The Neural Basis of Recursion and Complex Syntactic Hierarchy

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Language is a faculty specific to humans. It is characterized by hierarchical, recursive structures. The processing of hierarchically complex sentences is known to recruit Broca's area. Comparisons across brain imaging studies investigating similar hierarchical structures in different domains revealed that complex hierarchical structures that mimic those of natural languages mainly activate Broca's area, that is, left Brodmann area (BA) 44/45, whereas hierarchically structured mathematical formulae, moreover, strongly recruit more anteriorly located region BA 47. The present results call for a model of the prefrontal cortex assuming two systems of processing complex hierarchy: one system determined by cognitive control for which the posterior-to-anterior gradient applies active in the case of processing hierarchically structured mathematical formulae, and one system which is confined to the posterior parts of the prefrontal cortex processing complex syntactic hierarchies in language efficiently.

Keywords: Broca's area; hierarchy; recursion

1. Introduction

In the long-standing discussion of what it means to be human, language has always been considered a major component. Recently, the debate has clustered around the question to what extent recursion can be considered as the crucial part of language distinguishing human language from other communicative systems (Hauser *et al.* 2002, Jackendoff & Pinker 2005).

In the context of this discussion, a number of empirical studies on grammar processing have been conducted both in humans and non-human animals. A number of these have used very similar grammar types inviting a comparison between the different animals and cognitive domains. One of the studies directly compared grammar learning in humans and non-human primates, that is, cotton-top tamarins, and reported that non-human primates can learn a simple probabi-

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listic grammar $(AB)^n$, called Finite State Grammar, but not a more complex grammar A^nB^n, called Phrase Structure Grammar.

The recursive structure A^nB^n is derived from the two rewriting rules below.

(1) a. Rule 1 S → AB
    b. Rule 2 S → ASB (a rule for recursion),
    where S is a non-terminal symbol, and A and B are terminal symbols.

A^nB^n is derived for example as in (2):

(2) S → (with rule 1) ASB → (with rule 2) AASBB → … (repeating the rule 2) … → $A^{n-1}SB^{n-1}$ → (with rule 1) A^nB^n

Humans instead easily learned both types of grammar after short training periods (Fitch & Hauser 2004). Interestingly, songbirds were also shown to be able to learn both grammar types, but only after extensive training (Gentner *et al.* 2006). This finding suggests that different species may used different brain systems to solve the same task. The A^nB^n grammar used in these two studies was not declared to be a test for recursion, but it has been taken to be so by some scientists (Perruchet & Rey 2005, Gentner *et al.* 2006). A recent paper, tries to clarify this issue by defining the term 'recursion' as a rule "which has the property of self-embedding, that is, in which the same phrase type appears on both sides of a phrase structure rewrite rule" (Fitch 2010: 78)

When considering the biological basis of recursion, one has to take this definition into account. Thus it appears that whether an A^nB^n grammar is recursive depends on the underlying structure. An A^nB^n grammar could be described as recursive, but does not have to. Fitch (2010) discusses that in the latter case, the assumed processing mechanism, however, must go beyond a finite-state grammar process as it requires "some additional memory mechanism(s) to keep track of 'n'" (p. 87). We will keep this in mind when reporting some recent neuroimaging studies in humans which have tried to evaluate the neural basis of processing different types of grammar, including embedded structures which unambiguously qualify as a test for recursion. These studies used similar syntactic structures in artificial grammar, natural language and non-language domains.

2. Finite-State vs. Phrase Structure Grammar

In the first neuroimaging experiment referred to here (Friederici *et al.* 2006a), we investigated the neural basis of grammar processing in humans for the two types of grammar originally used in the behavioural study by Fitch & Hauser (2004) with human and non-human primates, namely an A^nB^n and an $(AB)^n$ grammar (see Figure 1).

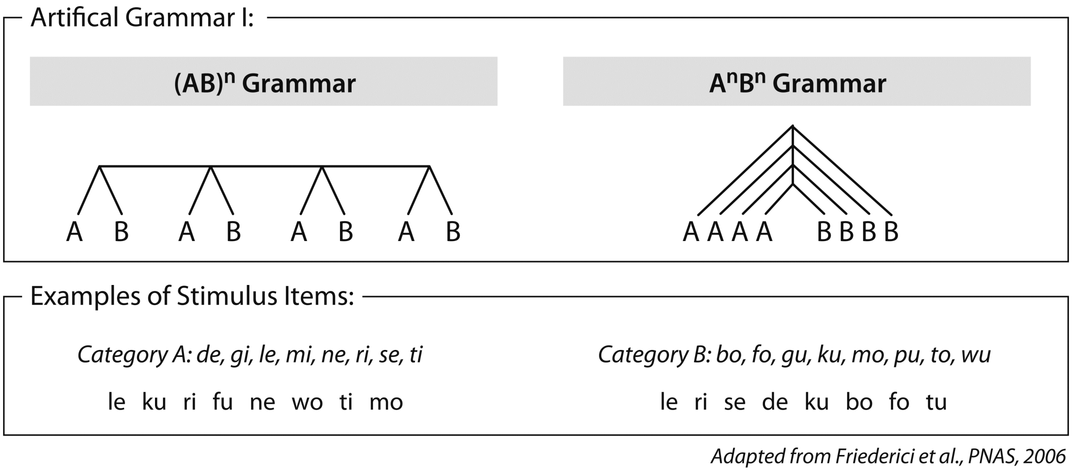


Figure 1: Processing hierarchy in Artificial Grammar I. Structure of sequences is given in the upper row. Category A syllables and Category B syllables used in the sequences as well as examples of an $(AB)^n$ sequence (left) and an A^nB^n sequence (right) are given in the lower row.

