

## Feature Review

# Evolution, brain, and the nature of language

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**Language serves as a cornerstone for human cognition, yet much about its evolution remains puzzling. Recent research on this question parallels Darwin's attempt to explain both the unity of all species and their diversity. What has emerged from this research is that the unified nature of human language arises from a shared, species-specific computational ability. This ability has identifiable correlates in the brain and has remained fixed since the origin of language approximately 100 thousand years ago. Although songbirds share with humans a vocal imitation learning ability, with a similar underlying neural organization, language is uniquely human.**

## Recent developments in the study of language

The understanding of language has progressed significantly in recent years and evidence regarding the neural correlates of human language has steadily accumulated [1]. The questions being investigated today could barely have been formulated half a century ago. A number of conclusions can be drawn with fair confidence from research in the past few decades. Human language appears to be a recent evolutionary development: archaeological evidence suggests that it arose within the past 100 000 years [2]. So far, no equivalent to human language has been found in other animal species, including apes and songbirds [3]. However, some of the systems required for language, such as the production of ordered sound sequences, have analogues in other species, such as vocal-learning songbirds [3] (Box 1). Furthermore, there is overwhelming evidence that the capacity for language has not evolved in any significant way since human ancestors left Africa, approximately 50 000–80 000 years ago [2]. Although there are some individual differences in the capacity to acquire language, there are as yet no firmly established group differences (Box 2). If so, then the human language faculty emerged suddenly in evolutionary time and has not evolved since.

Languages do change over time, but this describes change within a single species and is not to be conflated with the initial emergence of language itself. Famously, the 19<sup>th</sup> century 'Stammbaum' ('family tree') grammarians

were the first to articulate a view of human language relationships grounded on the reconstruction of ancestral language forms by collating sound changes among semantically similar ('cognate') words, for instance, 'two', 'duo', 'zwei', arriving at a phylogeny for all Indo-European languages [4]. This view inspired Darwin himself to note parallels between language and species 'family trees' ([5], p. 422–423). More recently, computational tools drawn from modern evolutionary biology and phylogenetics have been applied to language in an attempt to trace the spread of language diversity and pinpoint the times at which various languages diverged from one another, with some success [6–9]. For example, the frequency of word use seems to follow a clear pattern of 'descent with modification', mirroring Darwinian natural selection [9]. Other researchers [10], following the seminal work of Cavalli-Sforza [11], have begun to address the seemingly microscopically detailed variation that occurs from one language variant to another, even when in close geographic contact, aligning this with genetic variation.

However, other researchers have sounded cautionary notes regarding the validity of biological models of language variation because it can be difficult to ensure that biological model assumptions can be carried over intact into linguistic domains [12]. For example, the shared

## Glossary

**Context-free language:** a language (set of sentences) generated by a context-free grammar, namely, a grammar whose rules are all restricted to be in the form  $X \rightarrow w$ , where  $X$  is a single phrase name (such as VP or NP), and  $w$  is some string of phrase names or words.

**Externalization:** the mapping from internal linguistic representations to their ordered output form, either spoken or manually gestured.

**Internalization:** the computations that construct mental syntactic and conceptual-intentional representations internal to the mind/brain.

**Merge:** in human language, the computational mechanism that constructs new syntactic objects  $Z$  (e.g., 'ate the apples') from already-constructed syntactic objects  $X$  ('ate'),  $Y$  ('the apples').

**Nested dependencies:** the particular relationships between elements of a sentence; for example, in 'the starling the cats want was tired' – in an abstract form:  $a^1 a^2 b^2 b^1$  –,  $a^1$  ('the starling') matches up with  $b^1$  ('was tired'), whereas  $a^2$  ('the cats') matches up with  $b^2$  ('want').

**Phonology:** the study of the abstract sound patterns of a particular language, usually according to some system of rules.

**Syntax:** the rules for arranging items (sounds, words, word parts, phrases) into their possible permissible combinations in a language.

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### Box 1. Syntactic song structures?

Darwin [71] noted the striking parallels between birdsong learning and the acquisition of speech in human infants that appear to be absent in our closest relatives, the apes [63]. In both juvenile songbirds and human infants, individuals imitate the vocalizations of adults during a sensitive period early in life and they go through a 'babbling' stage before they reach the adult form [63,70]. In addition, in both cases, the FOXP2 gene is involved in vocalization [63,72,73] and songbirds have brain regions that are analogous (and perhaps homologous) with human cortical regions involved in speech and language [63]. There is a dissociation in the songbird brain between regions mainly involved in vocal production and those involved in auditory perception and memory, similar to a functional dissociation between Broca's area and Wernicke's area in the human brain [63,74]. Recently it was shown that songbirds have human-like left hemispheric dominance of these brain regions during birdsong learning [75,76].

Human language and birdsong both involve complex, patterned vocalizations, but does birdsong also have a human-like syntax? In human language, hierarchical structure can be assembled by combining words into higher-order phrases and entire sentences [3]. In birdsong, individual notes can be combined as particular sequences into syllables, syllables into 'motifs', and motifs into complete song 'bouts'. Variable song element sequences may be governed by sequential rules, what Marler [77] has termed 'phonological syntax'. A recent suggestion that artificial language sequences such as A<sup>n</sup>B<sup>n</sup> can be learned by songbirds [78] has been demonstrated to rest upon a flawed experimental design [64]. Consequently, at present there is no convincing evidence to suggest that birdsong patterns can form (strictly) context-free languages or exhibit the hierarchical structure that characterizes human language [64,69].

genetic endowment for language appears to be fixed within the human species, as discussed in the following section. Because this underlying 'language genotype' is fixed, it cannot be informative for phylogenetic analysis, which relies crucially on differences between species (here, languages) for its basic data (Box 2).

