

Language, mind and brain

Angela D. Friederici^{1*}, Noam Chomsky², Robert C. Berwick³, Andrea Moro⁴ and Johan J. Bolhuis^{5,6}

Language serves as a cornerstone of human cognition. However, our knowledge about its neural basis is still a matter of debate, partly because ‘language’ is often ill-defined. Rather than equating language with ‘speech’ or ‘communication’, we propose that language is best described as a biologically determined computational cognitive mechanism that yields an unbounded array of hierarchically structured expressions. The results of recent brain imaging studies are consistent with this view of language as an autonomous cognitive mechanism, leading to a view of its neural organization, whereby language involves dynamic interactions of syntactic and semantic aspects represented in neural networks that connect the inferior frontal and superior temporal cortices functionally and structurally.

Our conceptions of the neural mechanisms of language have developed in tandem with our understanding of the nature of the language faculty as a cognitive system. Initially, research focused on frontal and temporal cortical regions as being involved in vocal production and speech perception, respectively. Since speech is the main medium of language used for communication, it may seem natural to equate language with speech or even ‘acoustic communication’¹. This view, however, is too narrow. Speech is just one possible way of externalizing language (with sign or writing being other examples), ancillary to the internal computational system. In addition, ‘communication’ is merely a possible function of the language faculty, and cannot be equated with it. We argue that language is a species- and domain-specific human cognitive capacity (Box 1)^{2–6}. In essence, language is an internal computational mechanism that yields an unbounded array of structured phrases and sentences. These must be minimally interpreted at two interfaces—that is, internal thoughts on the one hand, and externalization via sounds, writing or signs on the other (Box 1)^{4,5,7,8}. Neurolinguistics focuses on the study of the neural substrates underlying the computational cognitive mechanism that lies at the core of human language. From a theoretical linguistic standpoint—that of generative grammar—language is posited to be a process described at a formal level, divided into functionally separable or autonomous components, such as syntax, morphology, and so on. The immediate question of interest that then arises is whether the formal representations exploited in generative grammar correspond to actual brain architecture. We will discuss independent lines of research converging on the result that syntactic processes are in fact independently computed in the brain^{9,10}.

Universal grammar in mind and brain

Human infants develop language remarkably quickly, independent of the particular language environment into which they are born^{11,12}. Just as with any other organic system, language development involves the three-way interplay of genetic endowment, external input, and some independent principles for computational systems such as language, at least principles of computational efficiency¹¹. For language, the genetic endowment includes a language-specific component, known as universal grammar (UG) (Box 1)¹³, which

interacts with other cognitive systems. UG dictates, in part, the possible ontogenetic outcomes of language development in the human brain, which are constrained so that only natural languages, but not other kinds of language, can result. Languages that do not conform to UG principles, known as ‘impossible languages’^{14,15}, should not be learnable by infants; only ‘possible’ languages abiding by UG rules should. Possible languages compute the hierarchical structures generated by basic operation of UG, called ‘merge’ (Box 2)^{4,5}. Merge is a universal language-specific combinatorial recursive binary operation that takes two syntactic objects, x and y , and generates a new one, z (see Box 2). At the brain level, studies using functional magnetic resonance imaging (fMRI) have revealed increased activation in Broca’s area (see Fig. 1 for its location) for possible languages only, and not for impossible languages, suggesting that Broca’s area is sensitive to this distinction that was originally developed by theoretical linguistics^{16,17} (for activation in Broca’s area, see Fig. 2). This finding cannot be attributed to simplicity of computation, because impossible languages with rules involving linear order are generally far simpler than possible languages with rules involving recursive hierarchical structures. The impossible rules appear to be absent from the human biological endowment for language and its acquisition¹⁵.

The involvement of Broca’s area (in particular its posterior portion Brodmann area (BA) 44) in syntax learning has been further supported by examining the processing of an artificial grammar that mimics ‘possible’ rules of generative grammar and uses novel words that are assigned to grammatical categories^{10,18}. Evidently, once grammar is acquired, Broca’s area is activated. Moreover, this is independent of semantics, since as long as the structured sequence to be processed follows a UG rule allowing the merge operation, Broca’s area is active, regardless of whether its ‘words’ are real or not^{16,17} (Fig. 2). A recent brain imaging study provided evidence for the localization of the neural substrate of a single application of the merge computation in the human brain¹⁹. The build-up of syntactic structures determined by single merge operations is, for example, a determiner phrase, consisting of a determiner (‘the’) followed by a noun (‘ship’). To investigate the merge computation independent of semantics, a semantic-free determiner phrase can be constructed (‘the pish’). The neural substrate of merge was localized to a very confined subpart of BA 44, namely the most ventral anterior portion

¹Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany. ²Department of Linguistics and Philosophy, Massachusetts Institute of Technology, Cambridge, MA 02139, USA. ³Department of Electrical Engineering and Computer Science and Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA. ⁴University School for Advanced Studies IUSS - Pavia, I-27100 Pavia, Italy. ⁵Helmholtz Institute and Department of Psychology, Utrecht University, 3584 CH Utrecht, The Netherlands. ⁶Department of Zoology and St. Catharine’s College, University of Cambridge, Cambridge CB2 3EH, UK. *e-mail: friederici@cbs.mpg.de

Box 1 | Language is all in the mind

Language is often equated with ‘speech’ or ‘communication’, a view often leading to an inappropriate focus on just the neural mechanisms underlying auditory perception and vocal motor behaviour—all abilities that we share with other mammals and birds^{91,122}. By contrast, we propose that the core human language faculty consists of a biologically determined computational cognitive mechanism that recursively assembles a potentially infinite array of hierarchically structured expressions, an ability apparently unique to humans⁶. Each expression is assigned an interpretation at two ‘interfaces’: a sensory–motor interface involved with the generation of sequential forms serving as an interface spoken or signed language; and a conceptual–intentional interface, involved in generating instructions for inference, reasoning and semantic meaning^{4,5,7,8}. In this sense, language is primarily an autonomous computational system for generating complex thought⁵, which needs to be distinguished from its possible externalization as speech or sign as well as its potential functional use in communication^{7,8}.

Language as a cognitive mechanism develops remarkably rapidly in the human infant without overt instruction, acquiring the grammar and lexicon of the specific languages that are used in the environment in which they grow up^{11,12,102,122}. The distinctive development of a child’s language arises from the interplay of three factors: innate mechanisms, external experience and language-independent properties^{11,12}. The child’s biological endowment is known as universal grammar (UG)¹³. Experience-driven input determines whether the child acquires, for example, Japanese as opposed to German or English. Language-independent properties include general learning mechanisms and principles of computational efficiency¹¹. Ample empirical evidence from infant studies^{12,103} as well as theoretical modelling^{11,123} demonstrates that experience alone without prior constraints provided by UG is insufficient for successful language acquisition. Conversely, experience can be relatively impoverished, and infants often build linguistic structures that they cannot have heard from adults in their environment¹².

Box 2 | Minimalist structure building

In linguistic theory, it was obvious that human language expressions have a hierarchical structure, and the discovery of the specific mathematical regularities behind this structure are at the very origin of the so-called generative enterprise⁵. That is, the observable linear sequence of words or gestures in externalized human language is a linearized version of the hierarchical syntactic structure in the mind^{5,7}. Towards the end of the previous century, certain generative grammar theories have arrived at a much more narrowly defined and precise characterization of human language syntax, adopting the strong minimalist thesis (SMT)³. Instead of a complex rule system, it was proposed that human language syntax can be defined in an extremely simple way, involving a basic operation called ‘merge’^{3,4}. Merge involves a single operation that takes exactly two (syntactic) elements x and y and puts them together to form the set $[x,y]$. Crucially, merge is a recursive operation, that is, it can apply to the results of its own output so that a further application of merge to z and $[x,y]$ yields the set $[z,[x,y]]$, and so on, in theory ad infinitum. For instance, merge can take the words ‘the’ and ‘book’ to form the set $[the, book]$. A further application of merge may then combine that set with ‘read’ to form $[read, [the, book]]$ —that is, the English verb phrase ‘read the book’. The recursive use of merge automatically generates the full range of hierarchical structure that is characteristic of human language and distinguishes it from all other known human and non-human cognitive systems^{5,6}. The SMT^{5,6} holds that the merge function, along with a general cognitive requirement for efficient computation and minimal search for agreement and labelling operations, suffices to account for much of human language syntax. For instance, the syntactic category of a linguistic object constructed by merge is determined by one of its terms, conventionally referred to as the head—hence $[the, book]$ is a noun phrase and $[read, [the, book]]$ is a verb phrase¹¹. Current research within the SMT framework focuses on how the labelling of syntactic objects is determined by general principles of efficient computation that apply in the derivation of syntactic structures¹²⁴.

of BA 44, with a very high consistency across individuals¹⁹ (Fig. 3). In contrast, the processing of two-word sequences without syntactic hierarchy (for example, ‘apple, ship’ or ‘apple, pish’) was localized to the frontal operculum/anterior insula²⁰—a phylogenetically older brain region than BA 44 itself^{21–23}. Thus, from all these empirical results, it appears that the processing of syntactic hierarchy selectively involves a phylogenetically recent cortical region, namely BA 44, with little variance across individuals.

