



Review article

The neurobiological nature of syntactic hierarchies



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ABSTRACT

The review focuses on the neurobiological literature concerning the specific human ability to process linguistic hierarchies. First, we will discuss current ethological studies dedicated to the comparison between human and non-human animals for the processing of different grammar types. We will inspect the functional neuroanatomical structures of human and non-human primates more closely, including human developmental data, thereby suggesting interesting phylogenetic and ontogenetic differences. We then examine the neural reality of the Merge computation, being the most fundamental mechanism regulating natural language syntax, and offer new evidence for a possible localization of Merge in the most ventral anterior portion of BA 44. We conclude that BA 44, with its strong neural connection to the posterior temporal cortex, provides a recent evolutionary neurobiological basis for the unique human faculty of language.

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1. Introduction

The evolution of language has been discussed for centuries, but until now there is no consensus on the ultimate origin of human language. Through lack of direct evidence, one approach taken to contribute to this open question is to determine the neurobiological basis of language in the human and to evaluate this brain-behavior relation against data from non-human animals. In such an interspecies comparison, our close relatives, the chimpanzees and macaques, have long been in focus. When looking at production contexts, one of several studies indicates that compared to linguistic structures in humans, non-human primates fails to combine signs into higher-order hierarchical assemblies (Pearce, 1987). By observing the production capability of a normal hearing child, a deaf child, and a chimpanzee respectively, it was shown

that the two children produce sequences of more than two words by the age of 3 and 3;5 years, whereas the chimpanzee almost never produces an utterance that is longer than one word (Pearce, 1987; Terrace, 1979). Crucially, on the rare occasions where the chimpanzee produced longer utterances, these were word list arrays lacking any hierarchical combinatorial system (Yang, 2013). More recently, studies investigating the communicative system of Campbell's monkeys for example, have shown that these guenons exhibit some rudimentary form of combinatorial sequencing by combining pairs of individual calls into context-specific call types, as for example in the case of surrounding predators or neighboring groups (Arnold and Zuberbühler, 2006; Ouattara et al., 2009). Additional evidence in favor of call combinations within the primate kingdom has been reported for several other species including putty nosed monkeys (Arnold and Zuberbühler, 2008), Diana monkey (Candiotti et al., 2012), bonobos (Clay and Zuberbühler, 2011) and chimpanzees (Crockford and Boesch, 2005). Given the limited number of combined vocalizations—either one or two—it has been claimed that the vocal combinatorial strategies used by these primates might reflect some simple transition probability mechanism across

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adjacent dependencies, rather than correspond to some underlying hierarchical process as in human language (for a deeper discussion on the topic also see [Clarke et al., 2006](#); [Petkov and Jarvis, 2012](#)). Because of the limitations found for production capabilities, sensory learning abilities in animals and in non-human primates are generally taken to constitute a much more reliable experimental environment to systematically evaluate cross-species comparisons against the syntactic linguistic ability found for humans ([Petkov and Wilson, 2012](#)). See “2. Cross-species comparisons and linguistic specificity”.

The syntactic ability to combine words into higher-order structures is at the root of human language. This capacity enables humans to establish specific grammatical dependencies between words forming syntactic sequences of increasing length. As such, language is not merely about whether sequences can be processed, but crucially, about the type of syntactic structure underlying these sequences ([Everaert et al., 2015](#)). A fundamental distinction, often found in the literature, has been made between two grammar types, namely finite state grammars (FSG) following an $(AB)^n$ rule and phrase structure grammar (PSG) following an A^nB^n rule ([Fitch and Hauser, 2004](#); [Hauser et al., 2002](#)). See [Fig. 1](#). The distinction between these two grammars is based on the possibility to either learn adjacent dependencies in $(AB)^n$ grammars or non-adjacent dependencies in A^nB^n . The latter grammar may induce hierarchical processing, but the build-up of a minimal hierarchy is not necessarily required. The artificial grammar sequences of the A^nB^n type, as those used in [Fitch and Hauser \(2004\)](#) and in [Friederici et al. \(2006\)](#) could have been processed by a simple counting mechanism (e.g., four A-elements are followed by four B-elements) together with the cognitive ability to memorize a string of elements.

