

Opinion

Evolutionary neuroanatomical expansion of Broca's region serving a human-specific function

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The question concerning the evolution of language is directly linked to the debate on whether language and action are dependent or not and to what extent Broca's region serves as a common neural basis. The debate resulted in two opposing views, one arguing for and one against the dependence of language and action mainly based on neuroscientific data. This article presents an evolutionary neuroanatomical framework which may offer a solution to this dispute. It is proposed that in humans, Broca's region houses language and action independently in spatially separated subregions. This became possible due to an evolutionary expansion of Broca's region in the human brain, which was not paralleled by a similar expansion in the chimpanzee's brain, providing additional space needed for the neural representation of language in humans.

Evolution of language

The evolution of language remains a challenging area of investigation, as our closest living evolutionary relatives, the great apes, do not possess human-like language abilities. Recent attempts to approach this issue have often considered auditory processing or action processing present in human and non-human primates as precursors of speech and language, with a special focus on their neural basis.

Some researchers view auditory processing as a central precursor, and have considered the vocal learning abilities in songbirds and mammals to be at the roots of speech and language [1–3]. Anatomical features of the auditory and premotor cortex as well as the brain pathways connecting these regions have been compared between songbirds, non-human primates, and humans, leading to interesting observations on cross-species similarities and dissimilarities. In particular similarities were found for the auditory cortex as well as the pathway connecting the auditory cortex and the premotor cortex when comparing human and non-human primates [4,5]. However, while this connection is present in non-human primates as well as in humans, it is much stronger in humans in the left language-dominant hemisphere than in the right hemisphere [5,6]. This connection can be viewed as the evolutionary precursor for auditory-to-motor mapping abilities necessary for speech, but not for human language, I would argue (Box 1). The reason is twofold: first, there can be language without speech, as evidenced in human sign language [7]; and second, neuroanatomically language and speech rely on different circuits [8]. Thus, auditory processing is an important, but arguably not the most important aspect of human language and its evolution. One of the most crucial aspects of human language is syntax – the ability to combine words into phrases and sentences (Box 2).

Other researchers considered the relation between language and action planning as the crucial aspect when discussing the evolution of language. While language is clearly a human trait, action

Highlights

Language and action have adjacent, but distinct localizations in the human brain within Broca's region, with language recruiting an anterior part Brodmann area (BA) 44 and action recruiting posterior part of BA 44.

In humans, Broca's area, and in particular the cytoarchitecturally defined BA 44, shows an anterior expansion when compared to chimpanzees.

The expansion of Broca's area in humans compared to non-human primates provides additional cortical space for the human-specific function of language.

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Box 1. Vocal learning and spoken language

The human ability to acquire spoken language depends, in part, on the basic ability of auditory learning. Accordingly, in the discussion of the evolution of language, the hypothesis has been formulated that among other components, vocal and auditory learning is the most relevant one and evolved from an ancient motor learning pathway [1]. This pathway connecting the auditory cortex in the posterior superior temporal gyrus to the premotor cortex dorsally can be observed in human and non-human primates [4,5], and has been considered to support spoken language-related processes in humans [85]. Concerning its evolutionary brain basis, it is interesting to note that in the adult human brain there are two dorsal pathways, one auditory-to-motor pathway and a second dorsal pathway connecting the superior and middle temporal gyri to Broca's area in the inferior frontal gyrus [86,87]. While the former pathway supports auditory-to-motor mapping, the latter is taken to support syntactic processes.

The auditory-to-premotor pathway is present in vocal learning animals including some songbirds, non-human primates and humans, suggesting a continuum in this pathway during evolution [88]. Moreover, in humans, the auditory-to-motor pathway is already well developed at birth [86], whereas the dorsal pathway targeting Broca's area only matures much later as syntactic abilities increase [89]. When considering the continuous versus the discrete components of language, there are a number of components and brain systems which are continuous across evolution, but it seems that there is one component which is only present in humans. This is the ability to process hierarchical syntax, which is supported by Broca's area and its dorsal pathway connection to the posterior temporal cortex.