Neural language networks

Numerous neuroimaging studies have established that the processing of syntactic structures is not only based on Broca’s area but also involves a specific left frontotemporal neural network with two distinct brain regions: Broca’s area in the inferior frontal gyrus (IFG), and parts of Wernicke’s area in the posterior superior temporal cortex (pSTC), especially the superior temporal gyrus (STG) and sulcus (STS)^{24,25} (Fig. 1). Broca’s area consists of two cytoarchitecturally distinct parts. The posterior part (pars opercularis, BA 44) appears to subserve strictly syntactic processing^{26,27}, whereas its anterior portion (pars triangularis, BA 45) is known to mainly support lexical-semantic processing^{28–31}. These two subregions of Broca’s area are connected to the temporal cortex by distinct white matter fibre bundles. BA 44 is connected via a dorsally located pathway, whereas BA 45 is connected to the

temporal cortex via a ventral pathway (Fig. 1 and Box 3). Given their target regions, the dorsal pathway appears to support syntactic processes and the ventral pathway to support semantic processes²⁴. Note that lexical-semantic representations of a single word or a list of words are different from sentential semantics, which reflects the meaning relation between words and their thematic roles in a phrase or sentence. Sentential semantics thus depends on syntactic structure, and both types of information recruit the posterior temporal cortex³².

With respect to Broca’s area, the activation of BA 44 as a function of syntax has been confirmed in many studies across different languages by varying sentence syntactic ‘complexity’^{33–39}. Here, the term complexity refers to sentences that deviate from the basic, canonical word order, which in English is subject–verb–object—and also to sentences with varying degrees of hierarchical complexity such as, for example, embedded sentences (see the glossary in Box 4). The observed effect is clear: the greater the complexity, the greater the activation in BA 44^{26,33}.

Although BA 44 appears to be a core region for syntactic processing during sentence comprehension^{33,34}, its activation is sometimes reported to be accompanied by activation in BA 45^{35,36}. These studies used real words, so semantic information was unavoidably present to varying degrees, possibly triggering activation in BA 45. Moreover, most of the studies reporting major activation in BA 45

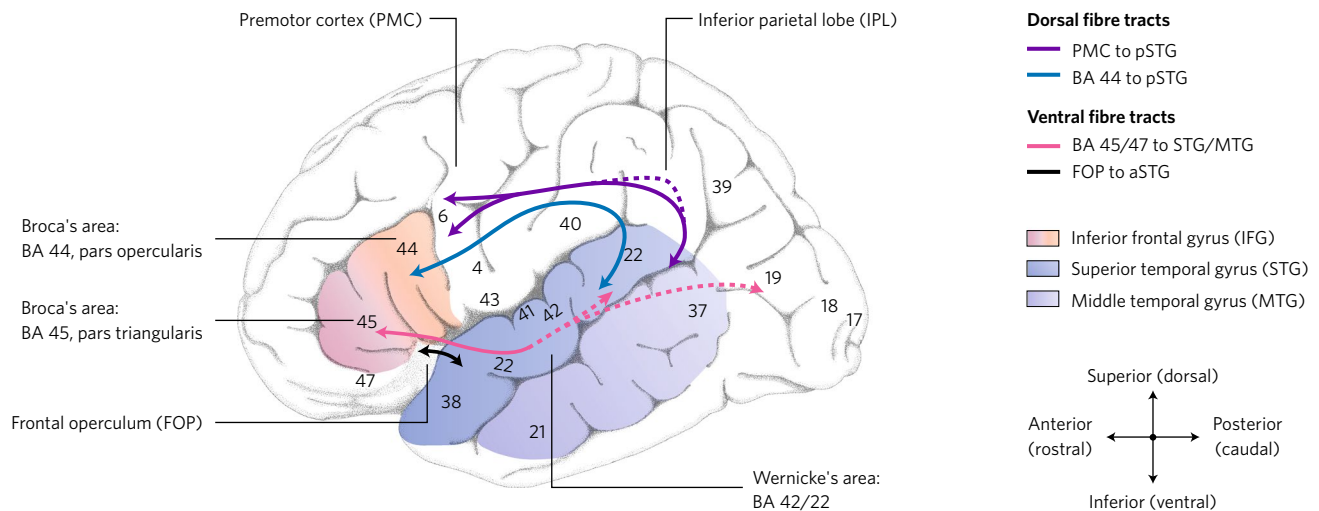


Fig. 1 | Structural connectivity between language regions. A schematic, condensed view of language-relevant brain regions and fibre tracts in the left hemisphere. The dorsal fibre tracts connecting the posterior temporal cortex (pSTG) with the frontal cortex involves the superior longitudinal fascicle and the arcuate fascicle. There are two streams with different termination points: one in the dorsal premotor cortex (PMC) (purple tract), and the other in BA 44 (blue tract). The ventral fibre tracts connecting the frontal cortex to the temporal cortex also consists of two streams: one going from BA 45 to the temporal, parietal and occipital cortex, involving the inferior fronto-occipital fascicle (pink tract); and the other going from the frontal operculum (FOP) to the anterior superior temporal gyrus (aSTG), involving the uncinate fascicle (dark grey tract). Adapted from ref. ²⁴.

and not BA 44 used control conditions that also allow merge operations (activating BA 44). In a direct comparison, BA 44 activation is, therefore, ‘subtracted away’⁴⁰. A clear functional segregation between BA 44 and BA 45 was demonstrated in a specially designed study in German showing that both regions were found to be active as long as even a minimal amount of semantic information in the form of morphological elements (such as ‘un-’ in ‘unhappy’), which alter the word meaning (derivational morphology for example, ‘happy’ versus ‘unhappy’), was present. However, in a semantic-free version in which only syntactic information (function words and inflectional morphology) was available, BA 44 alone was activated²⁷.

Taken together, these results support the view that BA 44 in particular subserves the build-up of syntactic structure during phrase and sentence processing.

The build-up of syntactic structure, however, is only one aspect of phrase and sentence comprehension. Sentence comprehension as a whole recruits a frontotemporal network that includes both Broca’s area and the pSTC²⁴. Within this network, the temporal cortex seems to support the integration of semantic and syntactic information, as it is active when natural sentences that include semantic and syntactic information are processed^{41–44}, but not when artificial grammar sequences lacking semantic information are processed⁴⁵. The coordination of activity in pSTC and left Broca’s area during sentence comprehension has been demonstrated by means of functional connectivity analyses^{42,43} as well as analyses of the synchronized neural activation as measured by brain oscillations (see Box 4)⁴⁴.

This coordination is implemented through a structural connection via the dorsal fibre tract connecting the pSTC to BA 44^{46,47} that can be measured by diffusion-weighted brain imaging (Fig. 1; blue dorsal fibre tract), which is to be differentiated from a dorsal fibre tract targeting the premotor cortex (Fig. 1; purple fibre tract; see also Box 3). The dorsally located pathway targeting BA 44 is crucial for the processing of syntactically complex sentences. This inference is supported by ontogenetic data indicating a direct correlation between the pathway’s maturational status—as reflected in its diffusion properties such as, for example, the increase of myelin, and behavioural performance on processing such sentences⁴⁸, as well as by patient data revealing an inverse correlation between the

pathway’s integrity and deficits in behavioural performance in syntactic processing⁴⁹. Thus, the dorsal frontotemporal network consisting of BA 44 and the pSTC connected by the dorsal pathway subserves mastery of hierarchically complex sentences.

