correction for the nonsphericity. Main effects and interactions were tested with the linear contrasts (*t* tests, instead of *F* tests). Since we had specific hypotheses on the activities in the posterior LIFG, the statistical inferences for activation in this region were drawn with the search volume confined to the posterior LIFG. The volume of interest for the posterior LIFG was build with a cytoarchitectonic map. The cytoarchitectonic map is a digitized 3-dimensional population map of cytoarchitectonic areas created with 10 postmortem human brains in which borders of areas were determined by statistically significant changes in laminar density patterns of neuronal cell bodies (40–42). We truncated a population map of area 44 and 45 of the left hemisphere at 30% and created a mask image by combining the 2 volumes. (Fig. S2). Statistical inferences were drawn at $P < 0.05$ (corrected for LIFG VOI) at cluster level: the statistical maps (SPM{T}) were thresholded at $P < 0.01$ (not corrected), and then thresholded by the cluster size.

See *SI Methods* for PPI analysis and anatomical connectivity analysis.

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- Chomsky N (1956) Three models for the description of language. *IEEE Trans Inf Theory* 2:113–124.
- Fitch WT, Hauser MD (2004) Computational constraints on syntactic processing in a nonhuman primate. *Science* 303:377–380.
- Gentner TQ, Fenn KM, Margoliash D, Nusbaum HC (2006) Recursive syntactic pattern learning by songbirds. *Nature* 440:1204–1207.
- 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.

- 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.
- Bahlmann J, Schubotz RI, Friederici AD (2008) Hierarchical artificial grammar processing engages Broca’s area. *Neuroimage* 42:525–534.
- Fiebach CJ, Schlesewsky M, Friederici AD (2001) Syntactic working memory and the establishment of filler-gap dependencies: insights from ERPs and fMRI. *J Psycholinguist Res* 30:321–338.

8. Fiebach CJ, Schlesewsky M, Lohmann G, von Cramon DY, Friederici AD (2005) Revisiting the role of Broca's area in sentence processing: Syntactic integration versus syntactic working memory. *Hum Brain Mapp* 24:79–91.
9. Just MA, Carpenter PA (1992) A capacity theory of comprehension: Individual differences in working memory. *Psychol Rev* 99:122–149.
10. Waters GS, Caplan D (1992) The capacity theory of sentence comprehension: critique of Just and Carpenter (1996). *Psychol Rev* 103:761–772.
11. Caplan D, Waters GS (1999) Verbal working memory and sentence comprehension. *Behav Brain Sci* 22:77–94; discussion 95–126.
12. 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.
13. Fiebach CJ, Vos SH, Friederici AD (2004) Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers. *J Cogn Neurosci* 16:1562–1575.
14. 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.
15. Hashimoto R, Sakai KL (2002) Specialization in the left prefrontal cortex for sentence comprehension. *Neuron* 35:589–597.
16. Waters G, Caplan D, Alpert N, Stanczak L (2003) Individual differences in rCBF correlates of syntactic processing in sentence comprehension: Effects of working memory and speed of processing. *Neuroimage* 19:101–112.
17. 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.
18. Smith EE, Jonides J (1998) Neuroimaging analyses of human working memory. *Proc Natl Acad Sci USA* 95:12061–12068.
19. Daneman M, Carpenter PA (1980) Individual difference in verbal working memory and Reading. *J Verbal Learn Verbal Behav* 19:450–466.
20. King JW, Kutas M (1995) Who did what and when - using word-level and clause-level ERPs to monitor working-memory usage in reading. *J Cogn Neurosci* 7:376–395.
21. Vos SH, Gunter TC, Kolk HH, Mulder G (2001) Working memory constraints on syntactic processing: An electrophysiological investigation. *Psychophysiology* 38:41–63.
22. Friston KJ, et al. (1997) Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6:218–229.
23. Friederici AD (2004) Processing local transitions versus long-distance syntactic hierarchies. *Trends Cogn Sci* 8:245–247.
24. Waters GS, Caplan D (2004) Verbal working memory and on-line syntactic processing: Evidence from self-paced listening. *Q J Exp Psychol A* 57:129–163.
25. Fedorenko E, Gibson E, Rohde D (2006) The nature of working memory capacity in sentence comprehension: Evidence against domain-specific working memory resources. *J Mem Lang* 54:541–553.
26. Gordon PC, Hendrick R, Levine WH (2002) Memory-load interference in syntactic processing. *Psychol Sci* 13:425–430.
27. Van Dyke JA, McElree B (2006) Retrieval interference in sentence comprehension. *J Mem Lang* 55:157–166.
28. Perruchet P, Rey A (2005) Does the mastery of center-embedded linguistic structures distinguish humans from nonhuman primates? *Psychon Bull Rev* 12:307–313.
29. de Vries MH, Monaghan P, Knecht S, Zwitserlood P (2008) Syntactic structure and artificial grammar learning: The learnability of embedded hierarchical structures. *Cognition* 107:763–774.
30. Gibson E (1998) Linguistic complexity: Locality of syntactic dependencies. *Cognition* 68:1–76.
31. McElree B, Foraker S, Dyer L (2003) Memory structures that subserve sentence comprehension. *J Mem Lang* 48:67–91.
32. Grodzinsky Y, Santi A (2008) The battle for Broca's region. *Trends Cogn Sci* 12:474–480.
33. Lewis RL, Vasishth S, Van Dyke JA (2006) Computational principles of working memory in sentence comprehension. *Trends Cogn Sci* 10:447–454.
34. Miller GA, Chomsky N (1963) Finitary models of language users. *Handbook of mathematical psychology*, eds Luce RD, Bush RR, Galanter E (Wiley, New York), pp 419–491.
35. Lewis RL (1996) Interference in short-term memory: The magical number two (or three) in sentence processing. *J Psycholinguist Res* 25:93–115.
36. Santi A, Grodzinsky Y (2007) Working memory and syntax interact in Broca's area. *Neuroimage* 37:8–17.
37. Vigneau M, et al. (2006) Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *Neuroimage* 30:1414–1432.
38. Amici S, et al. (2007) Anatomical correlates of sentence comprehension and verbal working memory in neurodegenerative disease. *J Neurosci* 27:6282–6290.
39. Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
40. Roland PE, Zilles K (1998) Structural divisions and functional fields in the human cerebral cortex. *Brain Res Brain Res Rev* 26:87–105.
41. Amunts K, et al. (1999) Broca's region revisited: Cytoarchitecture and intersubject variability. *J Comp Neurol* 412:319–341.
42. Eickhoff SB, et al. (2005) A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage* 25:1325–1335.