Neurobiology of Syntax as the Core of Human Language

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1. Introduction

The human language capacity appears to be rooted in the ability to combine words into hierarchical structures making up phrases and sentences. There is substantial evidence that this ability is specific to humans. Other animals can use words or symbols to refer to objects and actions, and can even memorise sequences of syllables and symbols, but only humans create syntactic hierarchies to build up phrases and sentences. In humans syntactic rules and representations together with words constitute the basis of the language system which allows the construction of sentences that carry and convey meaning. The present article focuses on syntax as the hierarchy building component which is unique to humans and thought to be part of their neurobiological endowment (Friederici et al. 2017).

This view was already formulated about 50 years ago by Erich Lenneberg (1967) in *Biological Foundations of Language*. He claimed that there must be an innate biological representation of the abstract structure of language in the human nervous system, and that language was characterised by "concatenations" which obey syntactic principles. Both claims have found supportive evidence in the past 50 years. While Lenneberg formulated his views mainly on the basis of behavioural language data from patients with brain lesions, today's knowledge is based on data from functional brain imaging, measurements of the grey and white matter structures of the living brain as well the correlation of these with behavioural language measures.

2. The Computation Merge: Broca's Area

These days the syntactic principle to which all languages adhere can be described according to Noam Chomsky (Chomsky 1995; Berwick et al. 2013) as a most basic computation, called Merge. Merge is a universal language-specific combinatorial operation that takes two syntactic objects to create a new one. For example, it takes two words (a determiner *the* and a noun *ship* to create a determiner phrase *the ship*, or it takes a determiner phrase *the ship* and a verb *sinks* to create a sentence *the ship sinks*. Crucially, Merge is a recursive operation allowing the generation of the full range of hierarchical structure that is characteristic of human language distinguishing it from other human and non-human cognitive systems (Chomsky et al. 1982, Bolhuis et al. 2014).

At this point two questions arise: What kind of evidence can we find to support the claim that the syntactic operation Merge is grounded in the human brain

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and what is the brain basis for the ability to deal with sentence structures beyond a single Merge operation? It is clear that the generation of a sentence like *the ship sinks* requires not only the neural representation of the syntactic operation Merge but, moreover, a set of words. Together, syntax and a set of words make up the basis of the language system. In a basic model of language this language system is connected to the external world and to the internal mental world by two interface systems. The former system called external sensory-motor interface supports perception and production of speech and the latter system named internal conceptual-intentional interface relates to concepts and intentions (Berwick et al. 2013). Clear neurobiological evidence for the internal conceptual-intentional interface system is still missing. For the external interface system, however, there is ample evidence as it relates to the respective modalities in which language is realized: the auditory-articulatory system for spoken language and the visual-gesture related motor system for sign language (Levelt 1989, Guenther 2016, Zatorre et al. 1992, Emmorey et al. 2003, Petitto et al. 2001).

Here I will mainly focus on the language system and its neural representation. The language system consisting of syntax and lexical items is mainly represented in the perisylvian cortex of the left hemisphere involving the inferior frontal and temporal cortex. These brain regions are connected by white matter fibre tracts constituting dorsal and ventral pathways (see figure 1) that allow the transmission of the information from one region to the next.[1] The brain areas which are connected by the ventral pathway are involved in processing words and semantic information (Binder et al. 2009, Patterson et al. 2007, Thompson-Schill et al. 1997, Newman et al. 2010, Weiller et al. 2009, 2011, Turken & Dronkers 2011). The processing of syntactic information, in contrast, is related to the dorsal pathway that targets BA 44 in Broca's area. Note that the figure displays two dorsal fibre tracts. One is terminating in BA 44 and discussed in detail here. A second fibre tract terminating in the premotor cortex (PMC) is involved in sensory-motor mapping and assumed to be essential for the sensory-motor interface system briefly mentioned above, but not discussed further in this article.

Since we learned that single words as such do not make up language, I will not report neuroscientific studies on the processing of single words, but only discuss those studies in which words become part of a hierarchical structure.