In this functional magnetic resonance imaging (fMRI) experiment, category membership was coded by a particular combination of consonants and vowels, and not by pitch information as it was done in the original experiment. Stimulus sequences were presented visually syllable-by-syllable (for details see Friederici *et al*. 2006a). The two grammars were learned by different groups of participants to prevent possible confusion between the two grammars in the participants. During learning, feedback was given. Learning took place two days before scanning.

In the scanning session, grammatically correct and incorrect sequences were presented. The two grammar types led to different activation patterns. The comparison of incorrect versus correct sequences led to activation in the frontal operculum for the $(AB)^n$ grammar, whereas the comparison of incorrect versus correct sequences for the A^nB^n grammar revealed activation in Broca's area (BA 44) in addition to activation in the frontal operculum. This difference was considered interesting in its own right, but, moreover, to be of special phylogenetic importance, since the frontal operculum is considered a phylogenetically older cortex than the more laterally located Broca's area (Sanides 1962).

Thus, it appears that the processing of the more complex artificial grammar with the A^nB^n structure recruits the phylogenetically younger cortex, namely Broca's area stronger than the processing of the less complex grammar. Broca's area is known to support syntactic processes in natural language comprehension as evidenced in several studies across different languages (for reviews, see Friederici 2004, Grodzinksy & Friederici 2006, Vigneau *et al.* 2006). The sentences used in the different studies reviewed in these articles include a broad variety of complex syntactic structures such as cleft sentences, passive sentences, scrambled sentences and others, thereby suggesting that Broca's area is involved in the processing of complex hierarchically structured sequences.

From the data reported in Friederici *et al.* (2006a), however, it is not clear whether participants in this experiment did reconstruct a hierarchical embedded structure while processing the A^nB^n sequences, or whether the A^nB^n sequences were processed by a simple counting mechanism. For example, counting the number of A elements which then have to be followed by the same number of B elements. Such a mechanism has been claimed to account for the successful processing of the sequences used by Fitch & Hauser (2004) and by Friederici *et al.* (2006a) (see Perruchet & Rey 2005, de Vries *et al.* 2008).

This point is well taken, but given the available literature on syntactic processing which systematically shows an involvement of Broca's area, the observed activation in Broca's area in the present fMRI experiment may suggest that participants did build a hierarchical structure on the basis of which the violation was detected. But this had to be shown in an additional experiment. Moreover, it had to be considered, that the activation in Broca's area could be due to memory processes which are more demanding for the processing of A^nB^n sequences than for the $(AB)^n$ sequences used in this study, since the A and B elements were always adjacent in the latter sequences, but not in the former. These open issues were addressed in two subsequent experiments.

3. Processing Syntactic Hierarchy

In order to answer the question about the nature of the underlying processes when dealing with $(AB)^n$ structures, a second fMRI experiment (Bahlmann *et al.* 2008) was conducted in which the sequences were build such that hierarchical processing for the A^nB^n structures was induced, e.g., $[A_1[A_2[A_3\ B_3]B_2]B_1]$. Each subcategory (e.g., A_1, A_2, etc.) had more than one member to prevent item-based learning. The crucial relations between the dependent elements in the structure were coded by phonological parameters of the respective syllables (see Figure 2).

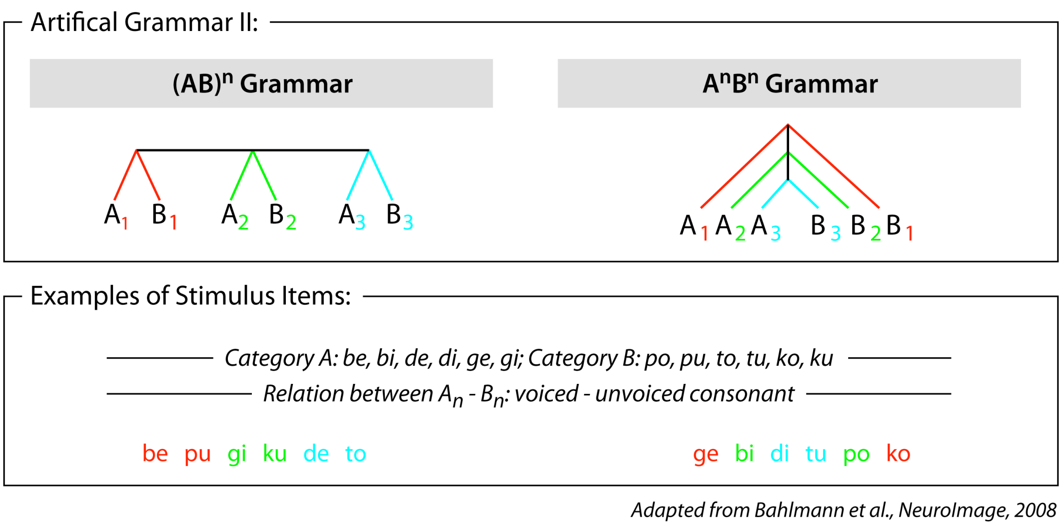


Figure 2: Processing hierarchy in Artificial Grammar II. Structure of sequences is given in the upper row. Category A syllables and Category B syllables used in the sequences as well as examples of an $(AB)^n$ sequence (left) and an A^nB^n sequence (right) are given in the lower row. Each subcategory (i.e. A_1, A_2, etc.) comprised two syllables. Note that the relation between A^n–B^n is defined by the voice-unvoiced dimension of the consonant of the respective syllable.

In this experiment, both grammar types were learned by the same participants to allow a direct comparison of the two grammar types in a within-subject design. This also enabled us to conduct analyses for the correct sequences only in order to evaluate to what extent the observed activations are triggered by grammar processing rather than by the detection grammatical incorrectness.