Natural language grammars, in contrast, are based on hierarchical structures even at the most basic level. The structural dependency between a determiner (D), for example, *the* and a noun (N), for example, *man*, as in *the man*, is processed through the computation *Merge* which brings the two elements together into a set prior a minimal hierarchical structure can be established based on the syntactic relationship between the two elements. As such, *Merge* generates unordered sets—which may contain possible points of symmetry (symmetric structures) to be rescued by movement before linearization ([Moro, 1997, 2000](#)). Therefore, the hierarchical nature of the assembly within the set—as in *the man*—is determined by the resulting label, in which D is said to project, consequently yielding a determiner phrase, DP ([Chomsky, 1995](#)). Formally, this computation is represented as $\text{Merge}(X,Y) = \{X,Y\}$, which means “take two elements X and Y, and string them together to form a new set containing both,” such as *the, man* $\rightarrow \{the, man\}$ ([Everaert et al., 2015](#)). The two elements in the input, X and Y, comprise words from any lexical categories, whose resulting label will then express the hierarchical relation between them, regardless of the superficial linear ordering. Recent theoretical developments on the cognitive status of *Merge* ([Chomsky, 2013](#); [Murphy, 2015](#)) have now shed new light on the possibility of splitting this computation into two distinct steps: (1) a sequencing phase in which words are strung into a set—for example $\{the, man\}$ —called *string-Merge*; and (2) a hierarchicalization phase in which a linearized asymmetric structure is processed by establishing a relation of dominance between the two elements in the set based on their grammatical relationship—here the determiner phrase $DP[the\ man]$ —called *hierarchy-Merge*. Cognitively, the combinatorial linguistic faculty expressed by *Merge* can be defined as the syntactic process containing rules that analyze linguistic structures into hierarchical structures, taking into account the lexical categories of words to be combined ([Grodzinsky and Friederici, 2006](#)). In this sense, *Merge* corresponds to the structure formation process and is considered to be the fundamental com-

putation over which linguistic productivity is based ([Berwick et al., 2013](#)).

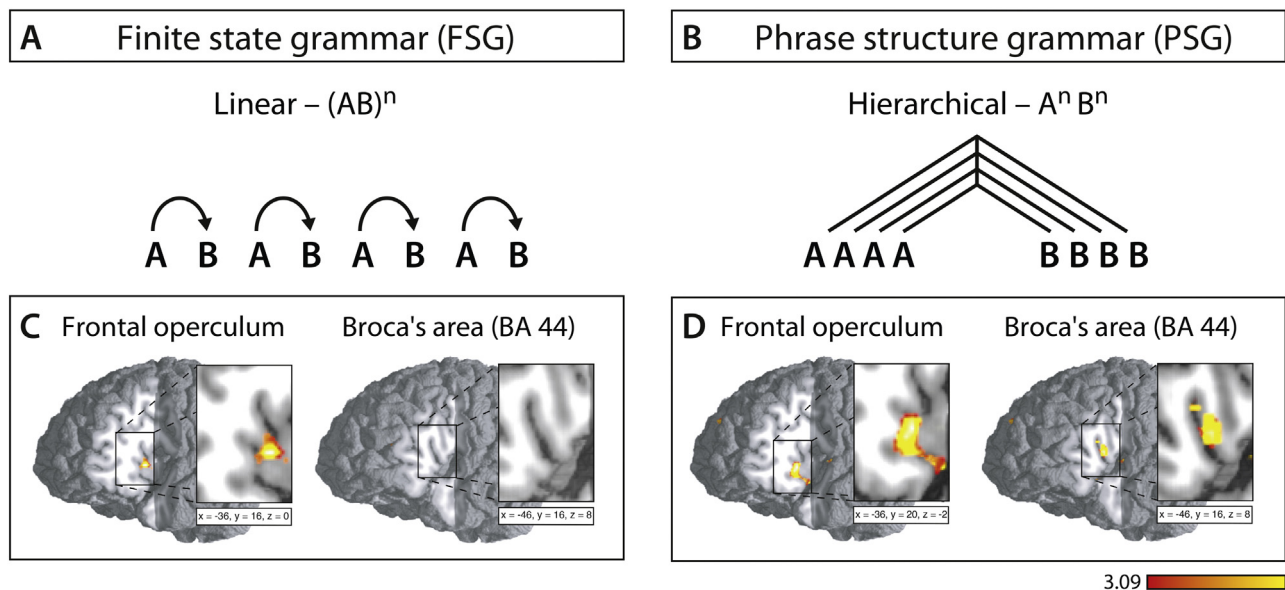
In the following, we will discuss phylogenetic and ontogenetic data concerning the language network and specify the functional localization of *Merge* with its possible substeps.

2. Cross-species comparisons and linguistic specificity

There are already a number of recent studies that investigated the ability to process sequences, in particular produced by $(AB)^n$ and A^nB^n grammars in humans and in non-human species, both in primates and in songbirds. Songbirds are equipped with an auditory-vocal learning system that allows them to learn sequences of a certain temporal order ([Abe and Watanabe, 2011](#); [Berwick et al., 2011](#); [Bolhuis et al., 2014](#); [Gentner et al., 2006](#)). Moreover, birdsongs have left-hemispheric dominance during a songbird's learning, which resembles the one found in adults and young infants ([Dehaene-Lambertz et al., 2006](#); [Friederici and Alter, 2004](#); [Pena et al., 2003](#)). It is clear that songbirds can learn rule-based adjacent dependencies, but there is no clear evidence that they are able to learn hierarchically structured sequences ([Beckers et al., 2012](#) for a critical discussion).