Cortical activity pertaining to the storage and retrieval of lexical items—which certainly has a central role in language—is thought to involve mainly the lateral temporal lobe⁵⁰ (in particular the middle temporal gyrus⁵¹), with a close link to a more medially located part of the temporal lobe, that is the medial temporal lobe involved in memory⁵². However, empirical investigation of semantic processes remains challenging, for two reasons. First, the processing of word-related lexical semantics cannot easily be teased apart from more holistic semantic concepts⁵³. Indeed, the two have sometimes even been considered together as ‘lexical-conceptual semantics’⁵⁴. However, the former may be thought of as a kind of abstract, under-specified representation such as ‘something to sit on’ for ‘armchair’⁵³, whereas the latter is typically construed more broadly as a representation incorporating various general semantic associations such as ‘chair, the most comfortable one’⁵⁵. The latter should result in broadly distributed brain activation patterns⁵¹ due to the possible associations triggered by the lexical element. Given this state of affairs, the brain basis of lexical semantics is still a matter of debate. Patient studies consistently reported semantic deficits both within and outside the language domain for patients with lesions in the left anterior temporal lobe, thereby suggesting that this may be a domain-general region⁵⁶. The anterior temporal lobe brain region, however, has also been thought to support semantic combinatorics in language^{57,58}. Structurally the anterior temporal lobe is connected to the frontal cortex—that is, to BA 45 and the frontal operculum (FOP) via ventral pathways consisting of the long-range inferior fronto-occipital fascicle and the short-range uncinate fascicle (Fig. 1; pink and grey ventral fibre tracts). The long-range ventral pathway connecting the temporal cortex with BA 45/47 in the IFG—a region that has been found to support semantic processes^{29,34,59,60}—is therefore taken to subservise semantic processing^{61,62}. The function of the uncinate fascicle connecting the anterior temporal lobe to the most ventral part of the frontal cortex is still under debate, with some researchers arguing for its involvement in language processing generally^{63,64} and others for its

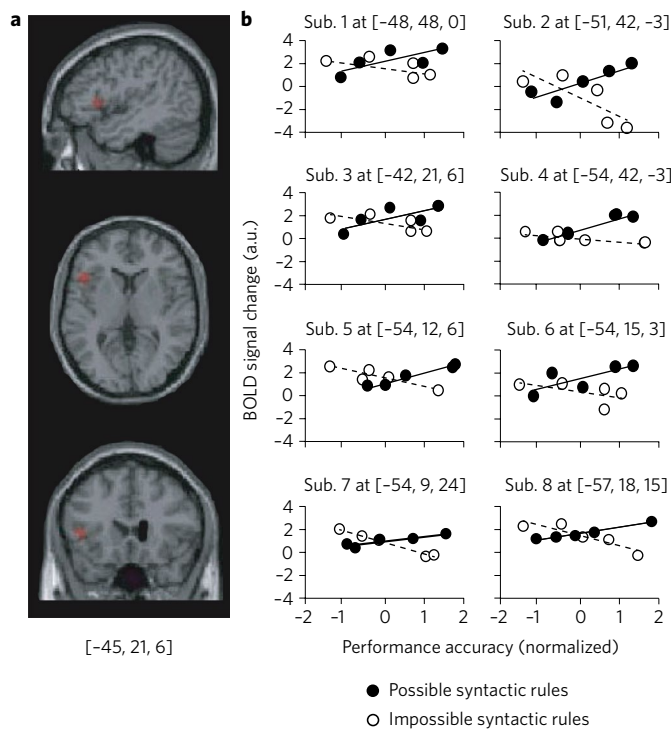


Fig. 2 | Brain recognition of impossible syntactic rules. Result patterns of the interaction between performance and the type of rule learning for different German native speaker subjects (Sub.) that learned a mini version of Italian. This version constrained both possible and ‘impossible’ syntactic rules, that is, rules that are based on a linear sequence rather than recursive hierarchical structures. **a**, The activation specific to possible rules resulting from the random effect analysis is displayed on selected slices of the MRI template available in SPM99 software. The threshold was set at $P < 0.05$ (corrected for multiple comparison). **b**, Plots of changes in blood-oxygen-level dependent (BOLD) signal in the left inferior frontal gyrus in each individual subject (Sub. 1 to 8, with the respective spatial coordinates) for possible and impossible syntactic rules. Similar activations were reported for impossible syntactic rules in Japanese (not shown). Adapted with permission from ref. ¹⁶, Nature Publishing Group.

involvement in the combinatorics of elements independent of hierarchy⁴⁵. Further research is required to clarify this issue.

The empirical analysis of the lexicon remains difficult with current neurobiological methods for several reasons. One is that the human language lexicon also contains so-called function words that serve purely syntactic or logical roles (for example, determiners, quantifiers, conjunctions and negation elements)^{65,66}. A more fundamental reason, however, is that even the simplest words in the lexicon⁶⁷—those typically considered as capable of referring to entities in the real world, such as ‘book’ or ‘river’—are in fact misinterpreted as involving a direct relationship between a mentally represented concept and an object in the real world: they should rather be considered as mental instructions for thinking about reality. The investigation of the lexicon, which together with the syntactic rules constitutes the core language system, thus remains a very challenging area for the neuroscience of language, both theoretically and empirically.

Language production and comprehension involves an external interface system, which, in contrast, is more directly accessible⁴. The neurobiological basis of this external interface system is represented in a particular dorsal fibre tract that connects the sensory system in the temporal cortex to the premotor cortex (Fig. 1; dorsal tract colour-coded in purple). In the adult brain, this fibre tract supports the oral reproduction of heard language sequences⁶¹. Notably

this fibre tract can be separated from the dorsal fibre tract targeting BA 44, although the two run partly in parallel (Fig. 1, dorsal fibre tracts). The difference between these two dorsal fibre tracts becomes most evident when looking at the newborn brain, in which the fibre tract terminating in BA 44 is not yet myelinated whereas the fibre tract terminating in the premotor cortex already is⁶⁸—the syntax-related fibre tract, in particular, matures late.

Language in the developing brain

The maturational status of a fibre tract depends on its myelination. Myelination is functionally critical, as myelin is essential for the transmission of electrical impulses⁶⁹, thereby determining the speed of information transfer from one brain region to another⁷⁰. During human development, different fibre tracts follow different maturational trajectories^{71–74}, with the dorsal fibre tract connecting the pSTC to BA 44 developing quite late during childhood^{48,75}. The maturation of this fibre tract is highly predictive of behavioural performance on processing nonstandard object-first sentences in certain languages⁴⁷, thereby providing evidence for its functional role in processing hierarchically complex sentences.

The functional connectivity between Broca’s area and pSTC, which reflects the coordination between these two areas⁷⁶, also develops slowly from infancy to adulthood. In contrast to adults, who show a marked intrahemispheric functional connectivity between these two brain regions in the left hemisphere, no such connectivity is observed in newborns⁶⁸. Instead, newborns show interhemispheric connectivities between the left Broca’s area and its right hemispheric homologue, and between the left pSTC and its right hemispheric homologue^{68,77}. Functional connectivity between the left IFG and the pSTC can be detected during task-independent brain activation, so-called resting state measures, around the age of 6 years, and is shown to become behaviourally increasingly relevant at that age⁷⁸.

Although Broca’s area and the pSTC are active quite early in life during speech^{68,79}, it takes until late childhood before the two regions in the left hemisphere work together efficiently for speech comprehension. The observed functional development of the neural language network from infancy to adulthood mirrors its structural development: the ventral pathway of the network is established early on, and so is the dorsal pathway targeting the premotor cortex. These pathways support word and phonological learning during early infancy^{80–83}. The processing of syntax in its mature state, however, depends on the full myelination of the dorsal fibre tract targeting BA 44⁴⁸ and the functional specificity of BA 44 for syntactic processes⁸⁴. The specificity of BA 44 to syntax only develops between 7 and 10 years of age; before this, syntactic and semantic processes are not yet segregated neurally, as both information types recruit the same brain regions⁸⁴. This finding can be related to behavioural data indicating an interaction of semantic and syntactic information during early childhood, with the full independence of syntactic from semantic information only being realized around the age of 10 years⁸⁵. Furthermore, analyses at the neural microstructural level also suggest a late maturation of BA 44 into its final adult status, since an adult-like cytoarchitectonic leftward asymmetry only emerges around the age of 10 years⁸⁶.