The direct comparison of brain activation for the two grammar types indicated activation of Broca's area (BA 44), both when collapsed over incorrect and correct sequences, and also when comparing only the correct sequences of the two grammar types (see Table 1 and Figure 4, below). This finding was taken to indicate that the processing of complex hierarchical structures in an artificial grammar involves Broca's area. The result provides support for the interpretation that the processing of the A^nB^n structures in the experiment by Friederici *et al.* (2006a) reported above was based on hierarchy building rather than on counting plus memory processes needed to keep track of 'n'.

4. Syntactic Hierarchy and Working Memory

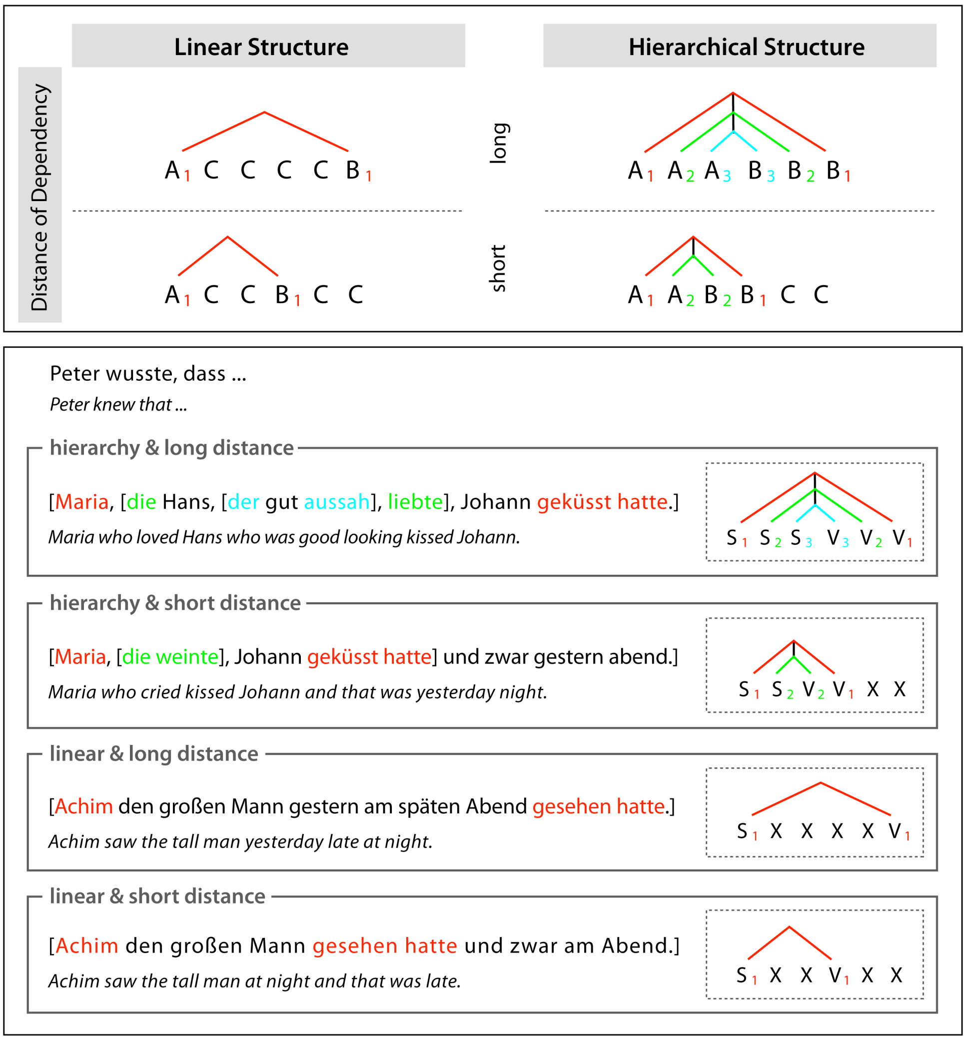
As a second open issue in the interpretation of our initial results, was the question to what extent the observed brain activation was due to working memory involved in the processing of embedded structures, rather than to the syntactic structures as such.

This question is of particular relevance since verbal working memory is known to activate the ventrolateral prefrontal cortex including Broca's area (Jonides *et al.* 1998, Smith & Jonides 1998, 1999), and since it has been claimed that working memory and syntax interact in Broca's area when syntactically complex sentences are processed (Cooke *et al*. 2001, Santi & Grodzinksy 2007). And indeed working memory needs to be considered, as the $(AB)^n$ and the A^nB^n structure sequences tested here not only differ in their underlying structure, but moreover in the distance between the dependent A-elements and B-elements. In the studies reported so far the $(AB)^n$ structure, the distance was always short, since A and B are adjacent, whereas this was not the case for the A^nB^n structure sequences. Thus, the issue of a possible involvement of memory processes is still unresolved by the prior experiments.

In a further fMRI study (Makuuchi *et al*. 2009, Friederici *et al.* 2009), we investigated to what extent activation in Broca's area is a response to processes of syntactic hierarchy or to working memory. Moreover, we wanted to see to what extent the brain activation pattern observed for artificial grammar processing generalizes to natural language.

The study used German as the testing ground as it allows the construction of sentences with multiple embeddings similar to the previous artificial grammar experiment, e.g., $[A_1[A_2[A_3\ B_3]B_2]B_1]$ in the form of subject–verb dependencies, e.g., $[S_1[S_2[S_3\ V_3]V_2]V_1]$ (Figure 3). In order to disentangle the possible confound of the factor syntactic hierarchy and the working memory resources required when dealing with long distance dependencies (e.g., A_3–B_3), we designed a sentence reading study in a 2x2 factorial design, with the factors *syntactic hierarchy* (number of embeddings) and *verbal working memory* (distance of dependent elements).