Monkeys seemingly also lack the ability to learn hierarchically structured sequences ([Fitch and Hauser, 2004](#); [Hauser et al., 2014](#); [Saffran et al., 2008](#)). Monkeys and humans were compared directly in a seminal study on artificial grammar learning using FSG and PSG grammars ([Fitch and Hauser, 2004](#)). By testing cotton-top tamarins and human adults in a behavioral grammar learning study, they found that humans could learn both grammar types easily, whereas monkeys were only able to learn the FSG. There are different possible mechanisms for learning such grammatical sequences. Learning adjacent dependencies, as in $(AB)^n$ grammars can be simply accomplished by extracting phonological regularities from the input and memorizing these for further use. Non-adjacent dependencies as in A^nB^n , however, can also be learned through the same mechanism, as long as no build up of a minimal hierarchy is required. The finding that the monkeys were not able to learn the A^nB^n grammar indicates that these animals used neither of the two strategies. Finally, true structural dependencies, such as those found in language, can only be accomplished by applying hierarchical rules, which in natural language grammar is processed through the computation *Merge* already described.

Being unable to trace back the neural basis for this sequence learning ability in cotton-top tamarins, due to the lack of functional and structural brain imaging studies on this type of monkey, [Friederici et al. \(2006\)](#) investigated the neural basis of the processing $(AB)^n$ and A^nB^n structures in humans in a functional brain imaging study comparing correct and incorrect sequences (see [Fig. 1](#)). Crucially, violations for both $(AB)^n$ and A^nB^n grammar types activated the frontal operculum (FOP; [Fig. 1C, D](#)), whereas only the A^nB^n grammar, which creates non-adjacent dependencies, activated the posterior portion of Broca's area (Brodmann area [BA] 44) ([Fig. 1D](#)). This is interesting for two reasons. Firstly, BA 44 has long been known to support syntactic processing ([Friederici, 2002](#) for a review) and secondly, BA 44 is a phylogenetically younger area than the FOP ([Amunts and Zilles, 2012](#); [Friederici, 2004](#)). In humans, because the artificial grammar A^nB^n is processed in a brain region which is known to be involved in processing syntactic hierarchies in natural languages ([Friederici, 2011](#); [Grodzinsky and Santi, 2008](#); [Hagoort, 2005, 2008](#)), it is likely that the A^nB^n grammar is processed similar to natural languages. In this respect, a learning study focusing on the mastering of rules either following or not following universal principles of natural grammars was able to show that activation in Broca's area increased only when participants were learning a novel language following real hierar-



Source: Adapted from Friederici et al., PNAS, 2006

Fig. 1. Neural basis of the processing of violations of different artificial grammar types in humans. (A) structure of Finite State Grammar $(AB)^n$ and (B) of Phrase Structure Grammar $A^n B^n$. (C) and (D) group-averaged statistical parametric maps of functional activation for different grammar types in the Frontal Operculum and in Broca's area (Brodmann area [BA] 44) in the left hemisphere ($P < 0.001$, corrected at cluster level). Adapted from Friederici et al. (2006).

chical rules, but not when they were learning a language following impossible rules based on linear order (Musso et al., 2003; also see Tettamanti et al., 2002). For a full discussion on the terminology referring to non-recursive/hierarchical rules see Moro (2015). Another direct evidence for the assumption that $A^n B^n$ grammars might be processed similar to real languages comes from a recent study using a natural language, namely German, with non-adjacent dependencies in the experimental sequences. In this functional brain activation, center-embedded sentences were used whose long distance dependencies are superficially similar to the artificial grammar $A^n B^n$ but are grammatically marked, thereby indicating syntactic hierarchy (Makuuchi et al., 2009) (see Fig. 2).