planning can be observed in human and non-human primates, allowing to investigate its brain basis across species. However, the discussion about the relationship between language and action led to two opposing views based both on theoretical and neuroscientific grounds. One view holds that language emerged from action. While ontogenetic arguments regarding communicative gestures [9] have been brought as support to this view, the main grounding for it comes from neuroimaging findings suggesting that language and action equally involve a particular region in the inferior frontal gyrus, namely Broca's area [10,11]. The second view sees language as a cognitive ability independent of action, mainly based on formal analyses indicating that human language is characterized by syntactic **hierarchy** (see [Glossary](#)) only found in natural language, but not in action [12,13]. This view therefore assumes Broca's area to be a separate uniquely language-related region. The proponents of these two different views have tried to support their theories with arguments at theoretical and empirical levels without, however, reaching a mutual agreement [14]. At the theoretical level, the discussion focuses on the structural hierarchy underlying language and action, but there is an ongoing disagreement on how to define the term hierarchy [15–20]. At an empirical level, **phylogenetic** cross-species behavioral and neural findings are considered under the premise that both human and non-human primates have action abilities, whereas only humans possess language. But even the latter has been called into question [21] arguing that animals have a kind of **syntax**, although not a hierarchically structured syntax of natural languages as in humans [22]. If only humans possess the ability to process hierarchical syntax and if this ability is represented in Broca's area, the question arises: how did this brain region emerge during evolution to support hierarchical structured language in humans?

I take up these issues in turn and propose a model that provides a possible solution to the longstanding debate between the two opposing views. To this end, I take an evolutionary brain perspective which suggests that in humans, both action and language involve Broca's area, but that both functions reside side-by-side though independently in this region. First, I review the major neuroanatomical findings for the functional representation of language and those for the functional representation of action. I then present the results from two studies directly comparing the functional neuroanatomy of language and action in humans [23,24]. Next, I review the available data on the neuroanatomical evolution of the prefrontal cortex and Broca's region, which point towards a spatial expansion of Broca's area from non-human to human primates. Finally, based on these functional and evolutionary findings, I propose that the anterior extension of Broca's area during evolution provided additional neural space for the human-specific function

Glossary

Brodman area (BA): a

cytoarchitecturally defined classification of the cortex according to Brodmann (1909).

Cytoarchitectonic: refers to the types of neuron and their density in different cortical regions.

Gray matter: area of the brain consisting of unmyelinated neurons and other cells.

Hierarchy: hierarchy in syntax refers to the dominance relation between elements within a phrase and within a sentence.

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

Phylogenetic: evolutionary history of the development of a species.

Receptorarchitectonic: refers to the distribution of neurotransmitter binding sites in different cortical regions.

Syntax: in human language, refers to the universal principles (the rules) governing the composition of linguistic elements (sounds, words, word parts, and phrases) into their possible permissible combinations in a given language.

White matter: area of the brain with fiber tracts (axons) that are surrounded by myelin serving as an insulating sheath.

Box 2. Hierarchical and nonhierarchical structured sequences

Language is a uniquely human trait. Other animals can learn words, but they cannot combine these into phrases and sentences. Humans, by contrast, generate phrases and sentences based on a set of grammatical rules. In linguistic theory, it was proposed that in human language the observable linear sequence of words is a linearized version of the hierarchical syntactic structure in the mind [90,91]. Generative grammar theories [29] described grammar as a complex rule system, but some of the recent conceptualizations describe grammar more simply as involving one basic operation called merge [13,29]. Merge takes exactly two (syntactic) elements x and y and puts them together to form the set $\{x,y\}$. Merge is a recursive operation, and can apply to the results of its own output so that a further application of merge to z and $\{x,y\}$ yields the set $\{z,\{x,y\}\}$. For instance, merge can take the words ‘the’ and ‘book’ to form the set $\{\text{the}, \text{book}\}$. A further application of merge may then combine that set with ‘read’ to form $\{\text{read}, \{\text{the}, \text{book}\}\}$ —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 other human and non-human cognitive systems [91,92] (Figure 1E).