(a) Experimental design & Examples of Stimulus Items



Adapted from Makuuchi et al., PNAS, 2009

(b) Tree structure of Stimulus Item (hierarchy & long distance)

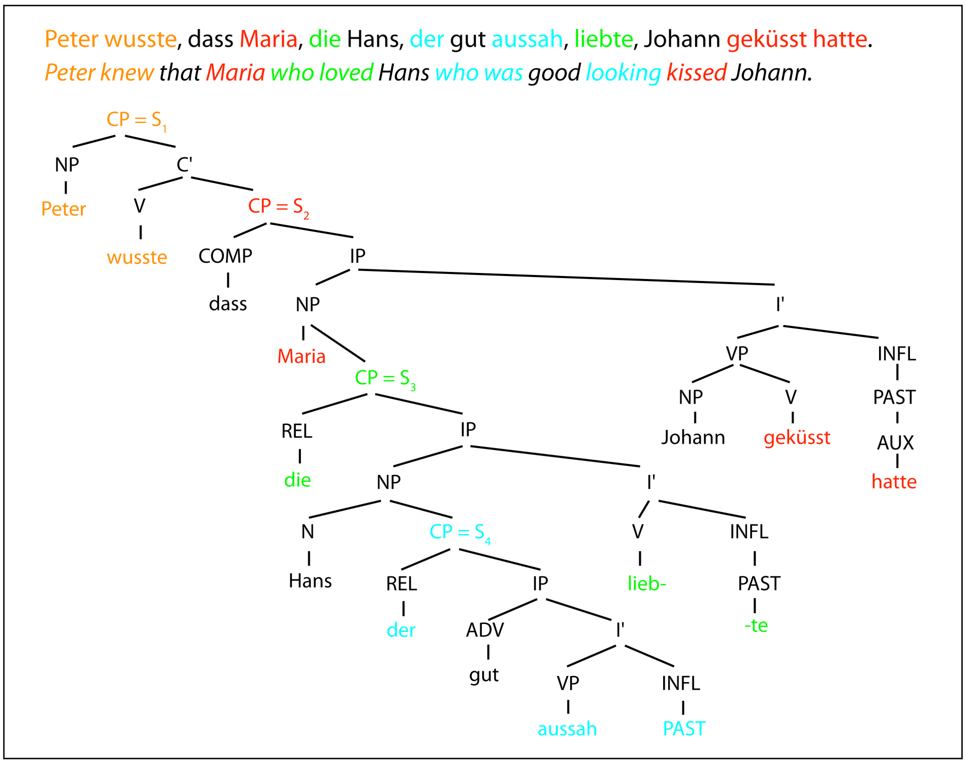


Figure 3:
(a) *Processing hierarchy in Natural Grammar. Top: Schematic view of the different conditions. Bottom: Examples of stimulus items for each condition and schematic view of relation between subjects (S) and verbs (V) of (embedded) sentences. "Linear" stands for "no embedding". Dependent items are color-coded (red, green, blue).*
(b) *The linguistic description of a sentence used in the natural grammar study (Makuuchi* et al. *2009). This sentence represents the most complex condition (Hierarchical Structure, long-distance dependency; compare Figure 2).*
Key: ADV = adverb, AUX = auxiliary, C = clause, COMP = complementizer, INFL = inflection, IP = inflectional phrase, N = noun, NP = noun phrase, PAST = past tense, REL = relative pronoun, S = sentence, V = verb, VP = verb phrase.

Syntactic hierarchy, as defined by the number of embeddings, activated Broca's area in the inferior frontal gyrus (IFG). In addition, the left superior temporal gyrus (STG) and the superior temporal sulci (STS) are also activated, indicating that these regions are part of the language network (Friederici *et al.* 2009). A region of interest analysis of the IFG (Makuuchi *et al.* 2009) revealed that the main effect of hierarchy was located in BA 44 as defined cytoarchitechtonically according to Amunts *et al*. (1999). In contrast, working memory operationalized by the factor distance between the dependent elements activated the left inferior frontal sulcus located dorsally to Broca's area (see Table 1 and Figure 4). A functional connectivity analysis revealed that these two areas strongly interact during processing multiple embedded sentences.

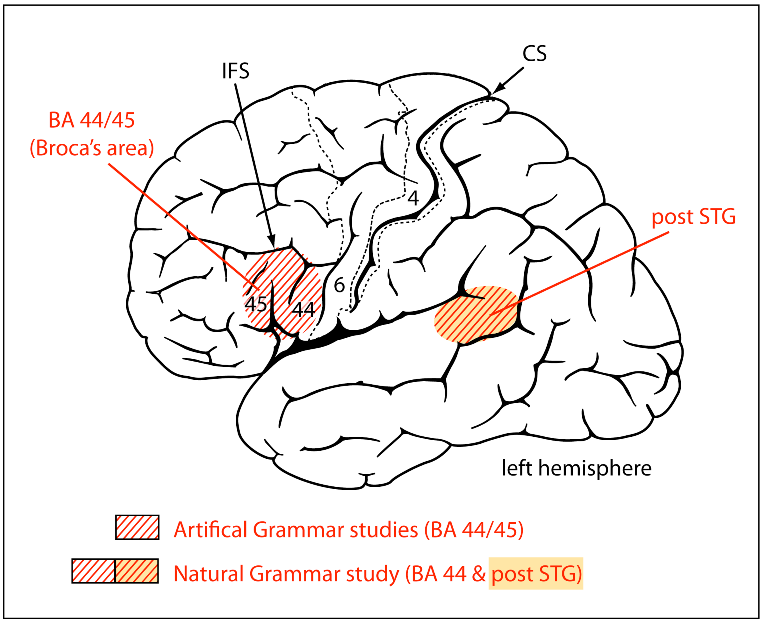


Figure 4: Schematic view of activation pattern for the main effect of hierarchy in the language domain. For Artificial Grammar I and II, the main effect of hierarchy was found in Broca's area (BA 44/45) (Friederici et al. *2006, Bahlmann* et al. *2008). For the natural grammar, the main effect of hierarchy was located in BA 44 (Makuuchi* et al. *2009) and in the posterior superior temporal gyrus (pSTG) extending into the superior temporal sulcus (Friederici* et al. *2009).*
Key: BA = Brodmann Area; CS central sulcus; IFS = inferior frontal sulcus; STG = superior temporal gyrus.