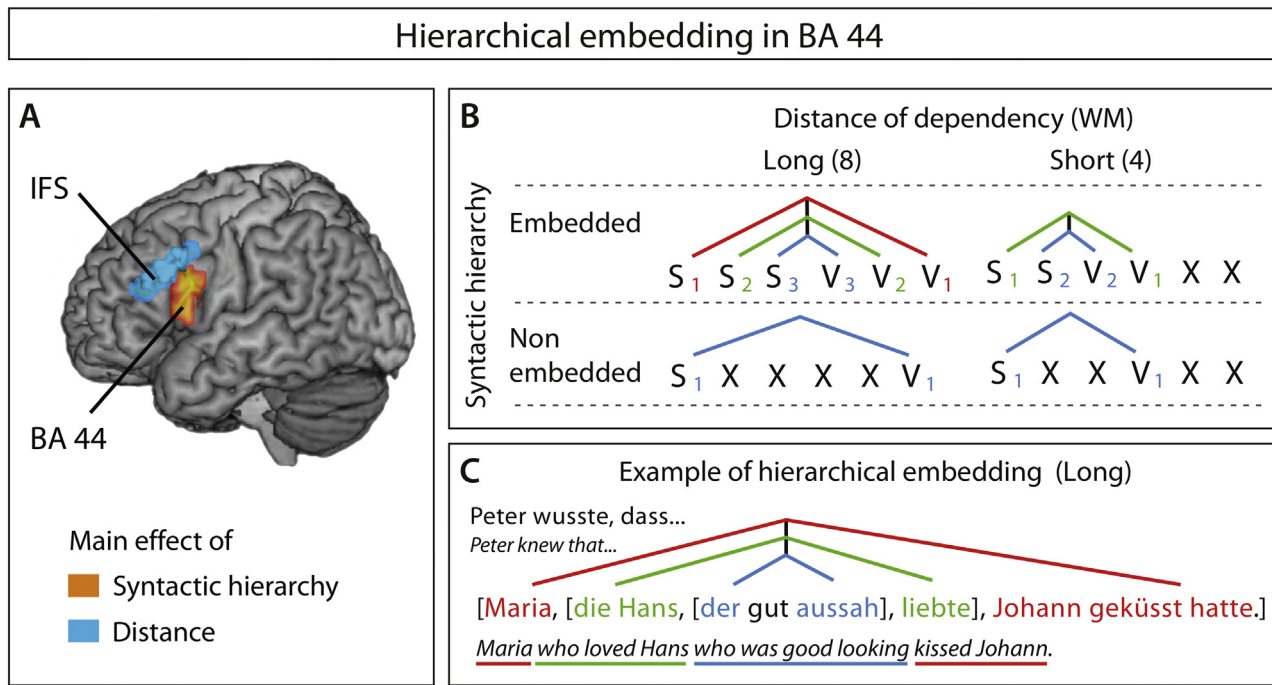
This study clearly demonstrates that the syntactic hierarchy in natural grammar is processed in BA 44. Based on these data, one might conclude that hierarchical structures are processed in BA 44 and that strings that lack syntactic hierarchy are processed in the FOP. Given the behavioral data discussed above (Abe and Watanabe, 2011; Fitch and Hauser, 2004; Saffran et al., 2008), the tentative hypothesis would then be that the sequences that monkeys and songbirds are able to process may be rule-based but do not involve syntactic hierarchies. On an evolutionary perspective, it is interesting to note that in humans two different brain regions process these two types of rule-based sequences: the frontal operculum which deals with the non-hierarchical sequences and BA 44 which instead deals dealing with the hierarchies.

Additional support for a dissociation between BA 44 and FOP comes from the analysis of the white matter structures in the Friederici et al. (2006) study. Based on the functional activation peaks in the FOP and BA 44 as seeds (starting points of the analyses), different pathways were observed. The FOP, housing the peak of activation for the $(AB)^n$ grammar, was connected to the temporal cortex via a ventrally-located fiber pathway, whereas BA 44, housing the peak of activation for the $A^n B^n$ grammar, was con-

nected to the posterior superior temporal gyrus and sulcus by a dorsally-located white matter fiber bundle (see Fig. 3). These findings provide a first indication that the processing of hierarchical syntactic structures is supported by BA 44 as a part of Broca's area, connected to the posterior superior temporal cortex via a dorsal white matter pathway. To evaluate this hypothesis in more detail, we consider phylogenetic data and ontogenetic data of this white matter pathway.

Phylogenetically, cross-species comparisons of the fronto-temporal white matter connections revealed interesting differences between human and non-human primates. Macaques and chimpanzees display a strong ventral and a weak dorsal pathway, whereas humans, in contrast, display a strong dorsal pathway in addition to a well-developed ventral pathway (Rilling et al., 2008). The dorsal pathway was, therefore, discussed as being the crucial pathway for the language ability in adult humans. In songbirds, a set of nuclei in the anterior forebrain pathway form the auditory loop, which is thought to interact with the motor regions to perform vocal and non-vocal motor responses, although it remains uncertain whether this neuroanatomical interaction also supports the evaluation of syntactic-like structural relationships, given the lack of clear behavioral evidence proving such ability (Berwick et al., 2011; Petkov and Jarvis, 2012).

Ontogenetically, the available evidence is twofold. First, for newborns it was shown that the dorsal pathway connecting Broca's area to the posterior temporal cortex is not mature at this stage in terms of myelination (Perani et al., 2011). However, a fiber tract connecting the posterior temporal cortex to the premotor area as well as the ventral pathway seems to be already fully myelinated at birth. Second, the dorsal pathway connecting BA 44 and the posterior superior cortex, which matures later, directly correlated with the behavioral performance on syntactically complex, hierarchically structured object-first sentences between the ages of three



Source: Adapted from Makuuchi et al., PNAS, 2009

Fig. 2. Hierarchical embedding effect in BA 44. (A) Activation main effect of syntactic hierarchy (orange) and main effect of working-memory distance (blue) projected onto the surface of the left hemisphere of the brain. Brodmann area (BA) 44; Inferior Frontal Sulcus (IFS). (B) Schematic view of sentence structures in the four experimental conditions. (C) Example sentences. $P < 0.05$ corrected for left Inferior Frontal Gyrus (LIFG) as the search volume. Adapted from Makuuchi et al. (2009).

to ten years (Skeide et al., 2015). This is strong evidence that this dorsal pathway is crucial for processing complex, hierarchically structured sentences. These developmental data are able to explain a long-standing unsolved problem of why children find it difficult to comprehend structurally complex sentences, such as object-first sentences (Dittmar et al., 2008; Skeide et al., 2014).