Given that the syntax-specific neural network of BA 44 and its connection to the pSTC only fully matures during late childhood, the question arises as to how young children generate and understand sentences. One possibility is that, during infancy, language processing is initially based on a system that allows the detection of statistical regularities without necessarily building syntactic hierarchies. During early childhood, syntactic performance may be based on a ventral syntactic system involving the most anterior ventral part of BA 44, supporting single application of the merge computation^{21,87}. This system would allow the processing of phrases and canonical sentences. Further research, however, is needed to

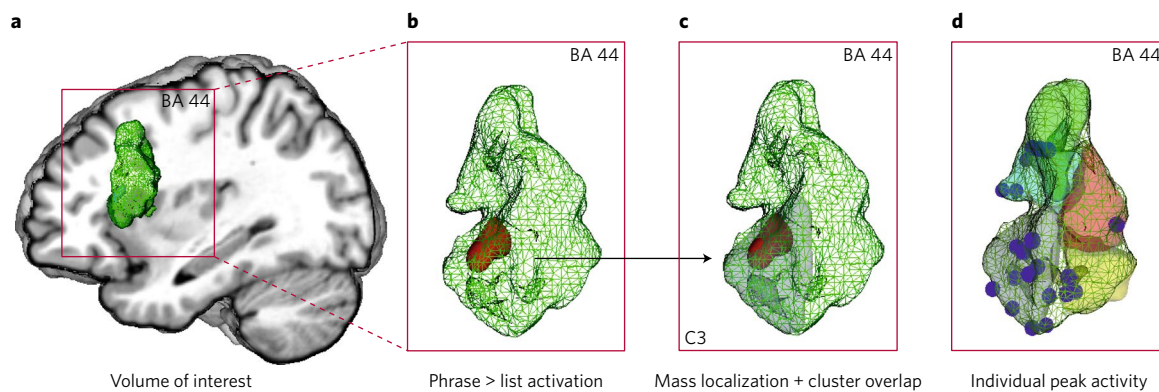


Fig. 3 | Activation of phrase structure building during a merge computation. The figure displays a volume of interest analysis for area BA 44. **a**, Activation contrast between a determiner phrase ('the pish') building condition compared with the processing of a two-word list ('pish, the') within BA 44 (green) in the whole brain. **b**, Extraction and enlargement of BA 44 with the mean activation shown, depicted in red (phrase condition compared to list condition). **c**, The shaded area represents one of five subclusters in BA 44 revealed by a meta-analysis¹²¹, namely the most anterior ventral cluster (C3). Activation, depicted in red, falls in cluster C3. **d**, Individual peak activity distribution within BA 44. Different clusters are colour coded. Significant accumulation of individual peaks (blue dots) are located in cluster C3 ($P < 0.01$). Adapted from ref. ¹⁹.

Box 3 | Neural pathways for language

Language-relevant brain regions such as Broca's area and Wernicke's area are connected by several white matter fibre bundles that transport information in the form of electrical signals from one brain region to the other. The white matter structure of the brain and its different functionally relevant anatomical pathways was first discussed for visual processing¹²⁵ and for auditory processing in the non-human primate¹²⁶, and later also for speech in humans¹²⁷. A dorsal pathway going from the sensory system through the parietal lobe to the dorsolateral prefrontal cortex was functionally linked to the so-called 'where' system, and a ventral pathway going through the temporal lobe to the ventrolateral prefrontal cortex was functionally linked to the so-called 'what' system. Hickok and Poeppel^{128,129} conceptually applied this differentiation to language, talking about dorsal and ventral processing "streams"—without, however, linking these streams directly to particular neuroanatomical fibre bundles. These approaches are distinct from the one presented here, as we consider two functionally distinct dorsal pathways and two ventral pathways²⁴ (see Fig. 1). The two dorsal pathways involve the arcuate fascicle and the superior longitudinal fascicle, which, although they partly run in parallel, can be distinguished by their target regions⁴⁶, in their maturational trajectory⁶⁸ and in their function²⁴.

One dorsal pathway targets the premotor cortex (PMC), and this supports auditory-to-motor mapping, similar to the dorsal processing stream proposed by Hickok and Poeppel^{128,129}. Another dorsal pathway targets BA 44 in Broca's area and supports syntactic processes, as evidenced by recent work in children⁴⁸ and patients¹³⁰. This pathway runs through the inferior parietal lobe known to be responsible for verbal working memory, which may come into play when processing distant syntactic dependencies³⁸. The functional relevance of the two ventral pathways for language is still a matter of discussion. Most researchers agree, however, that the ventral pathway connecting BA 45/47 to the superior and middle temporal gyrus (the inferior fronto-occipital fascicle) supports semantic processes^{61,62,131,132}. The ventral pathway connecting the frontal operculum (FOP) and the anterior superior temporal gyrus (the uncinate fascicle) is thought to subserve combinatorial processes in the semantic domain, and possibly assembling processes before syntactic hierarchy building¹³³.

uncover the exact neural basis of syntax development. The processing of non-canonical and embedded syntactic structures, demanding additional computations such as verbal working memory involve the inferior parietal lobe^{88–90} and most dorsal regions of BA 44 and BA 45^{33–35}, including the inferior frontal sulcus²⁶ as well as the dorsal fibre tract projecting from BA 44 via the inferior parietal cortex to the pSTC⁴⁸ (Fig. 1).

Comparative neurolinguistics

In principle, a computational syntactic system that generates hierarchical structure could have evolved in non-human species, either through descent from a common primate ancestor (so appearing in a non-human primate) or via evolutionary convergence with a more distantly related species (for example, songbirds)^{6,91–95}. However, so far, there is no empirical evidence that any non-human species has such a system^{6,92,96,97}, suggesting that language is human-specific. This is a challenge for comparative research, as there may be "not much to compare"⁶. Nevertheless, efforts continue to discover homologies in non-human primates.

Since Darwin⁹⁸, the comparative method applied to human and non-human primates has been taken as a standard approach to unravel the evolution of language. In a number of studies, human and non-human primates have been compared in terms of their ability to combine words (symbols) during production⁹⁹ and their ability to learn and process structured sequences^{100,101}. Sign language has also been tested, yielding the same result: no non-human primate approaches the linguistic abilities of generating or comprehending two-word phrases^{102,103}. A behavioural study demonstrated that non-human primates (cotton-top tamarins) can learn sequences generated by artificial grammars yielding patterns of a regular $(AB)^n$ type, but not artificial grammars yielding languages with non-regular A^nB^n -type patterns¹⁰⁴. As humans are able to learn both language types easily, it has been concluded that non-human primates differ from humans in that they cannot process recursive hierarchical structures¹⁰⁴. The human brain basis of the processing of $(AB)^n$ grammar was localized in the frontal operculum (FOP), whereas the neural substrate for the more complex A^nB^n grammar was localized in posterior Broca's area (BA 44)⁴⁵. Others have investigated the neural basis for learning linear sequences in both non-human primates and humans by using functional brain imaging¹⁰¹. Brain activation that results from a comparison of correct versus incorrect linear sequences, thereby revealing the violation effect, differed in

Box 4 | Glossary

BA: ‘Brodmann Area’ stands for a cytoarchitectonically defined classification of the cortex according to Brodmann (1909).

Canonical word order: Languages can be differentiated according to different basic canonical word order types. For English, the basic word order is subject-verb-object, which is relatively fixed. The canonical word order of German is also subject-before-object; however, this word order is not fixed. In German, the object can be moved from its original position, leading to object-before-subject structures, thereby deviating from the canonical basic word order.

Cytoarchitecture: Cytoarchitecture of the cortex refers to the type of neuron and their density in different cortical regions.

Diffusion-weighted brain imaging: A procedure used to track white matter fibre bundles in vivo in the human brain.

EEG: Electroencephalography measures the activation of neurons and neural ensembles at the scalp.

Embedding: The possibility for a linguistic dependency (for example, agreement between ‘the boy’ and ‘runs’ in a sentence, ‘the boy runs’) to have another dependency included within it (‘the boy (who smiles) runs’).

Functional brain imaging: Functional magnetic resonance imaging; a method that measures the changes in regional blood flow in relation to local neural activity in the brain.