This locus of activation in Broca's area for the embedded structures coincides with the view that Broca's area supports the processing of syntax in general (Grodzinsky & Friederici 2006). Most recently, a subdivision of syntactic computations within Broca's area for complex syntactic structures has been demonstrated with BA 44 activated for center-embedding and for sentences involving movement, and BA 45 selectively adapted to movement (Santi & Grodzinksy 2010). This finding is in line with the results reported by Makuuchi *et al.* (2009) for embedding and by Santi & Grodzinsky (2007) for movement.[1]

In the study by Makuuchi *et al.* (2009), working memory was neurally segregated from processing of center-embedding. The latter recruited BA 44, whereas working memory necessary to bind the respective A and B elements during processing recruited the inferior frontal sulcus located dorsally to Broca's area. This is in line with studies that report phonological processes and phonologically-based working memory processes to activate "the dorsal aspect of the inferior frontal gyrus near the inferior frontal sulcus" (Poldrack *et al*. 1999; see also Vigneau *et al.* 2006).

Thus, the activation data reported here point towards a functional subdivision in the inferior frontal cortex with respect to different computational subcomponents necessary to deal with syntactically complex recursive structures.

5. Processing Complex Hierarchy in a Non-Language Domain I: Visual-Spatial Event Sequences

When considering Broca's area as a brain region supporting the processing of complex structural hierarchies, the question arises whether this function is domain-specific or not. A direct way to approach this question is to investigate the processing of a hierarchical structure which matches that of the artificial grammars on syllable processing in a non-language domain.

We therefore conducted an fMRI study on the processing of hierarchical structures in a non-language domain (Bahlmann *et al*. 2009) using sequence structures just like those in the prior language studies. Category A and B elements were abstract visual stimuli whose membership was indicated by shape and texture. The dependency between A and B elements was encoded by rotation of the respective nonsense shape (see Figure 5).

[1] Note, that the statement that Broca's area supports the processing of complex hierarchical structures does not speak against the claim that Broca's area may also subserve the processing of non-hierarchical sequences (Petersson *et al.* 2010). Except for the first study reviewed here all findings stem from a direct comparison between a complex hierarchical condition with a condition which involves a dependency between adjacent elements. Thus Broca's area is shown to increase its activity as a function of increasing hierarchical complexity.

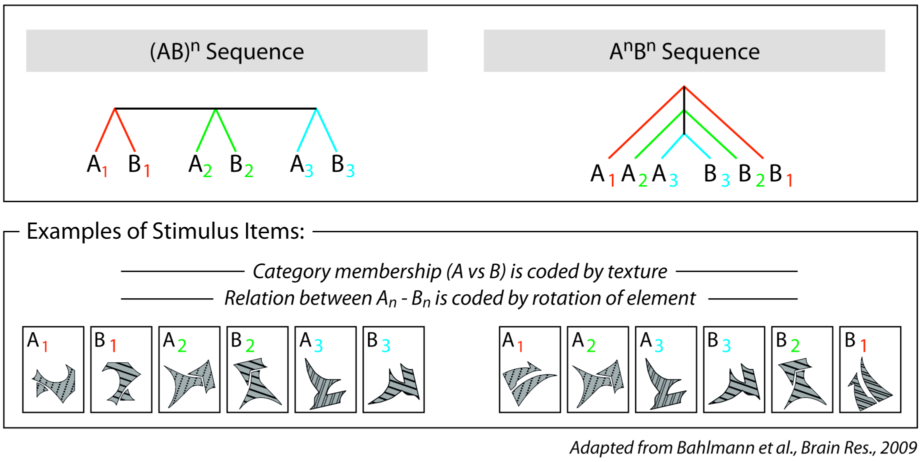


Figure 5: Processing of hierarchy in visuo-spatial event sequences. Top: Schematic view of the two structures. Bottom: Examples of stimuli. The relation between dependent elements is defined by rotation (B item has the identical shape as A item, but is spatially rotated). Dependency is color-coded (red, green, blue).

Processing of visual event-sequences in general (adjacent and hierarchical dependencies) activated the bilateral parietal lobe. A main effect of hierarchy was found for a whole brain analysis in the left pre-central gyrus (BA 6), the right pre-supplementary motor area and the right caudate. A hypothesis-driven region of interest analysis in BA 44 defined by a cytoarchitectonic probability map of area 44 (Amunts *et al.* 1999), however, revealed an increase of activation in BA 44 as a function of structural hierarchy (see Table 1 below and Figure 5 above). These data suggest that parts of the parietal cortex and pre-SMA together with BA 6 and BA 44 constitute the processing network for structured visual event sequences, and that BA 44/6 are involved when processing hierarchical dependencies.

From the present experiment in conjunction with those reported above, we may conclude that Broca's area receives its domain-specificity as a part of a particular neural network which differs from domain to domain. For example, Broca's area in a network together with the posterior superior temporal cortex subserves the processing of hierarchically complex natural language sentences, whereas Broca's area as part of a larger network involving the pre-motor cortex, the pre-SMA and parietal regions subserves the processing of non-linguistic visual-spatial event sequences.