The evolution of these syntactic processes cannot be directly investigated, because human-like language is not observed in non-human primates. Therefore, different types of artificial grammars (Figure 1A–D) were used to investigate the ability to process rule-based structured sequences in non-human primates. A simple $(AB)^n$ grammar containing adjacent dependencies was learnt by cotton top tamarins, whereas a more complex grammar (A^nB^n) leading to more non-adjacent dependencies was not [52]. Humans learn both grammars easily, suggesting an evolutionary step in the processing of rule-based sequences. Additional studies showed that non-human primates can process more complex sequences and nonadjacent dependencies [93–95], but not sequences following a repeated structure [96]. Humans are characterized by their ability to easily learn and process nested hierarchical dependencies early in development and across cultures [97]. In adult humans, the processing of recursive hierarchical structures in language recruit left Broca’s area [25,51]. Of note, Broca’s area has also been discussed to support the processing of musical syntax [62,98–101], although in contrast to language, music syntax is processed with a right hemispheric bias.

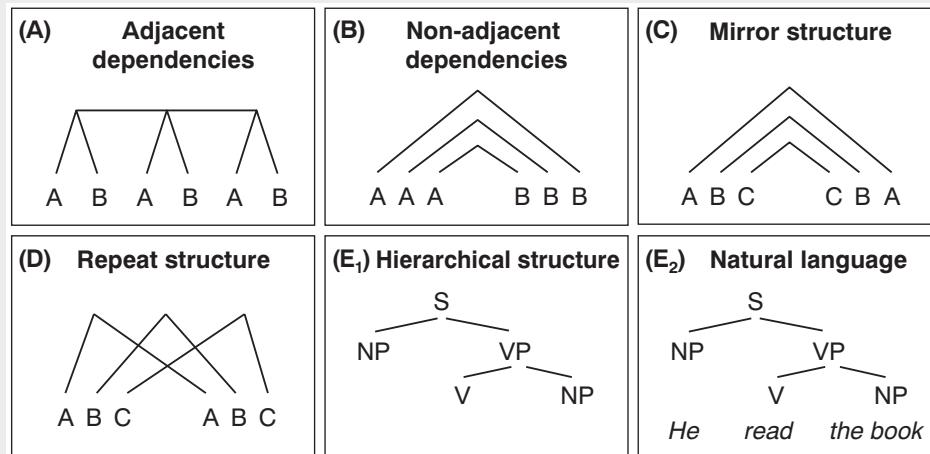


Figure 1. Structures of artificial grammar sequences and natural language. (A) Adjacent dependencies following the $(AB)^n$ rule. (B) Nonadjacent dependencies following the A^nB^n rule. (C) Sequences following a mirror structure. (D) sequences following a repeat structure. A, B, and C in the sequence stand for different item categories. (E) Hierarchical structure of natural language. Abbreviations: NP, noun phrase; S, sentence; V, verb; VP, verb phrase. Adapted from [13].

of language, allowing separate and independent neural representations of language and action in Broca’s region in humans.

Neuroanatomy of language

The core human neural language network has been shown to involve Broca’s area in the left inferior frontal cortex, the left anterior and posterior temporal cortex, as well as the **white matter** pathways connecting these regions [25–28]. Human language is defined to consist of a set of words and syntactic rules according to which words can be combined to build hierarchically

structured phrases and sentences [29]. This combinatorial ability is specific to humans. A strong version of this view holds that hierarchy building is grounded in a computational operation called merge, claimed to be at the root of every human language, and that multiple applications of it leads to hierarchical syntactic structures found in all natural languages (Box 1). Functional magnetic resonance imaging (fMRI) studies have shown that Broca's area is activated during processing syntactically complex sentences [30–36], as well as during processing syntactic hierarchy at the most basic level when applying a single merge computation in a simple two-word phrase [37,38]. Most researchers in the neuroscience of language hold that, in humans, syntactic computations are supported by Broca's area [25,28,30,39–41]. Broca's area [42] has been shown to increase its activation as a function of both increased syntactic complexity [30–36,43,44], and increased constituent structure [41,45]. Moreover, the posterior temporal cortex, as part of the language network, also seems to support sentence processing, in particular when semantic and syntactic information are to be integrated [26,46].