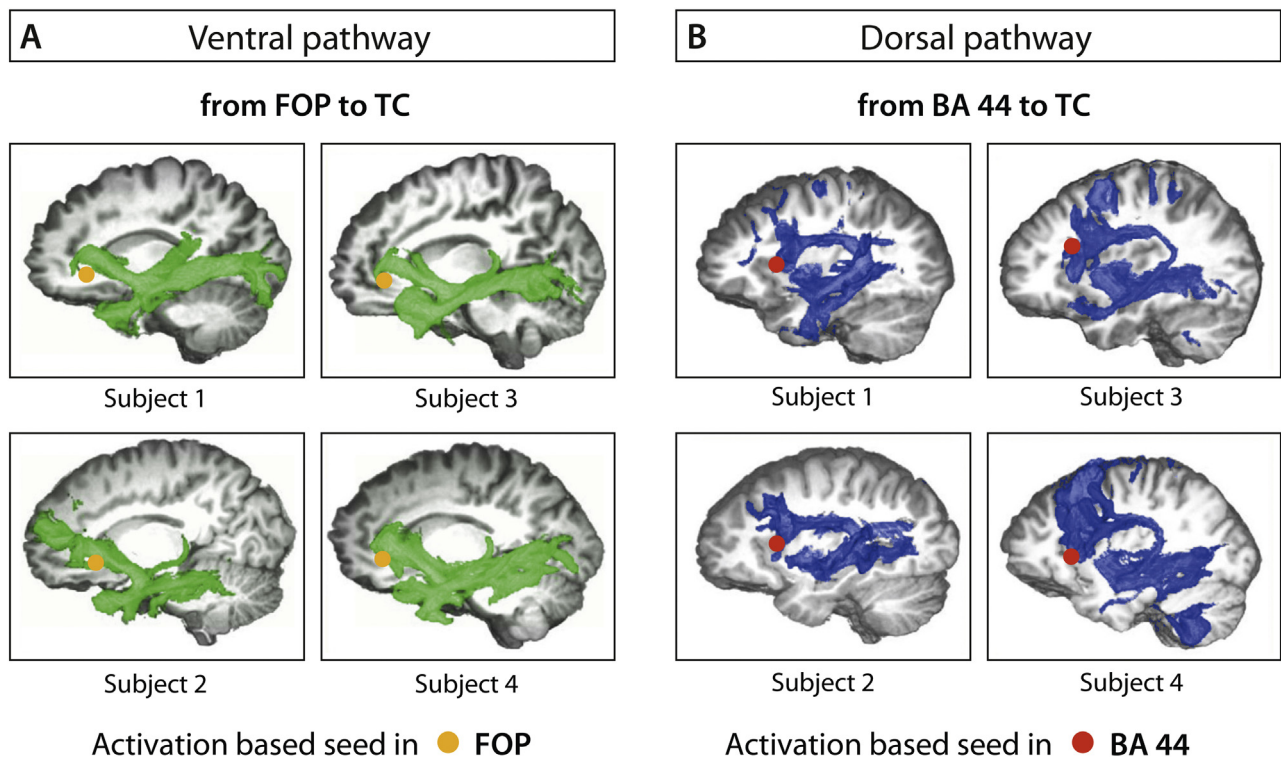
Together, both the phylogenetic and the ontogenetic data provide the basis for the conclusion that the dorsal fiber tract targeting BA 44 is crucial for processing complex hierarchies. But what about area BA 44 itself?

3. Neural reality for Merge and functional decomposition

Although there is ample evidence of an involvement of Broca's area (BA 44/45) in processing complex syntactic hierarchies, there is no clear evidence of a neural correlate of the most basic computation Merge (Zaccarella and Friederici, 2015c). Neurolinguistic investigations mainly focused on brain responses regarding the processing of increasing levels of structural complexity (e.g., scrambling phenomena, phrasal movement, sentential embedding). For a review see Friederici, 2011. Because of the type of manipulations used in these studies however, the effect related to the brain processing involved in Merge was not in focus, therefore offering no evidence in favor of a neural correlate for this most basic computation (Zaccarella and Friederici, 2015c). Complementary to complexity manipulations within the sentence-level, other studies used word-list control conditions to directly inspect the effect related to structure formation, often comparing syntactically structured stimuli against linguistic control stimuli lacking any syntactic structure. The rationale behind this type of experimental manipulation is that if the structure building processing is mandatory as soon as we process coherent linguistic constructions, the Merge mechanism should be detectable whenever normal structures are

compared to linguistic strings with no syntactic structure. This type of manipulation has been used in the literature across different languages, modalities, and experimental paradigms, using both PET and fMRI (Friederici et al., 2000; Humphries et al., 2006; Mazoyer et al., 1993; Snijders et al., 2009). From these experiments however, a rather unclear picture emerges, with the entire perisylvian language network believed to play a major role for syntax. The presence of several potential confounds in the stimulus materials could possibly explain the variation in the functional activation that was reported from the contrast between sentences and word-lists across the experiments. Confounds included the fact that word-lists themselves contained remaining syntactic chunks, which possibly cancelled out the Merge-related brain activations during signal comparison of the different conditions or lead to semantic anomalies triggering activation in non-syntax-related brain areas.