In the remainder of this article, we discuss these novel insights into the nature of language. After summarizing our views on the nature of language, we discuss the latest developments in the study of the neural mechanisms of language and evaluate recent evolutionary approaches.

### Human language has a shared computational core

We turn first to characterizing human language. Perhaps the core question about language is: what is its basic 'design'? As with any biological subsystem, the extent to which this question can be answered is indicative of whether one can tackle other basic questions, including how language is acquired and used, how the capacity for language evolved, how languages vary, and what the neural correlates of language are.

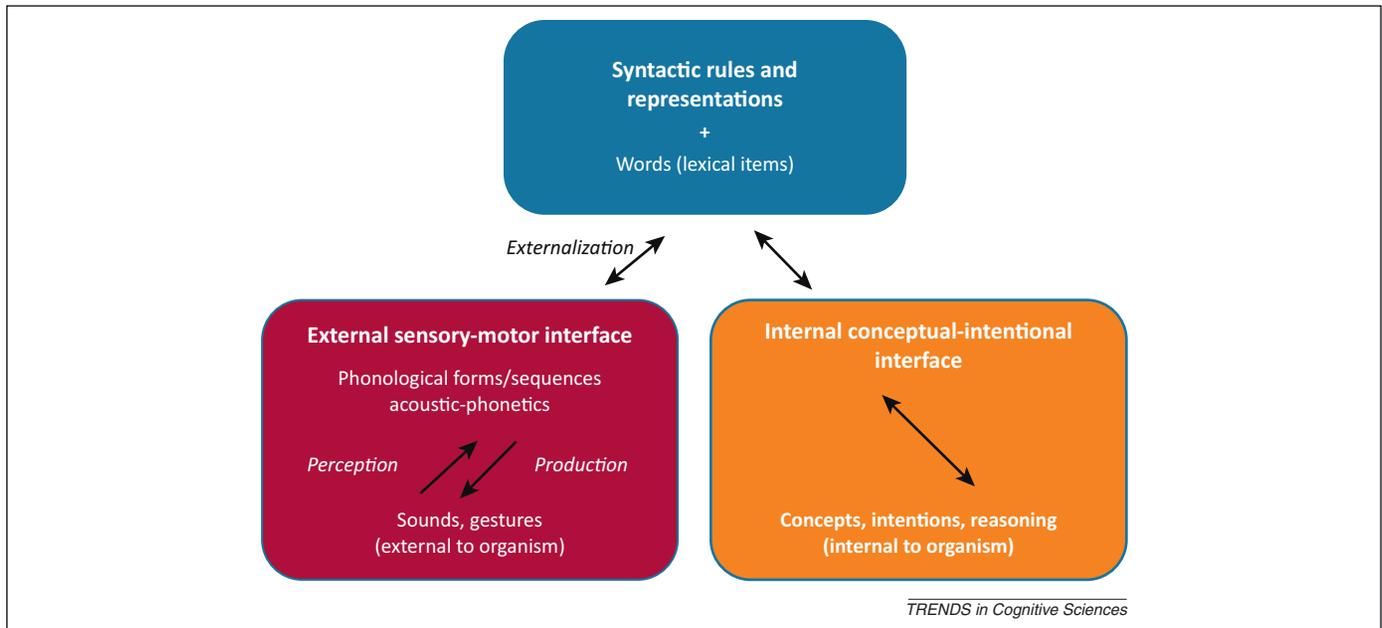
One way to approach this question is as follows. The most elementary property of human language is that knowing some variety of, say, English, each speaker can produce and interpret an unbounded number of expressions, understandable to others sharing similar knowledge. Furthermore, although there can be four and five word long sentences, there can be no four and a half word sentences. In this sense, language is a system of discrete infinity [13]. It follows that human language is grounded on a particular computational mechanism, realized neurally, that yields an infinite array of structured expressions.

### Box 2. Language variation, language change, and evolutionary models

Contemporary population genetics and computational phylogenetics provide powerful new tools to model the origin, historical divergence, and geographic spread of languages, similar to biological species [8,79,80]. However, the assumptions behind biological phylogenetics do not always hold for language, so such methods remain controversial [81,82]. Linguistic variation and biological variation may not always be comparable and we lack good population-based models for human language change coupled with phylogenetic models [81,83]. Human languages share a fixed common core and differ only within a small, finite menu of structures and sounds that have remained frozen as far back as written records exist – unlike the unlimited variation possible for the molecular sequences that have revolutionized modern phylogenetics. Such limits challenge phylogenetic methods because a language feature might appear many times in a single lineage, but there is no way to count how many and estimating evolutionary change becomes difficult. There is one exception: the number of words in a language is effectively unlimited. As a result linguistic phylogenetic analysis has generally proved more successful when applied to words [9]. Furthermore, the geographic contact of one language with another can result in the 'horizontal' transfer of traits from one language to another, creating a reticulated network rather than conventional branching trees. Here, too, special phylogenetic modeling is required, as with bacteria in biology [84]. Given these challenges, prominent researchers in the field argue that linguistic phylogenetic analyzes have not yet matured to the point that they 'are capable of accurate estimation of language family trees' ([81], p. 814) or that one can always disentangle the joint effects of change due to shared history from that due to shared geography [84]. Consequently, it remains to be seen whether these new tools will prove to have as dramatic an impact in linguistic analysis as they have in evolutionary biology.