At the neuroanatomical level, two different subregions of Broca's area have been identified in the adult brain: a posterior portion comprising the **cytoarchitecturally** defined **Brodman area (BA) 44** covering the left pars opercularis, and an anterior portion comprising the cytoarchitecturally defined BA 45 covering the left pars triangularis [47]. The cytoarchitecturally defined BA 44 is recruited in particular when dealing with linguistic hierarchies in natural language [25,26], whereas BA 45 supports the processing of semantic aspects [48]. Moreover, the two subregions BA 44 and BA 45 have also been shown to differ **receptorarchitecturally** with respect to their neurotransmitter distribution [49]. During human **ontogeny**, BA 44 and BA 45 follow different trajectories with respect to their cytoarchitecturally defined leftward laterality seen in adults. While BA 45 reaches its left-larger-right laterality at the age of 5 years, BA 44 only reaches laterality at the age of 11 years [50]. This developmental difference is of functional interest, as in adults, BA 45 has been described to support semantic processes, which develop early, whereas BA 44 to support syntactic processes, which develop later during childhood [48].

Thus, in the human brain, Broca's area is part of a left frontotemporal language network in which BA 44 plays a central role in the human-specific ability of processing syntactic hierarchy [25,51].

Neuroanatomy of sequence processing across primates

Given that non-human primates do not possess the ability to process natural language, researchers have used artificial rule-based nonlinguistic sequences to compare human and non-human primates' behavioral language-related abilities, as well as their neuroanatomical representations. Behaviorally, it has been demonstrated that monkeys (cotton top tamarins) can process simple sequences following the $(AB)^n$ rule, but not more complex sequences following the A^nB^n rule [52] (Box 2). At the neuroscientific level, an fMRI study in humans investigating the processing of these two artificial grammar types [53] found that both $(AB)^n$ and A^nB^n grammars activated a phylogenetically older cortex, the frontal operculum, but that only the complex A^nB^n grammar, which monkeys could not process, additionally recruited in humans the phylogenetically younger cortical area, BA 44. Another fMRI study investigated the processing of simple rule-based sequences directly comparing monkeys to humans found an involvement of the opercular cortex and a homologue of Broca's area in monkeys, whereas human adults only activated the opercular cortex, but not Broca's area [54]. These two studies suggest that for the processing of simple rule-based sequences, human adults do not need to recruit Broca's area, and that Broca's area only comes into play once linguistic hierarchies are to be processed.

Additional across-species comparisons focused on the core functional language network, and the relation between Broca's area and the posterior temporal cortex. A comparison of resting-

state functional connectivity linking frontal and temporal brain regions revealed interesting differences between macaques and humans [55]. The functional connectivity of posterior temporal cortex to ventral inferior frontal cortex (including Broca's area) was systematically stronger in humans than in the macaque, particularly in the posterior part of Broca's region (BA 44) – an area which in humans is involved in syntactic hierarchy building. Given these functional connectivity findings, the question arises as to what extent are the observed functional connectivity differences across macaques, chimpanzees, and humans based on structural connectivity differences. Concerning the structural connectivities between Broca's region and the temporal cortex, it was found that the dorsal pathway is stronger in humans compared to chimpanzees and stronger in chimpanzees compared to macaques [6,56,57], and that it connects to the middle temporal gyrus only in humans [6,57]. Behaviorally, there are clear differences in the language abilities between humans and non-human primates including chimpanzees and macaques. Moreover, minor behavioral differences between chimpanzees and macaques have been reported, with more variability of vocal production in the chimpanzee [58]. Thus there are functional and structural differences across species in the connectivity of core language brain regions. The neuroanatomical changes of Broca's area itself during evolution will be discussed in a later section.

There are clear cross-species behavioral differences with respect to the ability of processing nonhierarchical and language-related hierarchical sequences and their neural basis. The processing of simple rule-based nonlinguistic sequences, which in non-human primates activates homologue regions of Broca's area, do not involve Broca's area in humans, but only the phylogenetically older frontal operculum. By contrast, linguistic sequences as in natural language, which can only be processed in humans, activate a left fronto-temporal neural network, with Broca's area being a major processing hub. These findings suggest an evolutionary step in the involvement of Broca's area and its connection to the temporal cortex when processing hierarchically structured linguistic sequences.