A recent study (Goucha and Friederici, 2015) approached this issue by designing a German study shortly after an English study (Tyler et al., 2010), which had reported a widespread activation in the left hemisphere for their syntax based contrast. Because semantic information was widely available in their conditions, the observed activation pattern could have resulted from the additional semantic processes. Therefore, the German study systematically reduced semantic information from the sentences ranging from full sentences to purely syntactic sequences. For real word conditions, which included semantic information, the German study also found a broad activation in the left hemisphere, including the inferior frontal gyrus (BA 44/45/47), the anterior temporal lobe and posterior superior temporal gyrus (pSTG), and sulcus (pSTS). For pseudoword sentences, a similar activation pattern was found when derivational morphology conveying semantic meaning (such as *un-* in *unhappy* or *-hood* in *brotherhood*) was present. However, for pseudoword sentences in which only inflectional morphology (such as verb endings [-s in *paints*]) was present, only BA 44 was



Source: Adapted from Friederici et al., PNAS, 2006

Fig. 3. Ventral and dorsal pathway in the left hemisphere. Three dimensional rendering of the distribution of the connectivity values using the two regions as seeding point in four representative subjects. (A) Frontal Operculum (FOP, orange); tractograms from FOP to the temporal cortex (TC) revealing the ventral pathway (green); (B) Brodmann area (BA) 44 (red); tractograms from BA 44 to the TC revealing the dorsal pathway (blue). Adapted from Friederici et al. (2006).

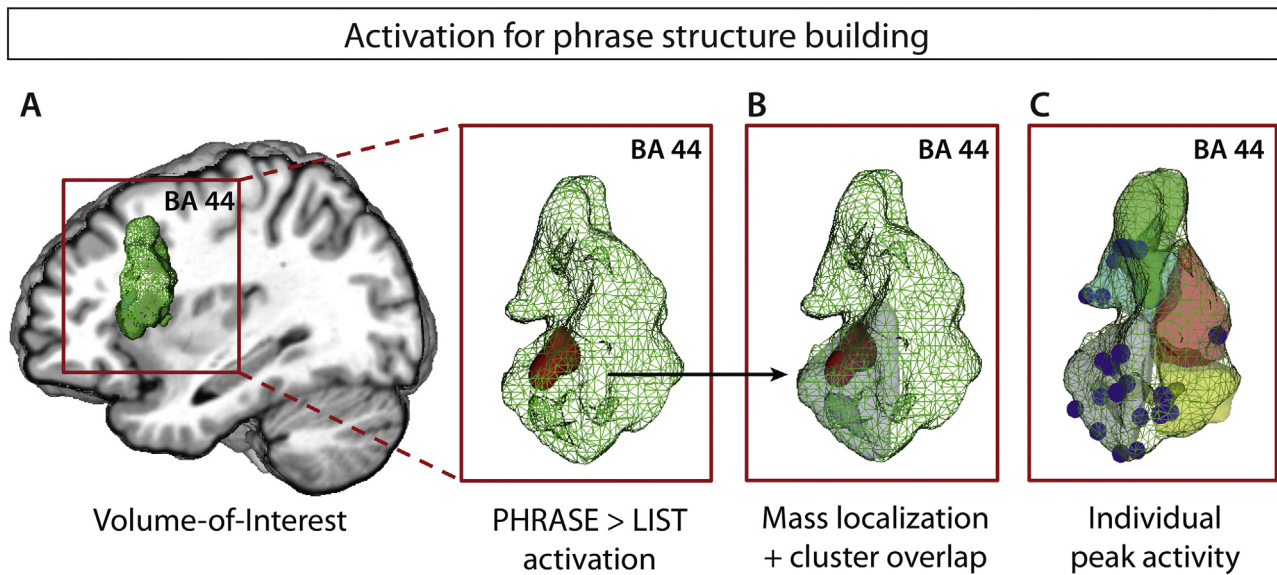
found to be active. These findings confirm that BA 44 is a core area for processing pure syntactic information.