The natural language experiment by Makuuchi *et al.* (2009) most directly indicates the BA 44 is part of the neural basis of linguistic recursion. The left posterior superior and middle temporal cortex seem to come into play when processing natural language sentences which require the assignment of thematic and semantic relations (Bornkessel *et al*. 2005, Snijders *et al*. 2009, Newman *et al*. 2010).

The present results for the non-language domain indicate that the view that Broca's area supports the processing of syntactic hierarchy in language does not preclude the involvement of Broca's area in other processing domains, be it the processing of visual-event sequences (Bahlmann *et al*. 2009), the processing of action sequences (e.g., Pulvermüller & Fadiga 2010), the processing of abstract action rules (e.g., Badre *et al.* 2010), or the processing of hierarchically ordered control signals (e.g., Koechlin & Summerfield 2007). In these cases, however, Broca's area is part of a different neural network than the one observed for language processing. The view that Broca's area receives its specificity for syntactic processes as part of a specific network has previously been discussed in the literature (Friederici 2002, Marcus *et al.* 2003, Friederici 2006, Petersson *et al.* 2010).

6. Processing Complex Hierarchy in a Non-Language Domain II: Mathematical Formulae

Before a general conclusion with respect to the relation between Broca's area and the processing of complex structural hierarchy can be drawn, consideration needs to be given to whether the assumed relation also hold for hierarchies that do not mimic as the embedded structure used in the previous study. It has been proposed that recursion as assumed for language might also underlie mathematics and the processing of mathematical formulae (Hauser *et al.* 2002, Fitch 2010).

The goal of the next experiment was to see whether Broca's area is involved in the processing of structural hierarchy in mathematical formulae (Friedrich & Friederici 2009). There is no doubt that in mathematics, a person familiar with the respective rules can make grammaticality judgements such as evaluating the correctness of a recursive structure. This experiment was, therefore, conducted with experts in mathematics. The formulae used in this experiment had either a hierarchical structure or a "linear" structure (see Figure 6). The hierarchical structure of these formulae was not primarily determined by embeddedness, but by the number of levels in the tree structure.

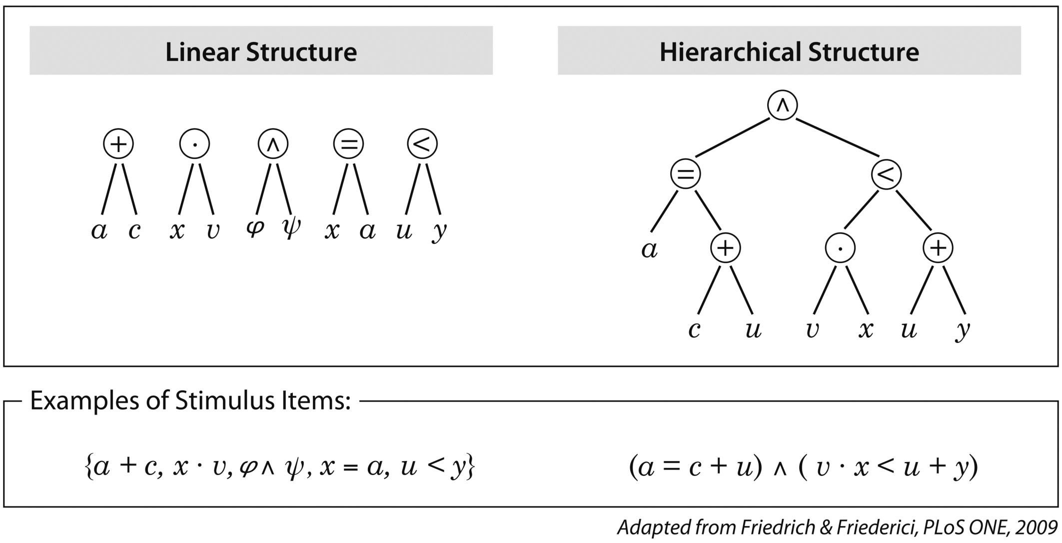


Figure 6: Processing of mathematical formulae. Top: Schematic view of the two structures. Nodes (circled) indicate the operator. Bottom: Examples of stimulus items.

It should be noted that hierarchy in mathematical formulae tends to differ from hierarchy in natural languages. Language structures are usually asymmetric whereas mathematical structures need not necessarily be so, as exemplified in Figures 3b and 6. While Figure 3b displays the linguistic description of a center-embedded sentence used in the natural language study (Makuuchi *et al*. 2009), Figure 6 shows the structure of mathematical formulae used in the mathematical study (Friedrich & Friederici 2009). Crucially, the nodes in the mathematical formulae (circled in Figure 6) contain an operator indicating the operation between the respective elements, i.e. = means 'equals', < means 'larger than', etc. These operators require that the two elements under the respective node must be put into a logical relation. This may require the activation of additional or even different brain regions than those observed in the processing of the hierarchical structures in the previous experiments.

The formulae used as stimuli in the mathematical study did not contain numbers, in order to abstract from the issue of numerosity and related number-based calculation processes. The formulae presented in the fMRI experiment were either correct or incorrect. Participants were students of mathematics and physics and were therefore highly familiar with mathematical formula processing. They were required to make judgements regarding the correctness of the visually presented formulae. Whole brain analysis of the brain imaging data for the processing of these mathematical formulae revealed a clear effect of hierarchy in left BA 47 bordering BA 45 and in parietal regions, as well as the right precuneus (see Table 1 below and Figure 7).