Each expression is assigned an interpretation at two 'interfaces', as depicted in Figure 1, which envisions an abstract system block diagram for the language faculty. The first interface appears at the left side of Figure 1, a sensory-motor interface that connects the mental expressions formed by syntactic rules at the top of the figure to the external world, via language production and perception. The second, a conceptual-intentional interface, depicted on the right-hand side of Figure 1, connects these same mental expressions to semantic-pragmatic interpretation, reasoning, planning, and other activities of the internalized 'mental world'. In this respect, language satisfies the traditional Aristotelian conception as a system of sound with meaning [14].

As with other biological subsystems, such as vision, the ontogenesis of language ('language acquisition') depends on the interplay of three factors, familiar to biologists [15]: (i) the shared initial genetic endowment; (ii) external data (e.g., environmental stimuli, such as the language spoken to children); and (iii) general principles, such as the minimization of computational complexity, and external laws of growth and form. Factor (i) in turn has several components: (a) language- (and human-)specific components (often called 'universal grammar' [16,17]); (b) conditions imposed by the structure of the brain; and (c) other cognitive preconditions (e.g., a statistical analytical capacity). At a minimum this computational mechanism must be able to combine one linguistic representation (e.g., 'ate') with others (e.g., 'the apples'), yielding new, larger linguistic objects (e.g., 'ate the apples'). On a general level, therefore,



**Figure 1.** The basic design of language. There are three components: syntactic rules and representations, which, together with lexical items, constitute the basis of the language system, and two interfaces through which mental expressions are connected to the external world (external sensory-motor interface) and to the internal mental world (internal conceptual-intentional interface).

the computational mechanism for human language includes some operation that constructs new representational elements  $Z$  from already-constructed elements  $X, Y$ . This operation can be called ‘merge’ [18].

Absent contrary evidence, we assume that this combinatorial operation is as simple as possible, so that ‘merge’ takes just two arguments. The result of  $merge(X, Y)$  is therefore an (unordered) set of two elements  $\{X, Y\}$ , with  $X$  and  $Y$  unmodified. In our example, this would be simply the set  $\{ate, the\ apples\}$  (where ‘the apples’ must be further decomposed, a detail that we do not cover here). In turn, this suggests that wherever linear order appears in language, it is a reflection of the physical constraints imposed on the sensory-motor system’s input-output channel – words must be pronounced sequentially in time. For example, the plural of ‘apple’, ‘apples’, must be pronounced with the ‘s’ following ‘apple’, rather than the reverse, ‘sapple’. Similarly, the words in a complete sentence must necessarily be pronounced one after another rather than simultaneously, thus giving rise to the various basic word order patterns in the world’s languages, such as Subject-Verb-Object order in English. The same holds for language perception, where listeners analyze sequentially ordered acoustic sequences. We will call the mapping from the internal linguistic representations to their ordered output versions ‘externalization’ (see [Glossary](#)). In marked contrast, linear sequential order does not seem to enter into the computations that construct mental conceptual-intentional representations, what we call ‘internalization’ [12]. If correct, this calls for a revision of the traditional Aristotelian notion: language is meaning with sound, not sound with meaning. One key implication is that communication, an element of externalization, is an ancillary aspect of language, not its key function, as maintained by what is perhaps a majority of scholars (cf. [19,20], among many others). Rather, language serves primarily as an internal ‘instrument of thought’ [18].

Further, it should be evident that, although any two arbitrary syntactic objects, including words, may be merged, the result is not always meaningful at one or the other of the interfaces. For example, while the merge of ‘ate’ and ‘the apples’ results in a new, interpretable structured object, ‘ate the apples’, this is not always the case; combining ‘sleep’ and ‘the apple’, ‘sleep the apple’, results in a structured object that the conceptual interface rejects as malformed.

What licenses some combinations but not others? Valid combinations work somewhat like the notion of electron donors and acceptors that form chemical bonds and so chemical compounds – for instance, an oxygen atom needs to accept two electrons, which are provided by two hydrogen atom donors, to complete its orbital shell, forming the chemical compound  $H_2O$ . Analogous to this, merged structures act like chemical compounds: one property (or feature) of a word such as ‘ate’ is that it requires something that is eaten, if only implicitly, here ‘the apples’ (the Object of the sentence). Additionally, considered as a predicate, ‘ate’ can specify who is doing the eating (the Subject). Here, ‘ate’ plays a role analogous to that of oxygen, requiring two ‘electron donors’ (the Object and the Subject), whereas ‘the apples’ and, for example, ‘Charlie’ (the Subject) act like the hydrogen atom ‘donors’. In linguistic parlance, ‘ate’ is the kind of word that ‘probes’ (or seeks) a ‘goal’ with certain features – namely, the goal must be the kind of syntactic object that can be, for instance, an Object, such as ‘the apples’.