Neuroanatomy of action across primates

Action has been considered an important testing ground for complex behavior across species, in particular when discussing the function of Broca's area. There is empirical evidence that in humans, Broca's area is involved not only in language but also in some aspects of action [18,23,59]. However, the human action network clearly differs from the language network in that it engages the parietal cortex in addition to Broca's area [60] rather than the temporal cortex as in language [25].

Functional neuroimaging studies in humans showing activation in Broca's area gave rise to the claim that Broca's area is equally supporting both action and language [9,61,62]. However, action-related neuroimaging studies comparing human and non-human primates often do not investigate all aspects of action, but focus on the observation of object-directed grasping actions as the test paradigm. In humans, a distributed frontoparieto-occipitotemporal neural network was identified underlying this process [63–65]. Cross-species studies using the same paradigm revealed a similar network in macaques, but with a relatively greater prefrontal activation and less parietal activation compared to humans [66]. For intransitive actions, homolog brain regions were reported for macaques and humans [64,67], but not for actions consisting of movements without results on objects [68]. A direct comparison of humans and non-human primates revealed that human activation is mainly distributed across more posterior parietal brain regions, whereas activation in non-human primates has a prefrontal bias including area BA 44 and BA 45 [69]. This suggests that, during evolution, the neural representation of action may have undergone a shift from a more frontally biased network in non-human primates to a more parietally biased network in humans.

In summary, these functional neuroanatomical data of action-related processes suggest a phylogenetic shift within action-related frontoparietal network from a higher involvement of prefrontal regions in macaques and chimpanzee to a higher involvement of parietal regions in humans, thereby possibly setting free frontal regions for the representation of additional functions, such as language.

Direct comparison of action and language in Broca's region

Only two studies, to my knowledge, have directly compared action and language in humans at the functional neuroanatomical level – a meta-analysis and an empirical study. These studies consistently report action and language to be represented in Broca's area though in nonoverlapping regions.

A recent meta-analysis conducted across more than 416 experiments on action processing revealed functional specificities for different action domains [23]. This is not surprising, since action consists of different subprocesses from the mental representation of the prospective action to the actual motor execution. The meta-analysis therefore grouped the experiments into six action domains, with only three of them activating Broca's area [23]. These were action execution, action imitation, and motor imagery; that is, all action domains that require a mental representation of the action. By contrast, observation of simple actions, motor learning, and motor preparation paradigms did not lead to activation in Broca's area, but rather to activation in motor and premotor cortices. The action-related activation that was found in Broca's area was located in a subregion of BA 44, namely its posterior part. This action-related activation was compared with language-related activation from independent meta-analyses [70,71]. The action-related activation was located in the posterior part of BA 44 (pBA 44) whereas the language-related activation was located in the more anterior part of BA 44 (aBA 44), with no overlap between the two subregions. A meta-analytic connectivity analysis revealed that these two different activation spots within BA 44 were part of two distinct functional networks in the human brain. The aBA 44 spot related to language was part of a fronto-temporal functional connectivity network whereas the pBA 44 spot related to action was part of a fronto-parietal network (Figure 1A,B). This activation difference together with the theoretical argument that action and language follow different principles in hierarchy lead to the view of independent systems for language and action in humans [72].

A more recent fMRI study comparing directly neural activation patterns for tool use and language processing also did not find an overlap of these two functions in Broca's area [24]. This study used syntactically complex sentences similar to those used in prior language studies and tried to construct a tool use paradigm of a particular complexity. The only neural overlap of the two functions was observed in the basal ganglia. In Broca's area, no functional overlap was found. Rather two separate activation spots were identified, with a more posterior activation for tool use and a more anterior activation for language (Figure 1C), much in line with the findings from the meta-analysis [23]. The authors of the fMRI study comparing tool use and language take their findings to indicate the existence of shared functional resources and to support theories of the coevolution of tool use and language [24]. However, the basal ganglia, the only region in which the neural overlap was found, is not very domain-specific, as it is also involved in emotional and reward-based learning [73]. Therefore, given the functional nonspecificity of this brain structure, it appears difficult to interpret the results of the study, as rendering support for the notion of coevolution of language and action.