Hierarchy: Hierarchy in syntax refers to the dominance relation between elements within a phrase and within a sentence. It is potentially infinite.

Impossible language: A language that does not follow the syntactic rules of a natural grammar.

MEG: Magnetoencephalography measures the magnetic field generated by the electrical current induced by neural activity.

Merge: An operation that takes exactly two (syntactic) elements — call them x and y — and puts them together to form the unordered set $\{x, y\}$. The elements x and y can be word-like building blocks that are drawn from the lexicon or previously constructed phrases that are assembled into an unbounded array of hierarchically structured internal representations (phrases and, ultimately, sentences). For example, two items such as ‘the’ and ‘paper’ are assembled as the set $\{the, paper\}$. Crucially, the merge function can apply to the results of its own output so that a further application of merge to ‘publish’ and $\{the, paper\}$ yields the set $\{publish, [the, paper]\}$. Through this recursive operation, the full range of characteristic hierarchical structure

that distinguishes human language from all other known non-human cognitive systems can be derived.

Morphological elements: parts of words that lead to variants of the original word forms.

Derivational morphology: Elements that allow the creation (derivation) of a new word on the basis of an old word such as ‘un-’ in ‘unhappy’.

Inflectional morphology: Elements that allow the formation of a grammatical variant of the same word such as ‘run’ and ‘runs’.

Myelin: The white tissue forming an insulating sheath around nerve fibres.

Neural oscillations: The rhythmic neural activity of single neurons or neural ensembles. At the level of neural ensembles, synchronized activity of a large number of neurons give rise to oscillations that can be observed in the electro- or magnetoencephalogram. Oscillatory activity arises from feedback connections between neurons or neural ensembles reflected in the synchronization of their firing.

Ontogeny: Development or course of development in an individual organism.

Phonology: The study of the abstract sound patterns of a particular language, and the systems of rules governing them.

Prosody: Sentence melody realized by a change in the acoustic parameters of pitch (range, height and variability), loudness and velocity.

Recursion: The property of some operations to reapply to their own outputs. In human language, recursion is usually discussed in relation to the embedding property and hierarchy (see also ‘Embedding’ and ‘Hierarchy’ above).

Resting-state fMRI: Resting-state functional magnetic resonance imaging measures the regional interaction of brain activity when a person is not performing a task. Resting-state functional connectivity can reveal general functional networks independent of specific tasks.

Semantics: The study of the meaning of individual words and the meaning resulting from the composition of words clustered together into phrases and sentences.

Syntax: The universal sets of principles (the ‘rules’) governing the composition of lexical items (sounds, words, word parts, and phrases) into their possible permissible combinations in a language.

humans and macaques in an interesting way. For humans, violation effects were found in the ventral frontal cortex, that is, the frontal operculum (FOP), but not in Broca’s area (BA 44/BA 45). Macaques, in contrast, showed neural activation in the homologue of Broca’s area for simple sequence violations¹⁰¹. Thus, human and non-human primates differ in the recruitment of brain regions in the left inferior frontal cortex for the processing of adjacent dependencies.

Non-human primates are also able to process simple rule-based dependencies between non-adjacent elements as in sequences ‘le-mi-to’, ‘le-gu-to’, in which the non-adjacent elements ‘le’ and ‘to’ are systematically related to each other with a variable element ‘x’ in between¹⁰⁵. Such sequences have been used to investigate precursors of language learning in infants^{106,107}. In the electrophysiological (EEG) studies using such syllable sequences, the processing of incorrect versus correct sequences is reflected in a violation effect

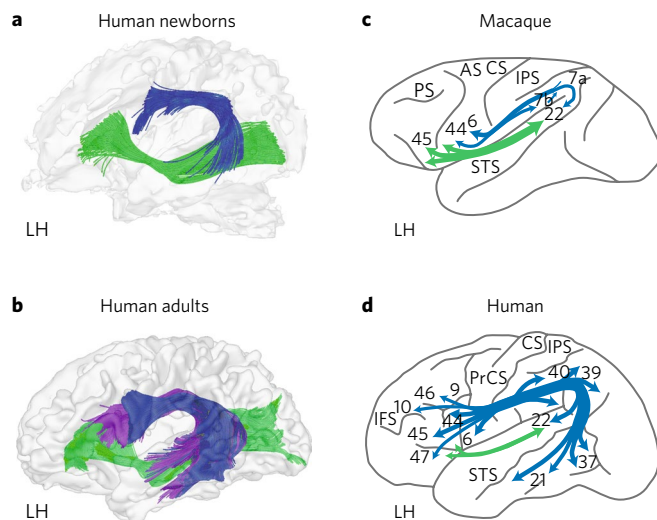


Fig. 4 | Fibre tract pathways in human and non-human primates. The figures shows the structural connectivity results for newborn humans, adult humans and macaques. **a, b.** The results of fibre tracking of diffusion tensor imaging data for human newborns (**a**) and adults (**b**) with seeds in Broca's area (BA 44) and the premotor cortex (PMC). In the adult brain, two dorsal pathways are detectable: one connects the temporal cortex (via the arcuate fasciculus and the superior longitudinal fasciculus) to the inferior frontal gyrus (that is, to the posterior portion of Broca's area (BA 44)) (purple tract); and the other connects the temporal cortex to the premotor cortex (blue tract). In newborns, only the pathway to the premotor cortex (blue tract) is detectable. The ventral pathway connecting the ventral inferior frontal gyrus via the extreme capsule to the temporal cortex (green tract) is present in both adults and newborns⁶⁸. **c, d.** A schematic summary of diffusion tensor imaging data in one human brain in vivo (**d**), and one rhesus macaque brain post-mortem (**c**). Results are shown in Fig. 2a of ref. ¹¹⁰. Dorsal fibre tract, blue; ventral fibre tract, green. In the macaque, the dorsal pathway terminating in BA 44 is not well developed, and in human newborns the dorsal pathway is not yet myelinated, and is therefore low in function. In the human adult, in contrast, the dorsal pathway terminating in BA 44 is strong, as can be seen in both the diffusion tensor imaging data (**b**) and the schematic data (**d**). It is only in the human adult brain that the connection between the posterior temporal cortex and BA 44 is fully developed. LH, left hemisphere; AS, arcuate sulcus; CS, central sulcus; IFS, inferior frontal sulcus; IPS, inferior parietal sulcus; PrCS, precentral sulcus; PS, principal sulcus; STS, superior temporal sulcus. **a, b** adapted from ref. ⁶⁸; **c, d** adapted from ref. ¹¹⁰, Nature Publishing Group.

that can be observed in human adults and infants as well as in non-human primates^{105,108}. Basically, the observed effects were similar in non-human primates and human infants, but they both differed from those observed for human adults. Thus, these data¹⁰⁸ demonstrate that simple rule-based linear sequences can be learned by non-human primates and by prelinguistic infants, possibly based on those pathways that are present in infants and non-human primates allowing phonological learning (Fig. 4).

So far there is no evidence that non-human primates or human newborns can process hierarchically structured phrases. To process such phrases, adult humans possess a specific network including a functionally specified BA 44 that is structurally and functionally connected to the left pSTC. The evidence indicates that this network is not fully evolved in non-human primates^{109–111}, and immature in young infants⁶⁸. Its myelination may follow a genetically determined maturational trajectory during development. Given that both non-human primates and human infants are not able to process

complex syntactic hierarchies, we conclude that the dorsal network consisting of BA 44 connected via the arcuate fascicle to the pSTC is crucial for this distinctive human ability.

Electrophysiology of the internal language code

Along with the intriguing findings from neuroimaging studies¹¹², empirical data relating to human language is emerging from electrophysiological measurements and the respective frequency analyses. The acquisition of this type of data from non-invasive techniques (such as EEG and MEG) or invasive procedures (during awake surgery)¹¹³ appears to be a very promising domain of research. This leads to the generation of qualitatively different data, allowing us to ask the question of how neuronal ensembles are activated when they are processing linguistic information, as opposed to where they are located. Together these different data types will provide a better understanding of the dynamics within the neural language network.

Due to ease of accessibility, the first important results have come from acoustic and phonetic observations. Neural activity in the STG is modulated to track the envelope of the acoustic stimulus with different frequency bands reflecting syllable and phoneme rates¹¹⁴. This correspondence between neural activity and the speech envelope in auditory regions permits recognition of the phonetic features that are heard during speech perception, and the reconstruction of simple words as well as linguistically defined phonological entities such as phonemes^{115–118}.