But what should be the name of the newly created ‘chemical compound’ formed by probe-goal assemblies such as ‘ate the apples’? In human language syntax, one can posit a labeling algorithm as part of the linguistic system itself: in a combination such as  $\{ate, the\ apples\}$  one element (‘ate’) is taken to label the newly-created compound. This representation distills much of what human language syntax requires for further syntactic computation: that ‘ate the

apples' forms a new syntactic object, a phrase (known in conventional grammar as a Predicate Phrase or a Verb Phrase), and that this structure is labeled with the verb-like features of 'ate', therefore having verbal properties, at least as far as linguistic syntax is concerned, as well as for any sound and meaning properties. This is so because the conceptual interface must know, for example, whether a syntactic object is a predicate or not, whereas the sensory-motor interface must know whether a word such as 'produce' is a noun or a verb in order to assign to it proper pronunciation with the correct stress (if the word 'produce' is a verb, then its stress falls on the second syllable, proDUCE, whereas as a noun the stress falls on the first syllable, PROduce). Crucially, in the case of one syntactic object that is a lexical item, such 'ate', along with another that is a more complex syntactic object, such as 'the apples', then the labeling algorithm selects the lexical item (in our example, the verb 'ate') as the label for the newly composed syntactic object, rather than, say, both elements.

In this sense, natural language phrases labeled with a lexical head (such as a verb, preposition, or adjective) plus some already-built phrase will exhibit the same characteristic structural pattern. Importantly, neural correlates and particular brain regions for this kind of structure-building have recently been discovered (see the following section).

Operating freely, 'merge' results in a ubiquitous human language phenomenon, the apparent 'displacement' of phrases from their normal positions of semantic interpretation. Consider a sentence such as 'Guess what he saw'. Oversimplifying, this sentence is produced by successive merge operations (forming 'he saw what', then 'what he saw what', and finally, 'guess what he saw what'). What is actually spoken arises by deleting the embedded occurrence of 'what', a simplification following the principles of factor (iii) above, reduction of computational complexity, yielding a sentence that is easier to pronounce because it contains only one copy of 'what'.

Unfortunately, the deletion of copies to make sentence production easier renders sentence perception harder, a fact familiar from the large literature on parsing human language [21]. For instance, in 'Who is too stubborn to talk to Morris?', 'who' must be interpreted as the Subject of 'talk', the person who is too stubborn to talk. However, if we encounter 'Who is too stubborn to talk to?', then 'who' must instead be interpreted as the Object of 'talk to'. Here, 'who' does not appear where expected, that is, after 'talk to', but rather at the beginning of the sentence.

Consequently, displacement results in a direct conflict between two competing functional demands: one that follows the computational dictates of factor (iii) above and a second that follows a principle of communicative efficiency. The former prevails, apparently in all languages and all relevant structures [12], again supporting the conclusion that externalization (*a fortiori* communication) is ancillary to language design.

The simplest version of 'merge' has many complex interpretive consequences, supporting the reality of the representations proposed above. Consider the examples in (i)–(iii), where we have left in place the copies that have been displaced in (iii):

- (i) they expect to see each other;
- (ii) guess which boys they expect to see each other;
- (iii) guess which boys they expect which boys to see each other.

Typically, a word such as 'each other' seeks the closest possible word(s) it refers to, where 'closest' is determined by sentence structure, not the number of intervening words. That holds true in (i), where 'they' is closest to 'each other'. However, in (ii) the word closest to 'each other', again 'they', is not selected as the antecedent of 'each other'. Rather, the antecedent of 'each other' is 'which boys'. Evidently, what reaches the mind for interpretation is not the form (ii), but rather the expression (iii), where 'which boys' is indeed closest to 'each other', as predicted by merge in conjunction with the computational principle that seeks the closest possible antecedent. Numerous and far more intricate examples similar to these, ranging across many different languages, illustrate that 'merge' operates in the way suggested earlier [12,13]. For an explicit formalization of 'merge' and this model of syntax, see [22].

In this way, much of the apparent complexity of language flows from externalization, with variation from one language to the next corresponding to different solutions to the way that internal syntactic representations 'surface' as sentences. These are precisely the aspects of language readily susceptible to variation and historical change, where models drawn from evolutionary biology have a role to play in accounting for language variation (Box 2). Whereas learning English requires acquiring from external experience the particular details for English sounds, word formation, word order, and the like, no individual needs to learn constraints such as those exhibited by examples (i)–(iii), which apply in all languages, apparently without exception. These come to us 'from the original hand of nature,' in David Hume's phrase [23] – derived from the human genetic endowment and its language-specific components, as well as from general computational principles.

### Language, words, and evolution

The computational procedure sketched above must include a set of atomic elements that are unanalyzable for the purposes of the computation – though, like atoms, they may be analyzable in different terms. For the core computations of language, this collection is called the 'lexicon', a set of roughly word-like elements. Although essential for language, these elements raise serious challenges for evolutionary analysis, rarely discussed, for one reason because they appear to be radically different from anything found in animal communication.

As an example of this gap, Laura-Ann Petitto, one of the leading researchers of primate communication and early language acquisition, observes that a chimpanzee uses the label for 'apple' to refer to 'the action of eating apples, the location where apples are kept, events and locations of objects other than apples that happened to be stored with an apple (the knife used to cut it), and so on and so forth – all simultaneously, and without apparent recognition of the relevant differences or the advantages of being able to distinguish among them' ([24], p. 86)

By sharp contrast, she continues, for human infants even the first words ‘are used in a kind-concept constrained way (a way that indicates that the child’s usage adheres to “natural kind” boundaries)’. Even after years of training, a chimpanzee’s usage ‘never displays this sensitivity to differences among natural kinds. Surprisingly, then, chimps do not really have “names for things” at all. They have only a hodge-podge of loose associations’ ([24], p. 86). This is radically different from humans.