The function of BA 44 was further pursued in a series of functional studies by Zaccarella et al. using a stepwise reductionist approach to probe Merge directly. Complexity was first pushed down to a three-word level to explore how Merge creates minimally hierarchical phrases and sentences (Zaccarella et al., 2015). The analysis then moved then to the most fundamental two-word level to directly assess the universal invariant nature of Merge, when complexity is fully excluded (Zaccarella and Friederici, 2015a). Finally, attention was directed to understand how the linguistic system organizes word pairs before Merge realization (Zaccarella and Friederici, 2015b). In a first study, three-word long prepositional phrases (*on the boat*) and sentences (*the boat sinks*), which involved Merge, were compared to word-lists of equal length, not involving Merge. The authors found functional selectively for Merge in BA 44 in the left inferior frontal gyrus (IFG) and in a smaller region in the posterior temporal sulcus (pSTS). Within the IFG, hierarchies at the sentential level engaged a more anterior portion of the area showing activity peak in the pars triangularis (BA 45) compared to hierarchies at the phrasal level, which showed activity peak in the pars opercularis (BA 44); (Zaccarella et al., 2015). In the second functional study (Zaccarella and Friederici, 2015b), simple two-word phrasal combinations (determiner + pseudo noun: *this flirt*), compared to simple lists (noun + pseudo noun: *apple, flirt*) were used. The use of pseudo nouns was intended to remove semantic processing from the signal, which could have interfered with syntactic processing at this very early stage, possibly confounding Merge with semantic combinatorics (Bemis and Pyllkanen, 2011). Two one-word condi-

tions (“this xxxxx”, “apple xxxxx”) were also employed as controls to understand which regions support two-word concatenation, regardless of the fact that they are phrases or lists. In this second study, it was found that the creation of minimal syntactic phrases, two-word phrases compared to two-word lists, corresponded to increased neural activity in the ventral-anterior portion of the left pars opercularis (BA 44). See Fig. 4A and B.

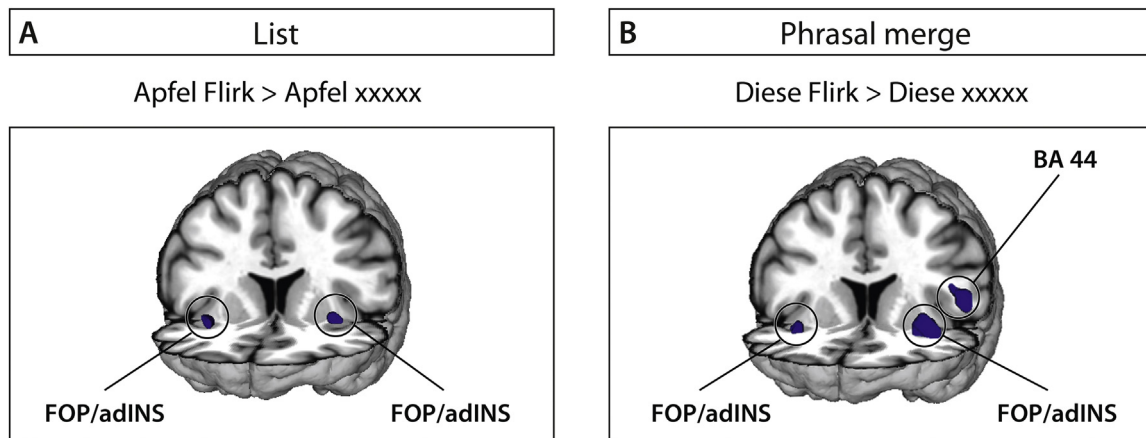
At a more fine-grained resolution, the neural correlate of Merge was found to be crucially confined in one of five predefined subregions within BA 44 (Clos et al., 2013), with high consistency across participants (Fig. 4C). Remarkably, this activation peak is only about 8 mm away from the activation peak reported in Friederici et al. (2006) for PSG rules, which is located in the same anterior-ventral cluster. In this respect, future research will have to clarify whether the two activation peaks would correspond to similar or slightly different connectivity pathways within the left fronto-temporal structural network. Nonetheless, these data not only conform to the general notion of BA 44 being activated as a function of structural linguistic hierarchy, but clearly goes beyond this view by suggesting that complexity can be broken down to its very basic computation (Zaccarella et al., 2015; Zaccarella and Friederici, 2015a).

In contrast, the deep frontal operculum/anterior-dorsal insula (FOP/anterior-dorsal INS), a phylogenetically older brain region, was found equally active for both phrases and word-lists (Zaccarella and Friederici 2015b), thereby indicating word-sequencing processing in the region, where the word is first accessed and then maintained on hold before further processing takes place (see Fig. 5). To note, such basic syntactic hierarchies do not seem to significantly trigger neural activity in more sub-cortical regions within the brain, suggesting that the basal ganglia may be engaged by more



Source: Adapted from Zaccarella and Friederici, *Front. Psychol.*, 2015

Fig. 4. Activation for Merge within BA 44. Volume of interest analysis in BA 44. (A) contrast phrase-list, (B) mass localization with cluster overlap (C3 cluster according to Clos et al., 2013). (C) Individual peak activity distribution within BA 44. Significant accumulations of individual peaks in cluster C3 ($p < 0.01$). Adapted from Figs. 1 and 3 in Zaccarella and Friederici (2015a).



Source: Based on data from Zaccarella & Friederici, *Brain & Language*, 2015

Fig. 5. Effect of phrasal Merge in BA 44 and frontal operculum/anterior-dorsal insula (FOP/adINS). Whole-brain activity distribution for (A) the list accumulation contrast (2-word list vs. one-word list, left) and (B) for the phrasal Merge contrast (2-word phrase vs. one-word phrase; right); (FWE-corrected; $P < 0.05$). Brodmann area (BA) 44. Based on data from Zaccarella and Friederici (2015b).

controlled reanalysis processing, as suggested by patient studies (Friederici et al., 1999; Frisch et al., 2003).