These two studies, which directly compare the neural basis of action and language, suggest that action-related processes activate the most posterior portion of Broca's area, namely pBA 44, and

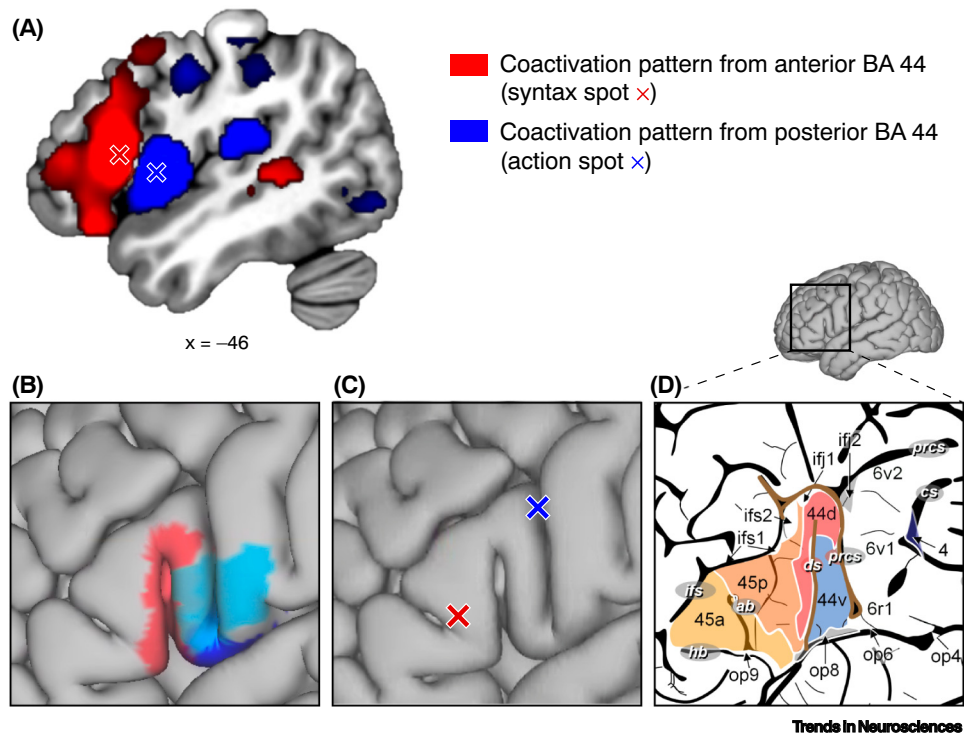


Figure 1. Language and action in Broca's area. (A) Coactivation patterns as revealed from a meta-analytic connectivity analysis for language and action were obtained from two different subregions centered within Brodmann area (BA) 44, with language localized in anterior BA 44 (red) and action in posterior BA 44 (blue) (centers are highlighted by a cross) [23]. Coordinates are in the MNI space. Coordinates were taken from different meta-analyses for language, anterior BA 44 (Cluster 3, Language) [70] and for action, posterior BA 44 from the meta-analysis [23]. (B) Activation maps for different functions, including syntax in red, and action in blue (adapted from [70]). (C) Activation spots (peak activations) for language (complex syntax) in red and for action (tool use) in blue as reported in [24]. (D) Receptor architectonic subregions in area 45 and 44. Area 44 is subdivided into an anterior–dorsal (44d) part color coded in red and posterior–ventral (44v) part color coded in light blue (adapted from [49]).

that this region is not overlapping with the language-related brain region located in aBA 44. Phylogenetically, Broca's region may have changed from a purely action-related area in non-human primates to an area which in humans house action and language side-by-side but independently in BA 44. The functional differentiation of the cytoarchitecturally defined BA 44 into an anterior and a posterior part may find a possible explanation in these subregions' receptorarchitectonic differentiation (Figure 1D) [49].

Thus, we are now left with two independent observations: (i) the phylogenetic shift of the action-related network reducing the involvement of the frontal brain regions in humans; and (ii) the phylogenetic shift of Broca's region from an action-only region in non-human primates towards a region supporting action and language in humans. These observations raise the question about the neuroanatomical evolution of Broca's region.