A closer look shows that humans also do not have ‘names for things’ in any simple sense. Even the simplest elements of the lexicon – ‘water’, ‘tree’, ‘river’, ‘cow’, ‘person’, ‘house’, ‘home’, etc. – do not pick out (‘denote’) mind-independent entities. Rather, their regular use relies crucially on the complex ways in which humans interpret the world: in terms of such properties as psychic continuity, intention and goal, design and function, presumed cause and effect, Gestalt properties, and so on. It follows that the meanings of even the simplest words depend crucially on internal cognitive processes and cannot be spelled out in strictly physical terms. Human words and concepts differ sharply from those in the rest of the animal world in just about every relevant respect: their nature, the manner of their acquisition, and their characteristic use.

What is true of simple words becomes far more mysterious when we move to more complex concepts or to acquisition of language under conditions of sensory limitation, for example, acquisition of language by the blind, who readily achieve exquisite understanding of words for what seeing individuals perceive, as Landau and Gleitman have shown [25]. Or, to take another example of Gleitman’s to illustrate the remarkable feats of language acquisition, consider ‘such words as *fair* (as in “That’s not fair!”), a notion and vocabulary item that every child with a sibling learns quickly, and in self-defense’ ([26], p. 25) – and a concept of considerable subtlety, a centerpiece of contemporary moral philosophy. As she and others have shown, that barely scratches the surface. Not only are the meanings of words intricate, far beyond any evidence available to the child, but they are also learned with amazing rapidity, approximately one per waking hour at the peak period of language acquisition.

Such facts pose extremely hard and crucial questions both for the study of acquisition of language and evolution of the human language capacity. Note that, as in the case of human language syntax, the usual tools for evolutionary analysis, the comparative method, cannot be applied, in an even more radical sense. Whereas analogies between human words and primate vocal calls have sometimes been drawn (see, e.g., [27] on vervet monkeys), it has become more apparent over time that if the minds of these creatures really had a human-like capacity for expression, then there should be no acoustic barrier to stop at just a handful of calls, yet that is what Seyfarth and Cheney [27] observed. Furthermore, there seems to be no vocal learning, so even if a new call was introduced in a group, accurate reproduction seems impossible. Moreover, such calls lack key properties of human words: no abstractions and no ‘displacement’ – calls remain linked to what monkeys are presently experiencing (exactly as with the chimpanzee use of the item ‘apple’ cited by Petitto earlier). Taken

together with the apparent absence of ‘symbolic behavior’ in the closest relative extinct species of *Homo* [2], there is scant evidence on which to ground an evolutionary account for words.

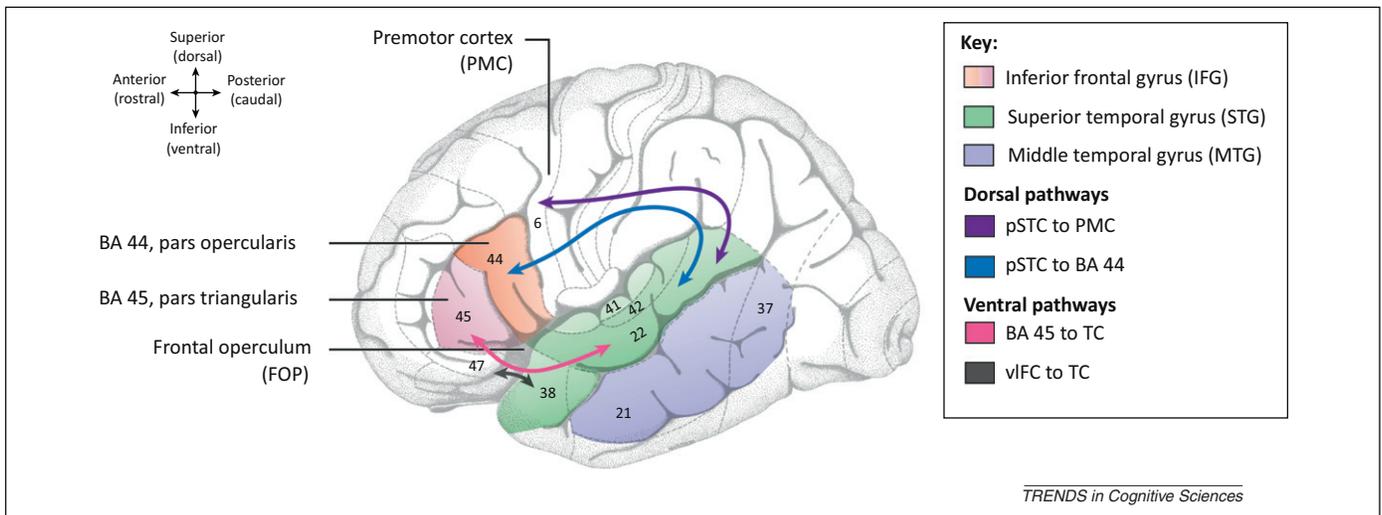
### Human language has a fixed neural architecture

Recent technical advances in neuroimaging have greatly increased our understanding of these language-related processes in the human brain. Natural language and artificial grammar studies have made it possible to determine the neural bases of processing hierarchically structured sequences. Results from studies of artificial grammar learning across species strikingly parallel the distinctions in linguistics between the structures that are characteristic of natural language and those structures involved in other kinds of cognitive processes.