The next problem that neurolinguistics faces deciphering the electrophysiological code that carries structural information such as the recursive hierarchical structure delivered by the merge operation. A first study carried out via awake surgery techniques¹¹⁹ revealed that the wave form of cortical activity in Broca's area and the wave form of the sound envelope of corresponding utterances correlate during reading aloud, starting before any sound was produced, and even in the absence of speech; that is, when patients read silently. This correlation between the sound envelope area and cortical activity around Broca's area is apparently sensitive to the theoretical linguistic distinction between words and sentences. Another study on auditory language perception using EEG measurements constructed sentences in which the normal joint presence of the syntactic and prosodic phrase boundary was broken, leading to a systematic mismatch between the syntactic and prosodic phrase boundary. In the EEG signal, delta band oscillations reflected that syntactic phrase rather than acoustic (prosodic) boundary cues were crucial¹²⁰. An internal linguistic bias for grouping words into syntactic phrases thus appears to be active during speech processing.

Approaching the issue of online structure building, a combined MEG and electrocorticographic study during surgery demonstrated that the processing of different hierarchical levels is reflected in different frequency bands⁴⁴. The processing of a sequence of syllables revealed different frequency bands depending on the internal representation of word phrases and sentences due to the underlying language knowledge that allows the construction of these from subphrasal units. This neural tracking of hierarchical linguistic structures appears to be dissociated from the encoding of acoustic cues. These results indicate that a hierarchy of neural processing timescales underlies the grammar-based internal construction of hierarchical linguistic structure.

Ideally, these findings open the door to identifying the electrical activity corresponding to the mental representation of syntax. The current research is a first step in integrating the results obtained in understanding fine-grained localization analysis and those of cortical activity pertaining to the merge operation¹⁹ and recursion, and finding the explanatory link between the neuroanatomical data, the electrophysiological data, and the formal properties of human syntax.

Conclusions and perspective

The study of language's neural mechanisms has received a new impetus from a focus on the key mechanisms underlying the human language faculty as described by linguistic theories. Only when we realize that language is essentially a cognitive computational system will we be able to fruitfully explore its neural mechanisms. Here, we have reviewed evidence consistent with the hypothesis that language is an autonomous computational system with a distinct neural underpinning. This system is grounded in a frontotemporal network in which the neural substrate for the basic recursive hierarchy building computation is localized in Broca's area, and which works together with the posterior temporal cortex to achieve language comprehension. We argue that this functional relationship is crucially supported by white matter fibre connections that are more prominent in the human than in the non-human primate brain. Progress in the formal analysis of the computational mechanisms of language as suggested by contemporary linguistic theory together with new neuroscientific data and methods have clearly extended earlier insights, and are now yielding new and original questions concerning the most important aspect of the human mind: language.

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References

- Ackermann, H., Hage, S. R. & Ziegler, W. Brain mechanisms of acoustic communication in humans and nonhuman primates: an evolutionary perspective. *Behav. Brain Sci.* **37**, 529–604 (2014).
- Chomsky, N. *Syntactic Structures* (Mouton, The Hague, Paris, 1957).
- Chomsky, N. *The Minimalist Program* (MIT Press, Cambridge, MA, 1995).
- Berwick, R. C., Friederici, A. D., Chomsky, N. & Bolhuis, J. J. Evolution, brain, and the nature of language. *Trends Cogn. Sci.* **17**, 89–98 (2013).
- Chomsky, N., Huybregts, R. & van Riemsdijk, H. *Noam Chomsky on the Generative Enterprise* (Foris, Dordrecht, 1982).
- Bolhuis, J. J., Tattersall, I., Chomsky, N. & Berwick, R. C. How could language have evolved? *PLoS Biol.* **12**, e1001934 (2014).
- Huybregts, M. A. C., Berwick, R. C. & Bolhuis, J. J. The language within. *Science* **352**, 1286 (2016).
- Huybregts, M. A. C. Phonemic clicks and the mapping asymmetry: how language emerged and speech developed. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2017.01.041> (2017).
- Embick, D., Marantz, A., Yasushi, M., O'Neil Wayne & Kuniyoshi, L. S. A syntactic specialization for Broca's area. *Proc. Natl. Acad. Sci. USA* **7**, 6150–6154 (2000).
- Moro, A. et al. Syntax and the brain: disentangling grammar by selective anomalies. *NeuroImage* **13**, 110–118 (2001).
- Yang, C., Crain, S., Berwick, R. C., Chomsky, N. & Bolhuis, J. J. The growth of language: Universal Grammar, experience, and principles of computation. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2016.12.023> (2017).
- Crain, S., Koring, L. & Thornton, R. Language acquisition from a biolinguistic perspective. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2016.09.004> (2017).
- Chomsky, N. *Cartesian Linguistics* (Harper and Row, New York, 1966).
- Moro, A. *Impossible Languages* (MIT Press, Cambridge, MA, 2016).
- Moro, A. *The Boundaries of Babel* 2nd ed. (MIT Press, Cambridge, MA, 2015).
- Musso, M. et al. Broca's area and the language instinct. *Nat. Neurosci.* **7**, 774–781 (2003).
- Tettamanti, M. et al. Neural correlates for the acquisition of natural language syntax. *NeuroImage* **17**, 700–709 (2002).
- Opitz, B. & Friederici, A. D. Brain correlates of language learning: the neuronal dissociation of rule-based versus similarity-based learning. *J. Neurosci.* **24**, 8436–8440 (2004).
- Zaccarella, E. & Friederici, A. D. Merge in the human brain: a sub-region based functional investigation in the left pars opercularis. *Front. Psychol.* **6**, 1818 (2015).
- Zaccarella, E. & Friederici, A. D. Reflections of word processing in the insular cortex: a sub-regional parcellation based functional assessment. *Brain Lang.* **142**, 1–7 (2015).
- Sanides, F. The architecture of the human frontal lobe and the relation to its functional differentiation. *Int. J. Neurol.* **5**, 247–261 (1962).
- Friederici, A. D. Processing local transitions versus long-distance syntactic hierarchies. *Trends Cogn. Sci.* **8**, 245–247 (2004).
- Amunts, K. & Zilles, K. Architecture and organizational principles of Broca's region. *Trends Cogn. Sci.* **16**, 418–426 (2012).
- Friederici, A. D. The brain basis of language processing: from structure to function. *Physiol. Rev.* **91**, 1357–1392 (2011).
- Hagoort, P. Nodes and networks in the neural architecture for language: Broca's region and beyond. *Curr. Opin. Neurobiol.* **28**, 136–141 (2014).
- Makuuchi, M., Bahlmann, J., Anwender, A. & Friederici, A. D. Segregating the core computational faculty of human language from working memory. *Proc. Natl. Acad. Sci. USA* **106**, 8362–8367 (2009).
- Goucha, T. B. & Friederici, A. D. The language skeleton after dissecting meaning: a functional segregation within Broca's area. *NeuroImage* **114**, 294–302 (2015).
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K. & Farah, M. J. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. USA* **94**, 14792–14797 (1997).
- Fiez, J. A. Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum. Brain Mapp.* **5**, 79–83 (1997).
- Démonet, J.-F., Thierry, G. & Cardebat, D. Renewal of the neurophysiology of language: functional neuroimaging. *Physiol. Rev.* **85**, 49–95 (2005).
- Price, C. J. The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann. NY Acad. Sci.* **119**, 62–88 (2010).
- Bornkessel, I., Zysset, S., Friederici, A. D., von Cramon, D. Y. & Schlesewsky, M. Who did what to whom? The neural basis of argument hierarchies during language comprehension. *NeuroImage* **26**, 221–233 (2005).
- Friederici, A. D., Fiebach, C. J., Schlesewsky, M., Bornkessel, I. & von Cramon, D. Y. Processing linguistic complexity and grammaticality in the left frontal cortex. *Cereb. Cortex* **16**, 1709–1717 (2006).
- Newman, S. D., Ikuta, T. & Burns, T. The effect of semantic relatedness on syntactic analysis: an fMRI study. *Brain Lang.* **113**, 51–58 (2010).
- Santi, A. & Grodzinsky, Y. fMRI adaptation dissociates syntactic complexity dimensions. *NeuroImage* **51**, 1285–1293 (2010).
- Tyler, L. K. et al. Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. *Cereb. Cortex* **20**, 352–364 (2010).
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D. & Grodzinsky, Y. The neural reality of syntactic transformations: Evidence from functional magnetic resonance imaging. *Psychol. Sci.* **14**, 433–440 (2003).
- Röder, B., Stock, O., Neville, H., Bien, S. & Röslér, F. Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: a functional magnetic resonance imaging study. *NeuroImage* **15**, 1003–1014 (2002).
- Kinno, R., Kawamura, M., Shioda, S. & Sakai, K. L. Neural correlates of noncanonical syntactic processing revealed by a picture-sentence matching task. *Hum. Brain Mapp.* **29**, 1015–1027 (2008).
- Zaccarella, E. & Friederici, A. D. The neurobiological nature of syntactic hierarchies. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2016.07.038> (2016).
- Friederici, A. D., Makuuchi, M. & Bahlmann, J. The role of the posterior superior temporal cortex in sentence comprehension. *NeuroReport* **20**, 563–568 (2009).
- Den Ouden, D. B. et al. Network modulation during complex syntactic processing. *NeuroImage* **59**, 815–823 (2012).
- Makuuchi, M. & Friederici, A. D. Hierarchical functional connectivity between the core language system and the working memory system. *Cortex* **49**, 2416–2423 (2013).
- Ding, N., Melloni, L., Zhang, H., Tian, X. & Poeppel, D. Cortical tracking of hierarchical linguistic structures in connected speech. *Nat. Neurosci.* **19**, 158–164 (2015).
- Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I. & Anwender, A. The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proc. Natl. Acad. Sci. USA* **103**, 2458–2463 (2006).
- Catani, M., Jones, D. K. & Ffytche, D. H. Perisylvian language networks of the human brain. *Annals Neurol.* **57**, 8–16 (2005).
- Anwender, A., Tittgemeyer, M., von Cramon, D. Y., Friederici, A. D. & Knösche, T. R. Connectivity-based parcellation of Broca's area. *Cereb. Cortex* **17**, 816–825 (2007).
- Skeide, M., Brauer, J. & Friederici, A. D. Brain functional and structural predictors of language performance. *Cereb. Cortex* **26**, 2127–2139 (2016).
- Wilson, S. M. et al. Neural correlates of syntactic processing in the nonfluent variant of primary progressive aphasia. *J. Neurosci.* **30**, 16845–16854 (2010).
- Davis, M. H. & Gaskell, M. G. A complementary systems account of word learning: neural and behavioural evidence. *Phil. Trans. Royal Soc. B* **364**, 3773–3800 (2009).
- Binder, J. R., Desai, R. H., Graves, W. W. & Conant, L. L. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* **19**, 2767–2796 (2009).