Traditionally, the processing of syntax has been investigated in the context of sentences with varying syntactic complexity (for a review see Zaccarella & Friederici 2015a). These studies systematically reported Broca's area in the left inferior frontal gyrus to support syntactic processes. Another approach chose to compare the processing of a 'possible' language that followed natural grammar rules to the processing of an 'impossible' language that did not follow such rules. Only the processing of 'possible' languages activated Broca's area, whereas the processing of languages which did not follow natural language rules did not (Musso et al. 2003, Tettamanti et al. 2002). Interestingly, the human brain uses Broca's area, in particular its posterior part BA 44, to process syntactic rules even in sequences that follow natural

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[1] The identification of fibre tracts is based on diffusion tensor imaging (DTI) allowing the measurement of the fractional anisotropy reflecting among other parameters the myelination in white matter which surrounds the fibre. It serves as an electrically isolating layer surrounding the fibre thereby increasing the propagation speed of the electrical signal and thus the information transfer between neurons and neuronal ensembles (Turner 2015).

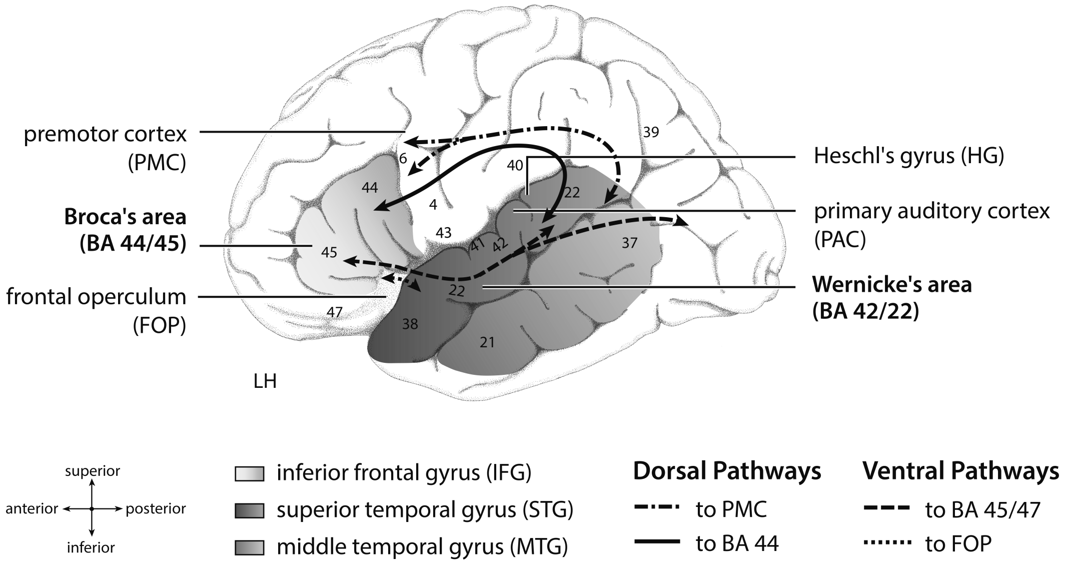

Figure 1: ***Neuroanatomy of language****. Anatomical details of the left hemisphere (LH). Top: Major language relevant gyri (inferior frontal gyrus (IFG), superior temporal gyrus (STG), middle temporal gyrus (MTG)) are shaded in grey. Numbers indicate language-relevant Brodmann Areas (BA) which Brodmann (1909) defined on the basis of cytoarchitectonic characteristics. The vertical coordinate labelled (see bottom left) superior/inferior indicates the position of the gyrus within a lobe or within a BA. The horizontal coordinate labelled anterior/posterior indicates the position within a gyrus. Broca's area consists of a posterior part (BA 44) and an anterior part (BA 45). Located anterior to Broca's area is area BA 47. The frontal operculum (FOP) is located ventrally and medially to BA 44, BA 45. The premotor cortex (PMC) is located in BA 6. Wernicke's area is defined as BA 42 and BA 22. The primary auditory cortex (PAC) and Heschl's gyrus (HG) are located in a lateral to medial orientation in the temporal lobe. White matter fibre tracts, i.e. the dorsal and ventral pathways connecting the language-relevant brain regions, are indicated by arrows. There are two dorsal and two ventral fibre tracts with respective different termination regions. (Adapted from Friederici 2011.)*

grammar rules, even when the 'words' are not real (Opitz & Friederici 2003, 2007, Goucha & Friederici 2015). These data provide suggestive evidence that BA 44 as part of Broca's area (see figure 1) is responsible for the processing of syntax in sentences as well as in sentence-like sequences.