In this context, the functional dissociation between FOP/adINS and BA 44 appears to converge with prior empirical data as well as to recent theoretical advancements on the cognitive status of Merge (Murphy, 2015). As such, the dissociation between FOP and BA 44 reported in humans for the processing of $(AB)^n$ versus A^nB^n , respectively (Friederici et al., 2006) indicates that the processing of $(AB)^n$ might not involve hierarchy building, but that it rather engages in FOP some evaluation strategy of transition probabilities across contiguous elements. Remarkably, studies comparing human and non-human primates for the functional activation of violations in rule-based non-hierarchical sequences revealed

interesting differences between the species. One study found that the processing of violations of transitions in finite state grammar sequences leads to activation in the ventral frontal opercular cortex (vFOC) in both species, and that only macaques additionally recruited Broca's area homologues; (Wilson et al., 2015). In humans, Broca's area was not systematically activated when evaluating transitions between adjacent elements, therefore supporting the hypothesis that the vFOC is specifically involved in the processing of sequential structures. In a second cross-species comparison, the brain areas involved in abstracting specific information from sequences of tones—number of items and tone-repetition patterns—were specifically investigated (Wang et al., 2015). Functional activation in humans revealed a simultaneous engagement of

the posterior IFG (BA 44)—together with the pSTS—for both types of processes, as revealed by conjunction analysis, compared to monkeys, for which no region was reported when joint effects were evaluated. When independently assessed, increased neural activity in monkeys included the ventral inferior parietal cortex (VIP), the anterior cingulate cortex (ACC), the supplementary motor area (SMA) and pSTS for the main effect of number of items, and the ventral premotor area 6/ventral part of dorsolateral prefrontal cortex (6VR), the pSTS, aSTS and the caudate for the main effect of sequence. Crucially, the authors view the neural network linking the IFG to the pSTS in humans as being critical for the emergences the human-specific capability to successfully process linguistic sequences. Reviewing neuroscientific studies on different processing domains across species, Dehaene et al. (2015) concluded that the capability to generate recursive structures by means of symbolic rules may be the critical aspect defining the uniqueness of human language.

At the theoretical linguistic level, the computation of Merge is now seen as complex process formed by a sequencing phase and a hierarchization phase (Murphy, 2015). In the first phase (*string-Merge*), words (e.g., *the* and *man*) are strung into a set, but no hierarchical structure is formed at this stage yet. This sub-routine is supported by the FOP/adINS. In the second phase (*hierarchy-Merge*), an asymmetric structure is created by translating a set into a labeled syntactic structure in which the hierarchical relation is finally established. This sub-routine appears to be implemented in (the anterior-ventral) BA 44 (Zaccarella and Friederici 2015a). Evolutionary, the main difference between human and non-human primates might be the ability to build hierarchical structures based on syntactic category information provided by the words in a language sequence. Thus, in its second phase, the computation Merge is comparable to the labeling algorithm leading to a hierarchical structure (Goucha et al., 2014). Future cross-species research should specify what the essential computational core of category information in human language is and to what extent these can be tested in non-humans, to see whether linguistic categories are special by themselves. Similarly, neuro-linguistic investigations in humans must necessarily determine at the neuroanatomical level how the labeling algorithm outputting rule-based syntactic structures in BA44 also rejects illegal structures—which fail to be labeled—based on same checking procedures, which might be internal to the Merge computation. In this respect, it is remarkable to note how consistent electrophysiological evidence exists, which assigns a major role to the left inferior frontal gyrus also for the detection of deviant syntactic structures in word-category violation studies, in which contiguous elements in linguistic strings cannot be fully integrated into a coherent labeled output (Hanna et al., 2014; Pulvermüller and Shtyrov, 2003). It is therefore plausible to hypothesize that the same checking procedures at work to form legal labeled structures in a specific language are equally involved during the exclusion of illegal strings in the same language.

4. Conclusion

Reviewing different neuroanatomical and neurofunctional studies across species, we can conclude that a fronto-temporal network is involved in evaluating rule-based structures, and recruited in humans to process syntactic hierarchies. In humans, BA 44 in the inferior frontal gyrus, which strongly connects to the temporal cortex via the dorsal pathway, appears to be particularly involved in hierarchy building. On a more fine-grained level, the computation Merge—the linguistic process responsible for combining words into hierarchical structures according to abstract rules—appears to be located in the most anterior-ventral portion of BA 44. The neurobiological validity of Merge as structure-building computation

offers strong support to the idea that linguistic structures consist of abstract mental representations, which are internally assembled on the basis of syntax (Ding et al., 2016). Here, we propose that the neuroanatomical implementation of Merge in humans may be an essential neural requisite of the human-specific capacity of language.

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