Evolution of Broca's region

Several attempts have been made to analyze the evolution of Broca's region, in the hope of shedding light on the structure–function relationship of this region. Neuroanatomical analyses have revealed interesting similarities and dissimilarities of Broca's region across primates [74] (Figure 2A). The available data reveal a difference between the human and the non-human

and temporal cortices from early *Homo* to *Homo sapiens* [76]. The enlargement of the prefrontal cortex during evolution has been discussed as being related to the emergence of higher cognitive functions in humans, and possibly language.

A cross-species neuroanatomical comparison of the prefrontal cortex revealed that the human prefrontal cortex, when compared to other association areas scaled to the visual cortex, is larger in the human than in the chimpanzee, and that both differ from monkeys, thereby delineating a clear phylogenetic trajectory enlarging the **gray matter** of the prefrontal cortex [77,78]. Comparing the gray matter volume of the prefrontal cortex using a tissue volume analysis it was found that this was 1.9-fold greater in humans than in macaques and 1.2-fold greater in humans than in chimpanzees [79]. A cross-species cytoarchitectonic comparison revealed that Broca's area in the left hemisphere – but not the right hemisphere – expanded in relative size during evolution from the chimpanzee to the human brain [80]. A more recent chimpanzee to human comparison used a method directly aligning the two species brains according to their sulcal and gyral structure and found that the cytoarchitectonically defined BA 44, in particular, expanded anteriorly in humans (Figure 2B) [49,81]. This anterior expansion of BA 44 in humans is the very part of BA 44 that receptorarchitectonically differs from its posterior part (Figure 2C) [74], and in which the language-related activation spot was found to be located in the meta-analyses (Figure 1) [70,71].

In addition to these phylogenetic differences in the gray matter, there are a number of cross-species differences in the structural white matter connection from Broca's region to language-related temporal regions as discussed above [6,57,82]. These cross-species differences in the structural aspects of Broca's area and its connection to the posterior temporal cortex of the language network make Broca's area a prime area for the evolution of language.

The foregoing discussions focussed on the phylogenetic trajectory across primates with respect to the growth of the prefrontal cortex, in particular Broca's area and its cytoarchitectonically defined subregions BA 44 and BA 45. The anterior expansion of BA 44 observed in humans compared to chimpanzees may have been crucial for the evolution of the neural basis of language, as it provides extra space for the representation of language in addition to action. It appears that during evolution language has invaded Broca's region functionally, which prior to humans, subserved action. This evolutionary expansion could be viewed as a case of partial neural reuse of phylogenetically older brain structures for the more recently emerging faculty of language [83,84]. This reuse may have been possible due to changes in the tissue's receptorarchitectonic structure, differentiating anterior and posterior BA 44. However, a number of crucial open questions remain to be addressed in future studies (see [Outstanding questions](#)).

Concluding remarks

The reported neuroanatomical differences of Broca's region between humans and chimpanzees could be relevant for the evolution of language as these species clearly functionally differ in their language ability. In humans, compared to chimpanzees, Broca's region, and in particular BA 44 anatomically expanded anteriorly. It is this anteriorly expanded part of BA 44 which in humans subserves language, whereas the posterior part of BA 44 also present in chimpanzees supports action, suggesting the independence of these functions in the human brain. Thus, it appears that the emergence of language in humans coevolved with the expansion of BA 44 in Broca's region providing additional neural space for the representation of language.

Outstanding questions

Can the functional neuroanatomical separation of language and action so far evidenced by meta-analyses over different studies between subjects be replicated in additional studies comparing language and action in a within-subject design?

Are there different neural networks for language and action whereby the language network involves Broca's area and the posterior temporal cortex whereas the action network involves Broca's area and the parietal cortex?

Can the functional neuroanatomical separation of language and action reported for the adult human brain, already be observed during childhood in the developing brain?

Does the extension of Broca's region in humans lead to cross-species differences in the short-range structural connectivities between Broca's area and the surrounding regions?

Can the receptorarchitectonic subdivision of area 44 observed in humans also be found in chimpanzees?

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Declaration of interests

The author declares no competing interests in relation to this work.

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