The question remains, however, whether this brain region should be viewed as the neural basis of the most basic linguistic operation Merge. It has been reasoned that if the neural substrate of Merge is the same independent of the number of recursive applications, the single application of Merge should also recruit BA 44 as part of Broca's area. Thus this brain region should be activated not only for the processing of sentences, but also for a single Merge operation. A recent study was able to provide support for this assumption. This study investigated the computation Merge of a determiner phrase using a semantic-free determiner (*the*) and a semantic-free noun (*bish*) in an fMRI experiment and found activation in the most ventral portion of BA 44 (Zaccarella & Friederici 2015b). This stood in clear contrast to the processing of two-word sequences without-syntactic hierarchy (*cloud*, *pish*) which activated the frontal operculum/anterior insula (Zaccarella & Friederici 2015c)—a phylogenetically older brain region than BA 44 itself (Sanides

1962, Friederici 2004, Amunts & Zilles 2012). These results suggest that the processing of syntactic hierarchy selectively involves a phylogenetically more recent cortical region, namely BA 44, independent of the number of recursive applications.

3. Beyond Merge: The Neural Syntactic Network

Although responsible for the syntactic operation Merge, Broca's area is not the only player when it comes to processing sentences. There is ample neuroscientific evidence that Broca's area in the inferior frontal gyrus and Wernicke's area in the posterior superior temporal cortex together constitute a fronto-temporal network that serves sentence comprehension (Friederici 2011, see figure 1). Within this network, BA 44 as the posterior part of Broca's area is responsible for syntactic processes whereas the posterior temporal cortex appears to support the integration of semantic and syntactic information (Friederici et al. 2009, den Ouden et al. 2012, Makuuchi & Friederici 2013, Ding et al. 2015). This conclusion is based on the observation that posterior temporal cortex is seen inactive when artificial grammar sequences lacking semantic information are processed (Friederici et al. 2006) but active when natural sentences are processed (for a review see Friederici 2011). It has been proposed that the posterior temporal cortex particularly comes into play for thematic role assignment, crucial for sentence comprehension (Bornkessel et al. 2005). In addition functional connectivity analyses observing a coactivation of Broca's area and the posterior temporal cortex revealed that these two regions work closely together when sentences are processed (den Ouden et al. 2012, Makuuchi & Friederici 2013).

Structurally, these two brain regions are connected by a white matter fibre tract relating the posterior temporal cortex and BA 44 in Broca's area via the arcuate fascicle and the superior longitudinal fascicle (Catani et al. 2005, Anwander et al. 2007). Empirical data from patients with deficiencies of this fibre tract (Wilson et al. 2010) and from young children in whom this fibre tract is still immature (Skeide et al. 2016) indicate that this dorsally located fibre tract is crucial for the processing of syntactically complex sentences. During development the function of this dorsal fibre tract becomes particularly obvious. It was shown that children's behavioural performance on processing syntactically complex sentences improves as the strength of this fibre tract increases (Skeide et al. 2016). The strength of a fibre tract is indicated by the status of the myelination of the fibres which in turn is essential for the transmission of electrical impulses to be sent from one brain region to another (Wake et al. 2011, Nave & Werner 2014).

This dorsal fibre tract is not yet myelinated at birth (Perani et al. 2011) and only matures slowly throughout childhood (Skeide et al. 2016), reaching its adult stage after puberty. This developmental trajectory is interesting in the context of Lenneberg's (1967) claim of a critical period of language acquisition whose window is thought to close in early puberty. He already drew suggestive parallels between the time course of language acquisition and the maturation of certain features of the human brain. Today we know that the maturation of the white matter of the dorsal fibre tract predicts processing of syntactically complex sentences (Skeide et al. 2016). Moreover, there is also evidence that the maturation of the grey matter is crucial for language development. It has been shown that performance on syntactically complex sentences during development is predicted by the maturation of the grey matter of BA 44 in particular, and the posterior temporal cortex (Fengler et al. 2016). These findings advance the view that the dorsal fibre tract together with its termination regions, namely BA 44 in Broca's area and the posterior temporal cortex, constitute the neural basis of the human syntactic capacity.