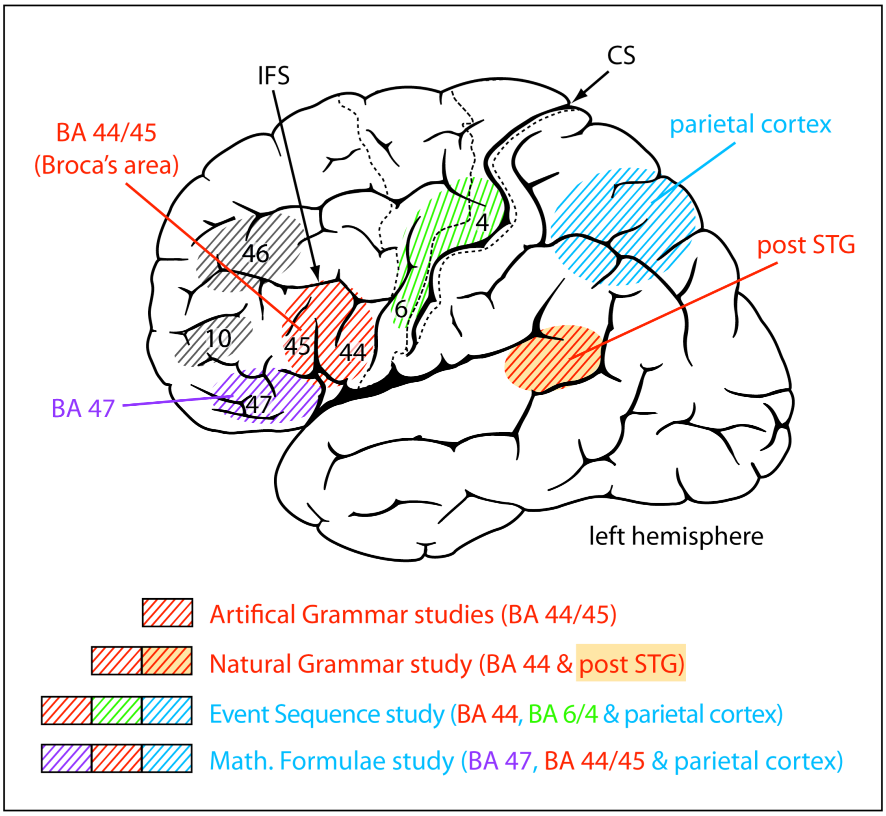


Figure 7: Schematic view of the activation pattern for the main effect of hierarchy in the language and non-language domains. For, explanation of activation for grammar studies, see Figure 4. For the visuo-spatial event sequence study, the main effect of hierarchy was found in the precentral gyrus (BA 6/4); a main effect of hierarchy in Broca's are (BA 44/45) was only found in a region of interest analysis (Bahlmann et al. *2009). For the mathematical formulae study, the main effect of hierarchy was found in BA 47 bordering BA 45 as well as in the medial frontal gyri (BA 10) and the most dorsal part of middle frontal gyrus (BA 6) (not depicted in the figure). In addition, a hierarchy effect was found in the parietal lobule bilaterally. For details, see Friedrich & Friederici (2009).*

Key: BA = Brodmann Area; CS central sulcus; IFS = inferior frontal sulcus; STG = superior temporal gyrus.

Given the previous analyses conducted by Bahlmann *et al.* (2009), which revealed an involvement of Broca's area for the processing of hierarchical structures in the visuo-spatial domain only in a region of interest analysis, we computed a similar analysis for the mathematical domain for the present article. This region of interest analysis for the voxels defined by the cytoarchitectonic probability map of area 44 by Amunts *et al.* (1999) revealed an effect of hierarchy for the correct formulae ($p< .05$) (see Table 1 below). Thus, BA 44 partly supports the processing of hierarchy in mathematical formulae, although the crucial area which most strongly subserves this process in the prefrontal region is located more anteriorly, namely BA 47 bordering on BA 45.

The obvious difference between hierarchical structures used in the mathematical formulae processing study (Friedrich & Friederici 2009) and the embedded structures used in the other studies (Bahlmann *et al*. 2008, 2009, Makuuchi *et al*. 2009) is that in the former, the nodes in the syntactic tree are operators calling for logical processes. Thus one of the crucial aspects in the comparison of hierarchically structured and linear mathematical formulae may be that for a successful judgment of the logical relations indicated by the operators, increased logical-semantic processes are necessary, recruiting BA 47 bordering on BA 45. This interpretation is in line with the view that BA 47 (and the anterior part of 45) mainly supports semantic processes, whereas the more posterior region, namely BA 44 (and the posterior part of BA 45) mainly subserves syntactic processes during language processing (see Bookheimer 2002, Friederici 2002, Hagoort 2005, Vigneau *et al*. 2006)[2].

In the context of cognitive control models of the prefrontal cortex (PFC), which assume a posterior-to-anterior gradient with a recruitment of more anterior portions of the PFC as hierarchies become more complex (for a recent review, see Botvinick 2008), the present data could make an interesting contribution.

7. Hierarchy in the Prefrontal Cortex

In order to see how far the present set of studies can be interpreted in the context of a general model of the PFC for the processing of hierarchies we compare the

[2] Note that a novel receptorarchitectonic study suggests a neuroanatomical subdivision of BA 45 into an anterior (area 45a) and a posterior (area 45p) part (Amunts *et al*. 2010). It seems likely that the receptorarchitectonic division of BA 45 is also functionally relevant.

different studies and the receptive activation in the PFC directly. Please note that the first Artificial Grammar Study I (Friederici *et al*. 2006a) is not included, as a direct test for the hierarchy effect was not possible due to the fact that the two grammar types (complex vs. simple) was a between-group factor. The other studies, with their location of the main effect of hierarchy, are listed in Table 1. The second artificial grammar study (Bahlmann *et al.* 2008) and the natural language study (Friederici *et al.* 2009, Makuuchi *et al*. 2009) revealed a main effect of hierarchy in BA 44. For the two non-language studies, a main effect of hierarchy in BA 44 was only seen in a ROI analysis. In the whole brain analysis for the visuo-spatial event sequences, a main effect of hierarchy was observed in the left precentral gyrus, the right pre-SMA and the right caudate, and for mathematical formulae in BA 47 and 45a.