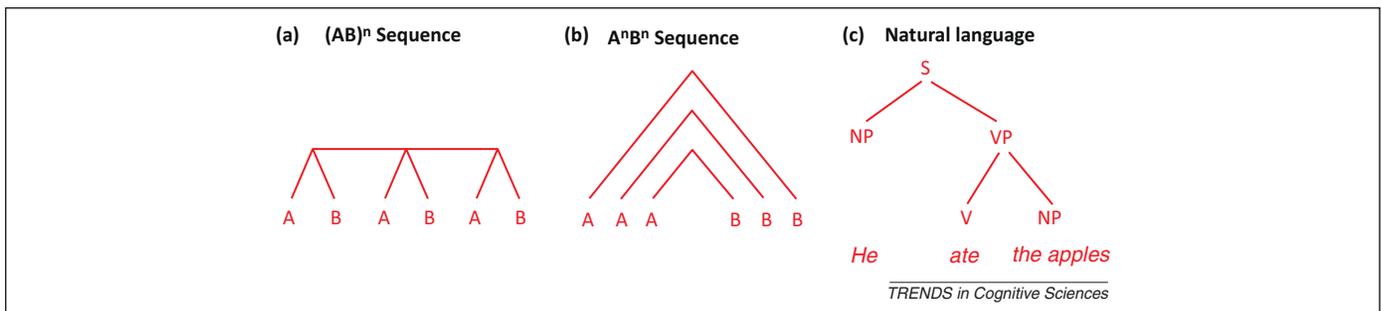
The study of the neural basis of language must consider those parts of the brain that represent the core computations which are thought to be universal, as well as those which constitute the interface systems that may vary across individuals, as these interfaces rely on individual working memory, reasoning, and conceptualization abilities (Figure 1). At the neural level, core computations may be differentiable from a sensory-motor interface and a conceptual system. Each of these systems consists of particular brain regions connected via specific fiber tracts forming a neural network. In this context, two different dorsally located pathways have been identified, one involving Brodmann area (BA) 44 and the posterior superior temporal cortex (pSTC) that supports core syntactic computations [28] and one involving the premotor cortex (PMC) and the STC that subserves the sensory-motor interface [29]. There are also ventrally located pathways which involve brain regions that support semantic processes. These are BA 45 in the inferior frontal cortex and portions of the temporal cortex (for discussion, see [30]; Figure 2). These networks will be specified below.

### Neural mechanisms for syntax and hierarchical structures

Human language contains hierarchical structures that are a product of multiple ‘merge’ operations. It has long been shown that the processing of hierarchically complex sentences involves Broca’s area, in particular, the pars opercularis (BA 44) in the inferior frontal gyrus (IFG; Figure 2) (for a review, see [1]). Recent artificial grammar studies investigating key differences between animals and humans [28,31,32] have often used two types of strings: one of the format  $(AB)^n$  (Figure 3a) and one of the format  $A^nB^n$  (Figure 3b). The processing of  $A^nB^n$  sequences activates Broca’s area (BA 44), whereas  $(AB)^n$  sequences activate the frontal operculum [28], a phylogenetically older cortical area than Broca’s area [33,34]. Note that  $A^nB^n$  sequences could, in principle, be processed without necessarily building hierarchically structured representations at all, by using a counting mechanism along with working memory that checks whether the same number of Bs follow the As [35]. Such a process could in principle be at work in animals and humans. Interestingly, in humans Broca’s area (BA 44) has been found to be activated for the processing of  $A^nB^n$  sequences [28] and for the processing of



**Figure 2.** Language-related regions and fiber connections in the human brain. Displayed is the left hemisphere. Abbreviations: PMC, premotor cortex; STC, superior temporal cortex; p, posterior. Numbers indicate cytoarchitectonically defined Brodmann areas (BA). There are two dorsal pathways: one connecting pSTC to PMC (dark red) and one connecting pSTC to BA 44 (blue). Moreover, ventral pathways connecting BA 45 and the ventral inferior frontal cortex (vIFC) to the temporal cortex (TC) have also been discussed as language-relevant.



**Figure 3.** Artificial strings and natural grammars. (a) Strings of the format  $(AB)^n$ , in which each A-category item is followed by a B-category item. (b) Consecutive sequences of equal numbers of A-category items followed by B-category items can be recognized without necessarily building hierarchical structure, by simply verifying that the number of A-category members to the left match the number of B-category members to the right. Such sequences can also be learnt by songbirds (Box 1). (c) By contrast, natural language structures are always hierarchical and must be processed as such.

complex hierarchical structures in natural languages (Figure 3c) [36–38]. In an elegant study by Moro and colleagues [39], German native speakers successfully learned either ‘real’ or ‘unreal’ grammatical rules of different languages (Italian or Japanese). In the ‘unreal’ versions of the unfamiliar language, the same lexicon was used as in the ‘real’ versions, but the sentences violated the rules of universal grammar. For instance, in a ‘real’ sentence, a literal translation of ‘I eat the pear’ from Italian is ‘Eat the pear’. An example of an ‘unreal’ negating sentence is one where the negative particle is placed after the third word, which does not happen in any natural language. Such an Italian negating sentence in English is ‘Paolo eats the no pear’. Using fMRI, the authors found that increased activation over time in Broca’s area during the learning task was specific for ‘real’ language that observed the principles of universal grammar, independent of the language used. These findings again suggest a role for Broca’s area in the processing of syntax. Importantly, the participants were able to learn the ‘unreal’ grammatical rules, as well as the ‘real’ ones, but, apparently, other brain regions were activated in the process, apart from Broca’s area, which suggested that language can be neurally dissociated from other cognitive capacities.

Natural sentence processing, in contrast to artificial grammar processing, involves the posterior superior

temporal cortex (STC) in addition to BA 44 as part of Broca’s area, to which it is connected via the arcuate fascicle (AF) and parts of the superior longitudinal fascicle (SLF) (Figure 2).