4. Comparing Human and Non-Human Primates

When considering syntax as a unique human ability, a comparison between human and non-human primates can add important aspects. Central to the discussion on sequence processing in human and non-human primates is not whether sequences can be learned, but rather what type of syntactic sequence can be learned. In this context a fundamental distinction is made between two grammar types, namely finite state grammars following an $(AB)^n$ rule and phrase structure grammars following an A^nB^n rule (Hauser et al. 2002, Fitch & Hauser 2004). The important difference between these two types of grammars is that sequences based on the $(AB)^n$ rule contain adjacent dependencies between an A-element and a B-element, whereas sequences based on the A^nB^n lead to non-adjacent dependencies. While it is open whether non-adjacent dependencies in artificial grammars necessitate the build up of hierarchies, it is clear that non-adjacent dependencies in a natural grammar require the build-up of syntactic hierarchies which is guaranteed by the computation Merge (Chomsky 1995).[2]

Fitch & Hauser (2004) were the first to investigate artificial grammar learning in human and non-human primates using such a finite state grammar $(AB)^n$ and phrase structure grammar (A^nB^n). Testing cotton-top tamarins and human adults in a behavioural grammar learning study, they found that humans could learn both grammar types easily, whereas monkeys were only able to learn the finite state grammar with its adjacent dependencies. More recently it has been shown that macaques can even learn non-adjacent dependencies in auditory syllable sequences of the A×B type (Milne et al. 2016). But note that the recognition of the dependency between the A-element and the B-element in such sequences does not necessarily require hierarchy building. Thus it appears that a crucial difference between human and non-human primates lies in the ability to process syntactic hierarchies.

Concerning the evolutionary aspect of a recent study investigated artificial grammar learning in two types of monkeys who differ in their evolutionary distance to humans: marmosets with a further distance and macaques with a closer distance to humans (Wilson et al. 2013). In the study both species had to learn an artificial grammar with non-deterministic word transitions. Marmosets showed sensitivity to simple violations in the sequence, whereas macaques showed sensitivity to violations of a higher complexity. This suggests an evolutionary interesting result with monkeys, namely that those that are closer relatives to us demonstrate a more advanced artificial grammar processing ability than those that are more distant.

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[2] It has been claimed, however, that A^nB^n artificial grammar sequences can in principle be processed by simpler cognitive processes such as counting and memorising. For a detailed discussion see Friederici 2017.

Human and non-human primates clearly differ in their abilities to process complex rule-based sequences. And so far there is no evidence that any other species except humans can process hierarchically structured sequences as they appear in syntactic structures of natural languages. This is interesting as the genetic difference between human and non-human primates is less than 2 % (The Chimpanzee Sequencing and Analysis Consortium 2005, Scally et al. 2012, Meyer et al. 2012), but there are differences in the basic neuroanatomy. These differences may be crucial and, therefore, deserve a closer look, both with respect to brain structure and brain function. A focused across-species look at the language-related brain structures as defined for humans may be of special interest here. These language-related brain regions in humans—as discussed above—are the inferior frontal gyrus and the posterior temporal cortex.

In humans, the language network with its posterior temporal region and Broca's area is lateralized to the left hemisphere. Neuroanatomically, it has long been reported that in the human brain the posterior temporal cortex is larger in the left than in the right hemisphere (Witelson 1982). For the planum temporale, a region that lies posterior to Heschl's gyrus and encompasses Wernicke's area, which has long been identified to support speech and language processing, a hemispheric asymmetry is consistently reported for humans (Geschwind & Levitsky 1968, Steinmetz et al. 1989, Watkins et al. 2001). It was shown in a recent meta-analysis that the anatomical asymmetry of the posterior temporal cortex is necessary for optimal verbal performances (Tzourio-Mazoyer & Mazoyer 2017). A cross-species comparison involving chimpanzees and three other non-human primate species, including macaques, focused on the grey matter asymmetry of the planum temporale. Analyses revealed that only chimpanzees as our closest relatives demonstrate an asymmetry of the planum temporale similar to humans (Lyn et al. 2011). The other crucial language-related brain region, Broca's area, known to be essentially involved in the human ability to process syntax, also deserves a detailed neuroanatomical evaluation. It has been demonstrated that a leftward asymmetry of Broca's area evidenced by a cytoarchitectonic analysis exists in the adult brain (Amunts et al. 2003). No such asymmetry can be found in the homologue of Broca's area in adult chimpanzees (Schenker et al. 2010). The observed neurobiological difference of these brain regions between the human and the non-human primate may be viewed as a crucial parameter for the evolution of language.