52. McCarthy, G., Nobre, A. C., Bentin, S. & Spencer, D. D. Language-related field potentials in the anterior-medial temporal-lobe. 1. Intracranial distribution and neural generators. *J. Neurosci.* **15**, 1080–1089 (1995).
53. Bierwisch, M. Formal and lexical semantics. *Linguistische Berichte* **80**, 3–17 (1982).
54. Jackendoff, R. *Semantics and Cognition* (MIT Press, Cambridge, MA, 1983).
55. Collins, A. M. & Loftus, E. F. Spreading activation theory of semantic processing. *Physiol. Rev.* **82**, 407–428 (1975).
56. Patterson, K., Nestor, P. J. & Rogers, T. T. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* **8**, 976–987 (2007).
57. Bemis, D. K. & Pykkänen, L. Simple composition: a magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *J. Neurosci.* **31**, 2801–2814 (2011).
58. Bemis, D. K. & Pykkänen, L. Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cereb. Cortex* **23**, 1859–1873 (2013).
59. Bookheimer, S. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu. Rev. Neurosci.* **25**, 151–188 (2002).
60. Kuperberg, G. R. et al. Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study. *J. Cogn. Neurosci.* **12**, 321–341 (2000).
61. Saur, D. et al. Ventral and dorsal pathways for language. *Proc. Natl Acad. Sci. USA* **105**, 18035–18040 (2008).
62. Turken, A. U. & Dronkers, N. F. The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front. Systems Neurosci.* **5**, 1 (2011).
63. Catani, M. & Mesulam, M. M. The arcuate fascicle and the disconnection theme in language and aphasia: history and current state. *Cortex* **44**, 953–961 (2008).
64. Duffau, H. The anatomo-functional connectivity of language revisited new insights provided by electrostimulation and tractography. *Neuropsychologia* **46**, 927–934 (2008).
65. Chierchia, G. *Logic in Grammar: Polarity, Free Choice, and Intervention* (Oxford Univ. Press, Oxford, 2013).
66. Tettamanti, M. et al. Negation in the brain: modulating action representations. *NeuroImage* **43**, 358–367 (2008).
67. Chomsky, N. in *From Grammar to Meaning: The Spontaneous Logicality of Language* (eds Caponigro, I. & Cecchetto, C.) (Cambridge Univ. Press, Cambridge, 2013).
68. Perani, D. et al. Neural language networks at birth. *Proc. Natl Acad. Sci. USA* **108**, 16056–16061 (2011).
69. Wake, H., Lee, P. R. & Fields, D. Control of local protein synthesis and initial events in myelination by action potentials. *Science* **333**, 1647–1651 (2011).
70. Nave, K.-A. & Werner, H. B. Myelination of the nervous system: mechanisms and functions. *Annu. Rev. Cell Dev. Biol.* **30**, 503–533 (2014).
71. Pujol, J. et al. Myelination of language-related areas in the developing brain. *Neurology* **66**, 339–343 (2006).
72. Lebel, C., Walker, L., Leemans, A., Phillips, L. & Beaulieu, C. Microstructural maturation of the human brain from childhood to adulthood. *NeuroImage* **40**, 1044–1055 (2008).
73. Lebel, C. et al. Diffusion tensor imaging of white matter tract evolution over the lifespan. *NeuroImage* **60**, 340–352 (2012).
74. Dubois, J. et al. Asynchrony of the early maturation of white matter bundles in healthy infants: quantitative landmarks revealed noninvasively by diffusion tensor imaging. *Hum. Brain Mapp.* **29**, 14–27 (2008).
75. Brauer, J., Anwender, A. & Friederici, A. D. Neuroanatomical prerequisites for language functions in the maturing brain. *Cereb. Cortex* **21**, 459–466 (2011).
76. Biswal, B., Yetkin, F. Z., Haughton, V. M. & Hyde, J. S. Functional Connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn. Reson. Med.* **34**, 537–541 (1995).
77. Lohmann, G. et al. Setting the frame: the human brain activates a basic low-frequency network for language processing. *Cereb. Cortex* **20**, 1286–1292 (2010).
78. Xiao, Y., Friederici, A. D., Margulies, D. S. & Brauer, J. Development of a selective left-hemispheric fronto-temporal network for processing syntactic complexity in language. *Neuropsychologia* **83**, 274–282 (2016).
79. Dehaene-Lambertz, G., Dehaene, S. & Hertz-Pannier, L. Functional neuroimaging of speech perception in infants. *Science* **298**, 2013–2015 (2002).
80. Kuhl, P. K. et al. Infants show a facilitation effect for native language phonetic perception between 6 and 12 months. *Dev. Sci.* **9**, F13–F21 (2006).
81. Gervain, J., Berent, I. & Werker, J. F. Binding at birth: the newborn brain detects identity relations and sequential position in speech. *J. Cogn. Neurosci.* **24**, 564–574 (2012).
82. Friederici, A. D., Mueller, J. L. & Oberecker, R. Precursors to natural grammar learning: preliminary evidence from 4-month-old infants. *PLoS ONE* **6**, e17920 (2011).
83. Friedrich, M., Wilhelm, I., Born, J. & Friederici, A. D. Generalization of word meanings during infant sleep. *Nat. Commun.* **6**, 6004 (2015).
84. Skeide, M. A., Brauer, J. & Friederici, A. D. Syntax gradually segregates from semantics in the developing brain. *NeuroImage* **100**, 206–111 (2014).
85. Friederici, A. D. Children's sensitivity to function words during sentence comprehension. *Linguistics* **21**, 717–739 (1983).
86. Amunts, K., Schleicher, A., Ditterich, A. & Zilles, K. Broca's region: cytoarchitectonic asymmetry and developmental changes. *J. Comp. Neurol.* **465**, 72–89 (2003).
87. Skeide, M. A. & Friederici, A. D. The ontogeny of the cortical language network. *Nat. Rev. Neurosci.* **17**, 323–332 (2016).
88. Meyer, L., Obleser, J., Anwender, A. & Friederici, A. D. Linking ordering in Broca's area to storage in left temporo-parietal regions: the case of sentence processing. *NeuroImage* **62**, 1987–1998 (2012).
89. Grossman, M. et al. Age-related changes in working memory during sentence comprehension: an fMRI study. *NeuroImage* **15**, 302–317 (2002).
90. Fengler, A., Meyer, L. & Friederici, A. D. How the brain attunes to sentence processing: relating behavior, structure, and function. *NeuroImage* **129**, 268–278 (2016).
91. Berwick, R. C. & Chomsky, N. *Why Only Us* (MIT Press, Cambridge, MA, 2016).
92. Bolhuis, J. J., Okanoya, K. & Scharff, C. Twitter evolution: converging mechanisms in birdsong and human speech. *Nat. Rev. Neurosci.* **11**, 747–759 (2010).
93. Gentner, T. Q., Fenn, K. M., Margoliash, D. & Nusbaum, H. C. Recursive syntactic pattern learning by songbirds. *Nature* **440**, 1204–1207 (2006).
94. Abe, K. & Watanabe, D. Songbirds possess the spontaneous ability to discriminate syntactic rules. *Nat. Neurosci.* **14**, 1067–1074 (2011).
95. Bolhuis, J. J. & Everaert, M. (eds) *Birdsong, Speech & Language. Exploring the Evolution of Mind and Brain* (MIT Press, Cambridge, MA, 2013).
96. Berwick, R. C., Okanoya, K., Beckers, G. J. L. & Bolhuis, J. J. Songs to syntax: the linguistics of birdsong. *Trends Cogn. Sci.* **15**, 113–121 (2011).
97. Beckers, G. J. L., Bolhuis, J. J., Okanoya, K. & Berwick, R. C. Birdsong neurolinguistics: songbird context-free grammar claim is premature. *NeuroReport* **23**, 139–145 (2012).
98. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
99. Pearce, J. M. in *Communication and Language* Ch. 8, 251–283 (Lawrence Erlbaum Associates, Hillsdale, NJ, 1987).
100. Fitch, W. T. & Hauser, M. D. Computational constraints on syntactic processing in a nonhuman primate. *Science* **303**, 377–380 (2004).
101. Wilson, B. et al. Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in macaques and humans. *Nat. Commun.* **6**, 8901 (2015).
102. Terrace, H. S., Petitto, L. A., Sanders, R. J. & Bever, T. G. Can an ape create a sentence? *Science* **206**, 891–902 (1979).
103. Yang, C. D. Ontogeny and phylogeny of language. *Proc. Natl Acad. Sci. USA* **110**, 6324–6327 (2013).
104. Hauser, M., Chomsky, N. & Fitch, W. The faculty of language: what is it, who has it, and how did it evolve? *Science* **298**, 1569–1579 (2002).
105. Mueller, J. L., Friederici, A. D. & Männel, C. Auditory perception at the root of language learning. *Proc. Natl Acad. Sci. USA* **109**, 15953–15958 (2012).
106. Saffran, J. R., Aslin, R. N. & Newport, E. L. Statistical learning by 8-month-old infants. *Science* **274**, 1926–1928 (1996).
107. Gervain, J., Macagno, F., Cognoi, S., Peña, M. & Mehler, J. The neonate brain detects speech structure. *Proc. Natl Acad. Sci. USA* **105**, 14222–14227 (2008).
108. Milne, A. E. et al. Evolutionary origins of non-adjacent sequence processing in primate brain potentials. *Sci. Rep.* **6**, 36259 (2016).
109. Schenker, N. M. et al. Broca's area homologue in chimpanzees (pan troglodytes): probabilistic mapping, asymmetry, and comparison to humans. *Cereb. Cortex* **20**, 730–742 (2010).
110. Rilling, J. K. et al. The evolution of the arcuate fasciculus revealed with comparative DTI. *Nat. Neurosci.* **11**, 426–428 (2008).
111. Neubert, F.-X., Mars, R. B., Thomas, A. G., Sallet, J. & Rushworth, M. F. S. Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex. *Neuron* **81**, 700–713 (2014).
112. Cappa, S. F. Imaging semantics and syntax. *NeuroImage* **61**, 427–431 (2012).
113. Ojemann, G., Ojemann, J., Lettich, E. & Berger, M. Cortical language localization in left, dominant hemisphere. An electrical stimulation mapping investigation in 117 patients. *J. Neurosurg.* **71**, 316–326 (1989).
114. Giraud, A. L. & Poeppel, D. Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.* **15**, 511–517 (2012).