The finding that the processing of natural syntactically complex sentences involves the posterior STC in addition to Broca’s area, in particular BA 44 [40,41], whereas the processing of artificial grammar sequences only involves Broca’s area [28], suggests that within this network BA 44 supports complex structure-building, whereas the integration of syntactic information and semantic information to achieve sentence interpretation is subserved by the posterior STC. This dorsal connection between BA 44 and the STC supports the processing of syntactically complex sentences [42,43]. Evidence for the relevance of the dorsal connection between BA 44 and the posterior STC for the interpretation of syntactically complex sentences comes from studies showing that, if this fiber tract is not fully matured [42] or not intact [43], processing such sentences is deficient.

In humans, there is an additional dorsal pathway that connects the auditory sensory regions in the STC with the premotor cortex (PMC) in the precentral gyrus [44–46]. In contrast to the other dorsal pathway, this second neural circuit is present in the infant brain at birth and remains

unchanged throughout life [47] (Figure 3). In adults this pathway is involved in oral repetition of speech [29] and in infants this sensory-to-motor mapping circuit appears to support phonology-based language learning demonstrated in infants during their first months of life [48,49]. Thus, although this pathway allows the detection of phonologically-coded rules in itself, this circuit is not sufficient to process the structure built by human grammars.

Thus, during ontogeny the dorsal connection between STC and the PMC is present at birth and probably supports auditory-based phonological learning during early infancy [48,50] – one component of the process of externalization. The full maturation of the dorsal connection between BA 44 and the STC, which only seems to happen around the age of 7 years [40], appears to be necessary to process syntactically complex sentences [51].

#### *Neural mechanisms for processing meaning*

The question of how the human brain achieves meaning assignment has been investigated at different levels: at the single word and at the sentence level. Many studies have investigated meaning at the word level (for a review, see [52]), but only few of these studies considered the fact that lexical-semantic and conceptual-semantic aspects during word processing are not easily distinguishable. Within this context, the anterior temporal cortex has been discussed as a region that represents semantic-conceptual knowledge independent of sensory, motor, and language aspects, which in turn are represented in other parts of the cortex, with words recruiting the inferior frontal and superior temporal cortex in particular [53].

Beyond the level of single words, a significant number of neuroimaging studies have focused on meaning assignment during sentence processing, but because this process involves inference, semantic-conceptual knowledge, and reasoning, the localization of its neural substrates is more variable across individuals and therefore more difficult to assess. Many researchers have approached the processing of meaning empirically by comparing normal sentences to so-called scrambled sentences or word lists containing pseudo-words. These studies mainly found activation in the pars orbitalis (BA 47) and the pars triangularis (BA 45) in the inferior frontal gyrus (IFG) and the anterior temporal cortex (for a review of these studies, see [1]). Recently, BA 45/47 has been described as being domain-specific for language [54] or as correlating with the size of linguistic constituents in particular [55]. In the latter study, regions in the temporal pole and anterior STC were activated in proportion to the size of the constituents only when they contained lexico-semantic information, which suggests that these regions are involved in semantic encoding [55]. Others have compared the processing of sentences with implausible and plausible meanings and found that BA 45 and BA 47 were activated as a function of implausibility and the anterior and posterior superior temporal cortex were activated as a function of plausibility (for a review, see [55]).

These inferior frontal and temporal regions are connected via ventral pathways which, however, are hard to differentiate neuroanatomically because they run in close vicinity when passing the insular cortex [56,57] (Figure 2). Within this ventral network, IFG activation is argued to

reflect semantic competition and controlled semantic processes, such as judgment and categorization, both at the word-level [58,59] and sentence-level [60]. Activations in the temporal cortex are reported for the anterior, as well as the posterior portion. The anterior temporal cortex has been associated with semantic combinatorial processes [61], whereas the posterior STC has been argued to support the integration of semantic information provided by more anterior temporal regions and syntactic information provided by Broca's area via the dorsal pathway [30]. Patient studies indicate that the ventrally located system is crucial for language comprehension [62]. It may reflect aspects of the internal interface, such as the retrieval and manipulation of semantic information.

In sum, neuroimaging studies suggest that, in addition to a sensory-to-motor mapping system, there are at least two other language-relevant systems at work in the adult human brain: a dorsal and a ventral language system. First, the dorsal system involves Broca's area (in particular BA 44), which supports core syntactic rule-based computation of hierarchical structure building and which, together with the posterior temporal cortex, subserves the comprehension of complex sentences. Second, the ventral system, which involves BA 45/47 and the temporal cortex, supports the processing of lexical-semantic and conceptual information. To what extent these two systems represent the assumed external and internal interfaces must be evaluated in future studies.

#### **Language evolution**

There is no equivalent to human language in other animal species [3], which poses a challenge for the mainstay of evolutionary explanation, the comparative method. Typically, evolutionary biologists examine species whose last common ancestor with humans is ancient, in order to search for evidence of convergent evolution, or conversely, species whose last common ancestor with humans is relatively recent, in order to search for features of shared, common descent with modification [63].

#### *Evidence of convergent evolution*

Songbirds provide an illustrative example of the former case. Songbirds are capable of sophisticated auditory learning and perception and of vocal production, in certain critical ways mirroring the developmental acquisition and production of human speech, even with analogous brain circuitry [63] (Box 1). However, speech is only an externalization of the internal representations of language as depicted in Figure 1, which limits the comparative power of the songbird model. Furthermore, songbirds lack two essential ingredients of human language: first, the link between word-structured sentences and distinct meanings; and second, the ability to process the hierarchical structures typical of natural language [3,35,64], as described in the previous section (Figure 3).