Moreover, the white matter connections between these brain regions should be of particular interest as they guarantee the information transfer between regions. There are a number of structural imaging studies on long-range white matter connections in macaques, chimpanzees, and humans which suggest interesting differences between human and non-human primates (Catani et al. 2002, Anwander et al. 2007, Rilling et al. 2008, Saur et al. 2008, Makris & Pandya 2009, Petrides & Pandya 2009). These studies indicate differences in the strength of the fibre bundles connecting the frontal and temporal regions known to be involved in language processing in humans. In these studies two major white matter pathways were analysed: the dorsal pathway connecting Broca's area to the posterior superior temporal gyrus/superior temporal sulcus and the ventral pathway connecting the most ventral part of the frontal cortex to the temporal cortex (Catani et al. 2005, Rilling et al. 2008). In humans this dorsal pathway is much stronger than in non-human primates. A direct comparison revealed that macaques and chimpanzees display a weak dorsal pathway but a strong ventral pathway, whereas humans display a strong dorsal pathway and a weaker though well-developed ventral pathway. The dorsal pathway was therefore discussed as the crucial pathway for the language ability in humans (Rilling et al. 2008; see also Rilling et al. 2012).

The difference in the strength of these fibre tracts is of particular interest in light of a combined functional and structural imaging study in humans (Friederici et al. 2006) which investigated that processing of artificial grammar types similar to those used in the behavioural study by Fitch & Hauser (2004). In humans, processing the $(AB)^n$ grammar, with its adjacent dependencies, activated the frontal operculum, whereas processing the more complex A^nB^n grammar, however, additionally recruited the phylogenetically younger Broca's area (Friederici et al. 2006). Furthermore, the structural imaging analyses conducted in this study found that the frontal operculum processing the $(AB)^n$ grammar was connected to the temporal cortex via a ventral pathway, whereas the posterior part of Broca's area computing the A^nB^n grammar was connected to the posterior temporal cortex via a dorsal pathway (Friederici et al. 2006). These data were taken to suggest that the posterior part of Broca's area (BA 44) and its dorsal connection to the temporal cortex, in particular, support the processing of higher-order hierarchically structured sequences relevant to language.[3]

5. Conclusion

The present review on neuroscientific studies of syntax processing revealed an intriguing overlap concerning the brain basis of syntactic processes. They culminate in the view that the human-specific ability to build syntactic hierarchies is neurobiologically anchored in BA 44 as part of Broca's area and the dorsally-located fibre tract connecting this brain region to the posterior temporal cortex. The empirical evidence for this view comes from neurofunctional and neuroanatomical observations in adult humans, in developing children and from cross-species comparisons of human and non-human primates.

The data show that within the language domain the posterior part of Broca's area, BA 44 is functionally unique in its involvement in the basic syntactic operation Merge. It can be functionally differentiated from BA 45 as the more anterior part of Broca's area involved in semantic processes and from the more ventrally located frontal operculum responsible for simple combinatory processes without building a syntactic hierarchy. Phylogenetically, BA 44 appears to be a more recent brain region than the frontal operculum, and this more recently evolved BA 44 reveals a structural difference between human and non-human primates (Sanides 1962, Friederici 2004, Amunts & Zilles 2012). Only in humans is BA 44 larger in the left than in the right hemisphere. Moreover, there are structural cross-species differences with respect to BA 44's connectivity in the larger language network. In

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[3] There is an ongoing debate whether Broca's area is involved in other cognitive processes. Broca's area has been shown to be activated during the processing of syntactic structure and hierarchies in music (Maess et al. 2001, Koelsch et al. 2013) and in mathematics (Makuuchi, Bahlmann & Friederici 2012). I have discussed this in several other publications (Friederici 2002, Jeon & Friederici 2013, Goucha, Zaccarella & Friederici, in press).

humans, BA 44 in Broca's area is connected via a dorsal fibre tract to the posterior temporal cortex including Wernicke's area, and its integrity is related to the ability to process syntax. This dorsal fibre tract is strong in human primates, but weak in non-human primates.

These observations support the view that BA 44 in the posterior part of Broca's area and its white matter connection to the temporal cortex is fundamental for the human language faculty with syntax as its core.

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