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The neural basis for human syntax: Broca's area and beyond

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Language is a uniquely human cognitive system which is biologically grounded in the human brain. Recent studies have shown that syntax processing in humans can be separated from sequence processing, a cognitive ability also present in non-human primates. Syntactic processing as the core of human language is subserved specifically by BA 44 located in the posterior portion of Broca's area in the left inferior frontal gyrus and its white matter connection to the posterior temporal cortex. It is only when this fronto-temporal system has emerged that full syntactic abilities are present — both in phylogeny and ontogeny.

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Introduction

Language is a uniquely human cognitive system. The consideration of language as a biological system is closely related to its neural basis. There are many studies on the neurobiology of language which cover a wide range of aspects, from single word processing to sentence comprehension in humans. However, when it comes to defining the uniqueness of the human language faculty, it seems essential to compare humans to other animals. Humans share a number of cognitive systems with other animals such as memory, attention, learning and sequence processing. Dogs, parrots and non-human primates can learn and use words and symbols to refer to objects and actions. Songbirds and non-human primates can learn and remember sequences of elements — be these tones or syllables — as reported in some more detail below. But only humans possess a biologically predetermined system of rules and operations that permits the combination of words into metastructures such as hierarchically structured phrases and sentences.

One prominent linguistic theory [1,2] proposed that syntax allowing the generation of larger sentence structures can be broken down into one single, most basic computational mechanism called 'Merge', which binds elements into a hierarchical structure. What does Merge refer to? An example may be the best way to clarify this. When you listen to a sentence and you hear the word *the* (determiner) followed by the word *ship* (noun), the computation Merge binds these two elements together to form a hierarchically structured determiner phrase (*the ship*). Then when you hear the word *sinks* (verb) next, the computation Merge again binds two elements together, that is, the determiner-phrase (*the ship*) and the verb (*sinks*), leading to a hierarchically structured sentence *The ship sinks*. Applying this computation recursively, over and over again, an infinite number of sentences of any length can be generated and mentally represented. Recent data suggest that this basic computation Merge has a well-defined localization in the human brain [3].

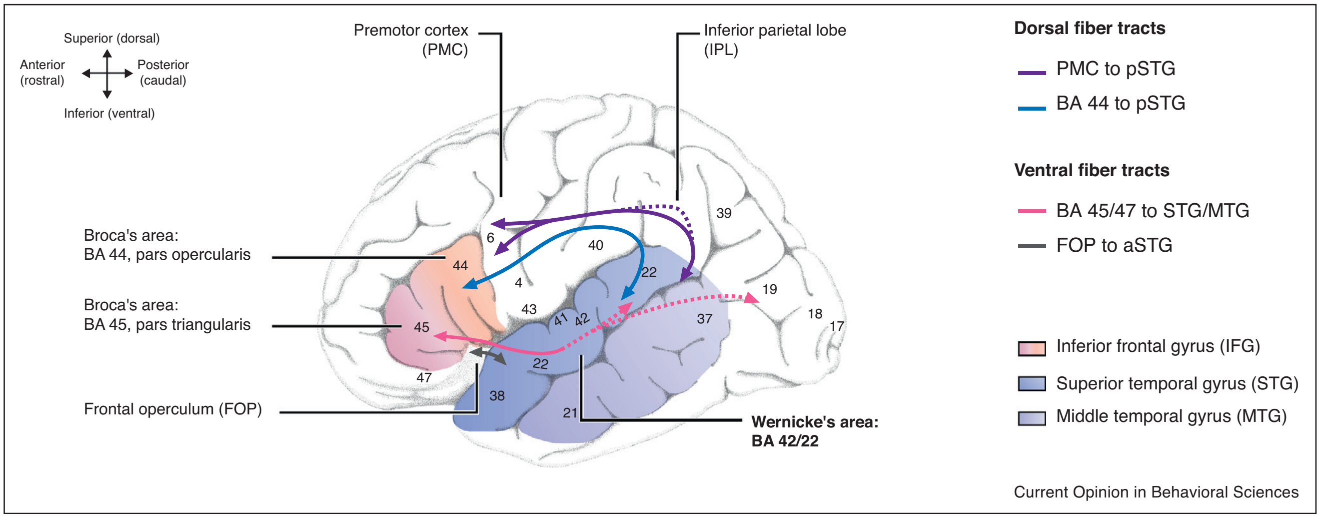
Syntax and Broca's area

A recent functional imaging study investigated the neural basis of Merge in a determiner phrase using a determiner (*the*) which is free of semantic information and a semantics-free noun (*pish*) and found brain activation localized in the most ventral portion of BA 44, the posterior part of Broca's area located in the inferior frontal gyrus (IFG) (see Figure 1) [3]. This stood in clear contrast to the processing of two-word sequences without syntactic hierarchy (*cloud*, *pish*), which activated the frontal operculum/anterior insula [4] — a phylogenetically older brain region than BA 44 itself [5–7]. This result suggests that the processing of syntactic hierarchy selectively involves a phylogenetically more recent cortical region, namely BA 44.