115. Nourski, K. V. et al. Temporal envelope of time-compressed speech represented in the human auditory cortex. *J. Neurosci.* **29**, 15564–15574 (2009).
116. Bouchard, K.-E., Mesgarani, N., Johnson, K. & Chang, E.-F. Functional organization of human sensorimotor cortex for speech articulation. *Nature* **495**, 327–332 (2013).
117. Mesgarani, N., Cheung, C., Johnson, K. & Chang, E.-F. Phonetic feature encoding in human superior temporal gyrus. *Science* **343**, 1006–1010 (2014).
118. Kubanek, J., Brunner, P., Gunduz, A., Poeppel, D. & Schalk, G. The tracking of speech envelope in the human cortex. *PLoS One* **8**, e53398 (2013).
119. Magrassi, L., Aromataris, G., Cabrini, A., Annovazzi-Lodi, V. & Moro, A. Sound representation in higher language areas during language generation. *Proc. Natl Acad. Sci. USA* **112**, 1868–1873 (2015).
120. Meyer, L., Henry, M. J., Gaston, P., Schmuck, N. & Friederici, A. D. Linguistic bias modulates interpretation of speech via neural delta-band oscillations. *Cereb. Cortex* **27**, 4293–4302 (2016).
121. Clos, M., Amunts, K., Laird, A. R., Fox, P. T. & Eickhoff, S. B. Tackling the multifunctional nature of Broca's region meta-analytically: co-activation-based parcellation of area 44. *NeuroImage* **83**, 174–188 (2013).
122. Beckers, G. J. L., Berwick, R. C. & Bolhuis, J. J. Comparative analyses of speech and language converge on birds. *Behav. Brain Sci.* **37**, 547–548 (2014).
123. Yang, C. D. Universal grammar, statistics or both? *Trends Cogn. Sci.* **8**, 451–456 (2004).
124. Chomsky, N. Problems of projection. *Lingua* **130**, 33–49 (2013).
125. Mishkin, M., Ungerleider, L. G. & Macko, K. A. Object vision and spatial vision — 2 cortical pathways. *Trends Neurosci.* **6**, 414–417 (1983).
126. Rauschecker, J. P. & Tian, B. Mechanisms and streams for processing of “what” and “where” in auditory cortex. *Proc. Natl Acad. Sci. USA* **97**, 11800–11806 (2000).
127. Rauschecker, J. P. & Scott, S. K. Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat. Neurosci.* **12**, 718–724 (2009).
128. Hickok, G. & Poeppel, D. Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* **92**, 67–99 (2004).
129. Hickok, G. & Poeppel, D. The cortical organization of speech perception. *Nat. Rev. Neurosci.* **8**, 393–402 (2007).
130. Wilson, S. M. et al. Syntactic processing depends on dorsal language tracts. *Neuron* **72**, 397–403 (2011).
131. Saur, D. et al. Combining functional and anatomical connectivity reveals brain networks for auditor language comprehension. *NeuroImage* **49**, 3187–3197 (2010).
132. Weiller, C. et al. How the ventral pathway got lost: and what its recovery might mean. *Brain Lang.* **118**, 29–39 (2011).
133. Friederici, A. D. *Language in our Brain: The Origins of a Uniquely Human Capacity* (MIT Press, Cambridge, MA, in the press).

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Competing interests

The authors declare no competing interests.

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