Study	BA	X	Y	Z
Artificial Grammar II Bahlmann *et al.* (2009) WB	44	–46	5	16
Natural Grammar Friederici *et al.* (2009) WB	44	–45	6	21
Makuuchi *et al.* (2009) ROI BA 44	44	n.a.		
Visuo-spatial sequence Bahlmann *et al.* (2009) WB	6/4	–50	–8	33
ROI BA 44	44	n.a.		
Mathematical Formulae Friedrich & Friederici (2009) WB	45 47 10	–47 –38 –38	19 52 52	6 –3 –3
ROI BA 44 (conducted for the present article)	44	n.a.		

Table 1: Anatomical areas, Brodmann Areas (BA) mean Talairach coordinates (X, Y, Z) for significant effect of hierarchy in left prefrontal cortex, WB = whole brain analysis, ROI = region of interest analysis based on cytoarchitectonic definition of BA 44 with a probability of 30% (Amunts et al. *1999), for which Talairach coordinates are not applicable (n.a.).*

Current models of the prefrontal cortex (PFC) assume a posterior-to-anterior gradient as the neural basis of hierarchically organized behavior. The posterior-to-anterior dimension in the lateral PFC has been considered a key in the temporal integration of behavior (Fuster 1990). Alternative models proposed a posterior-to-anterior functional gradient for executive control in action selection (Koechlin *et al.* 2003, Koechlin & Summerfield 2007, Badre 2008, Badre *et al.* 2010). The posterior-to-anterior gradient goes from the premotor cortex (BA 6) located in the posterior PFC, over the posterior dorsal lateral PFC (BA 44/45) to the anterior dorsolateral PFC (BA 46/47) and further to the polar portion of the PFC (BA 10), with more abstract, hierarchically structured processes recruiting more anterior regions (Koechlin & Jubault 2006, Badre 2008). It should be noted that both these latter theories lay no direct claim as to whether the models hold for the processing of hierarchical sequences in the language domain (but see Koechlin & Jubault 2006). If they did, these theories would be compatible with the studies discussed here only under a view assuming that the processing of mathematical formulae could require here more executive control than the processing of linguistic structures. If, however, the crucial parameter according to which the prefrontal cortex is functionally organized is 'complexity of hierarchy' of a given stimulus, the pre-sent data are not fully compatible with such theories, since the 'complexity of hierarchy' of the stimulus does not fully determine the localization of the activation in the prefrontal cortex.

It seems that the posterior-to-anterior gradient correlates with qualitatively different computations required. The computation of mathematical formulae, which include logical operations indicated by operators at the structural nodes, relies on the more anterior ventral part of the IFG, namely BA 47/45a, whereas the computation of hierarchical structures in natural language is localized in more posterior regions of the IFG, namely in BA 44/45p. Complexity of hierarchy of a given sequence does not fully determine the localization in the prefrontal cortex, as the structures tested in the natural language experiment are quite complex (for a linguistic description of such a sentence see Figure 3b). These linguistic structures, however, only recruit areas located in the most posterior part of the IFG, i.e. BA 44, which, according to the models above, are responsible for the processing of less complex hierarchies. Note, that other studies in the literature often report syntax-related activation in BA 45 (Ben-Shachar *et al.* 2004, Bornkessel *et al.* 2005, Santi & Grodzinsky 2007, 2010, Snijders *et al.* 2009, Pallier *et al.* 2011). It remains to be determined whether the cytoarchitectonically different regions BA 44 and BA 45 can be functionally separated or whether the receptor-architectonic separation between the more anterior portion of the IFG covering area 47/45a and the more posterior portion covering area 44/45p and is functionally relevant. Independent of this fine grained neuroanatomical distinction the present data show that highly hierarchically complex language structures can be dealt with by the posterior IFG, whereas the processing of hierarchical mathematical formulae requiring logical reasoning recruits more anterior brain regions.[3]

One important aspect of the processing of mathematical formulae as compared to language processing may be that even for mathematicians, the processing of mathematical formulae could be less automatic, requiring more cognitive control than the processing of language hierarchies. The data available do not allow us to ultimately decide to what extent the observed differences in the PFC activation are entirely driven by the difference in the processing domains, as it is conceivable that familiarity with language-like structures is considerably greater than with mathematical formulae even in mathematicians.

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[3] For a discussion of the function of Broca's in language and its role in Broca's aphasia, see Grodzinsky & Amunts (2006) and the contributions therein.

The present interpretation would call upon a view suggesting two parallel systems dealing with hierarchical structures, one which following the posterior-to-anterior gradient is determined by the degree of cognitive control leading to activation in the anterior PFC (BA 47/45a and 10) for highly complex sequences in different domains, and one which is confined to the posterior IFG (BA 44/45p) and which in the adult brain efficiently deals with highly complex hierarchically structured language sequences. When language processes are less automatic as during first and second language acquisition, however, more anterior regions of the PFC have to be recruited in addition to those seen in adults (Rüschemeyer *et al.* 2005, Brauer & Friederici 2007).

8. Conclusions

Language processing in adults is highly automatic and does not appear to be very challenging for the brain, even when the sequences to be processed are hierarchically complex. One intriguing conclusion is that humans are predetermined to compute linguistic recursion, with BA 44/45p being the neural correlate of this showing its functional primacy in the adult brain after long language exposure. Based on the studies discussed here, we propose that there are two different computational systems in the lateral PFC dealing with hierarchical structures: one system determined by cognitive control that follows the posterior-to-anterior gradient and one system confined to Broca's area which is able to process complex hierarchies in language efficiently.

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