Previous neuroimaging studies on syntax mostly investigated the processing of larger sentences structures varying their syntactic complexity (for a recent review see [8•]). Across different languages these studies consistently reported activation in Broca's area, in particular its more posterior part BA 44 [9]. Thus it appears that syntactic hierarchy building in natural languages is supported by this particular brain region in the IFG, independent of whether the syntactic structure is small as in a single phrase or large as in complex sentences.

Notably, Broca's area has also been shown to be involved in the processing of artificial grammars as long as these are phrase structure grammars which either require hierarchy building as in artificial grammars using natural grammar

Figure 1



Structural connectivities between language regions in the left hemisphere. A schematic, condensed view of language-relevant brain regions and fiber tracts connecting these. The dorsal pathway which connects the posterior temporal cortex (pSTG/pMTG) with the inferior frontal cortex via the superior longitudinal fascile and the arcuate fascile consists of two dorsal fiber tracts with different termination points: one in the premotor cortex (PMC) (purple tract going through the inferior parietal cortex (IPL)), and the other in BA 44 (blue tract going directly to BA 44). The ventral pathway which connects the inferior frontal cortex to the temporal cortex also consists of two ventral fiber tracts: one connecting BA 45 to the temporal, parietal and occipital cortex, involving the inferior fronto-occipital fascile (pink tract); and the other connecting the frontal operculum (FOP) to the anterior superior temporal gyrus (aSTG), involving the uncinate fascile (dark gray tract).
Adapted from Refs. [9,47].

rules [10,11•] or allow hierarchy building [12] although these latter grammars could in principle be dealt with by simpler processing strategies (for a discussion see [13]). Concerning the latter grammars a study by Friederici and colleagues [12] is of particular interest in a cross-species perspective as this study conducted with humans used stimulus material previously applied to non-human primates [14]. In the non-human primate study two grammar types were used, a finite state grammar following an $(AB)^n$ rule which requires sequencing and a phrase structure grammar following an A^nB^n rule which allows hierarchy building. Testing cotton-top tamarins and human adults in a behavioral grammar learning paradigm it was found that humans learn both grammar types easily, whereas monkeys were only able to learn the simpler finite state grammar with its adjacent dependencies, but not the phrase structure grammar with its non-adjacent dependencies [14]. The corresponding functional fMRI experiment with humans [12] revealed that the processing of the phrase structure grammar recruited Broca's area, whereas the simpler finite state grammar was processed by the frontal operculum [6,7]. The data from these studies suggest that the phylogenetically younger Broca's area serves as the neural basis for syntactic structure building.

Broca's area therefore deserves a detailed neuroanatomical evaluation when investigating the neurobiological basis of language. This should apply to this area's gray matter as well as its white matter connections to other regions within the larger language network. Concerning the gray matter it has been demonstrated that a leftward asymmetry of Broca's area (BA 45 and BA 44) evidenced by a cytoarchitectonic analysis exists in the adult human brain [15], but not in the brain of adult chimpanzees [16]. Moreover, BA 44 and 45 in humans compared to chimpanzees are much larger. Across-species differences were also reported concerning the long-range white matter connections. Structural imaging studies in macaques, chimpanzees, and humans indicate differences in the strength of the white matter fiber bundles connecting the frontal and temporal brain regions [17,18,19•,20,21] known to be involved in language processing in humans [22,23]. In the human brain Broca's area is connected to the posterior superior temporal gyrus/superior temporal sulcus via a strong dorsal white matter pathway which is much weaker in the brain of non-human primates [19•]. The ventrally located fiber tract connecting the frontal and the temporal cortex, in contrast, does not show such differences between species [19•].

The difference in the strength of the particular fiber tracts is of major interest when considering the function of the dorsal and ventral fiber tracts as revealed by their terminating regions (see Figure 1). In the adult human brain there are two subparts of the dorsal fiber tract, one targeting the premotor cortex and one targeting BA 44 in Broca's area. The latter subpart, in particular, seems responsible for syntactic processes [23,24]. The ventral