#### *Shared, common descent with modification*

Turning to the case of common descent and more closely related species, in primates, comparative phylogenetic studies of macaque, chimpanzee and human brains reveal fiber tract differences, in particular with respect to the

dorsal pathway that connects language-relevant areas in humans noted in the previous section. The dorsal pathway that connects Broca's area (BA 44) and Wernicke's area in STC undergoes considerable phylogenetic change: it is weak in non-human primates, but strong in humans [65]. Moreover, cross-species comparative studies on language learning reveal important differences in grammar processing, in particular for hierarchical structures. Comparisons between monkeys and humans indicate that monkeys can learn adjacent dependencies in  $(AB)^n$  strings but not non-adjacent dependencies in  $A^nB^n$  strings, whereas humans easily learn both [31]. Here, in non-human primates, the evidence is equivocal, since for small  $n$  the  $(AB)^n$  and  $A^nB^n$  patterns can both be learned simply by counting matching A's and B's. Whereas the processing of  $A^nB^n$  strings recruits Broca's area (BA 44) the processing of  $(AB)^n$  strings relies on a phylogenetically older cortex, the frontal operculum [28,33].

Taken together, the evidence on birds and primates suggests that three factors are important in the evolution of speech and language. First, there is neural and genetic homology: similar genes and brain regions are involved in auditory learning and vocal production, not only in songbirds and humans, but also in apes and monkeys. Second, there is evolutionary convergence with regard to the mechanisms of auditory-vocal learning, which proceeds in essentially the same way in songbirds and human infants, but not in apes or monkeys. Third, the combinatorial complexity of human language is unique in the animal kingdom [3,35,64]. It may be that the neural mechanisms that evolved from a common ancestor, combined with the auditory-vocal learning ability that evolved in both humans and songbirds, contributed to the emergence of language uniquely in the human lineage.

### Concluding remarks and future directions

The discussion regarding the cognitive capacities particular to human language as opposed to those found across many other animal species has shifted radically in recent years, not only in the domain of cognitive neuroscience, but also in linguistic theory. Over the past 60 years, linguistic theory has consistently sought to reduce what cognitive properties are human-language specific, moving more instead into the realms of general animal cognition or biophysical constraints. Perhaps the most dramatic reduction has been in the intricacy of the assumptions and stipulations required to formulate the linguistic grammars of the early 1950s [66] – drawing on complex Boolean rule conditions, rules, specific rule orderings, language-particular features, and similar devices. This has given way to a far simpler set of basic principles, in much the same way that the descriptively adequate, but overly-complex epicycle account of planetary motion was subsumed under Kepler's and Newton's handful of laws. If this work is on the right track, in effect only the simple 'merge' system plus words remain uniquely human, although too much at present is not understood to be confident about this bold conclusion.

From this standpoint, it is no surprise that researchers demonstrate with some regularity that, in the domain that we have called 'input-output' systems externalization, non-human animals can engage in such tasks as musical

rhythmic entrainment [67] or perception of degraded speech [68], formerly thought to be the sole province of humans. The realization that fewer aspects of language externalization are human-specific than previously thought has greatly improved the prospects for using animal models to understand this particular interface and has sharpened our ability to pinpoint neural mechanisms that in fact are human language specific. To be sure however, striking differences highlighted nearly sixty years ago remain: human reliance on sophisticated structure-building to assemble an unbounded array of interpreted expression, unlike the bounded call systems of any non-human animal.

To the extent that modern linguistic theory has revealed the underlying properties of language, it would seem appropriate to use these properties in future experimental probes of both non-human and human competences related to language, as well as to more nuanced accounts of language use and change. Similarly, the study of language historical change and phylogenetics must carefully distinguish between the fixed properties of human language and those that vary from language to language, perhaps culturally. Formulating accurate evolutionary analogues for language change seems key; here, unifying single-language population models with the cross-linguistic phylogenetics used so far would seem to be a crucial step.

Animal models for human language should move away from tests associated with the more superficial, external aspects of human language, such as simple  $A^nB^n$  strings, and instead probe for the hierarchical sequential structures described by linguistics and with known neural correlates, essential to language. Rather than non-human primates, songbirds and parrots are the most relevant animal models to study the neural mechanism of auditory-vocal learning and the production of structured vocalizations [63,64,69]. Convergent evolution of neural mechanisms underlying speech and birdsong suggests that there are optimal neural solutions to problems of auditory-vocal learning. Animal research thus has important heuristic value for the study of human speech and language and its disorders.

Regarding the neural mechanisms of human language, research should focus on distinguishing neural networks supporting the externalization of language from those engaged in core syntactic computations, such as 'merge'. Moreover, direct comparisons of language processing, as well as language learning, in the developing brain and in the mature brain should be more systematically considered as a window to the neurobiological basis of human language.

Recent developments in both animal and human research and comparisons between these suggest a novel approach to the study of language evolution. Of course, evolution in and of itself cannot explain the complete nature of language [70], but contemporary analyzes suggest that we need to rethink language evolution to begin with. First, regarding human-animal similarities in the domain of auditory-vocal learning, the fact that evolutionary convergence has been found to be more important than common descent has important consequences for the evolution of these capabilities [63]. Second, as we have

discussed, there are crucial differences between humans and any non-human species in terms of syntactic capabilities [3,64] that constrain evolutionary analyzes. Only then can we begin to understand the nature of language and its underlying neural mechanisms.

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