*Feature Review*

Evolution, brain, and the nature of language

Language serves as a cornerstone for human cognition, yet much about its evolution remains puzzling. Recent research on this question parallels Darwins 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, speciesspecific 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]](#_bookmark9). 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]](#_bookmark10). So far, no equivalent to human language has been found in other animal species, including apes and songbirds [[3]](#_bookmark11). However, some of the systems required for language, such as the production of ordered sound sequences, have analogues in other species, such as vocallearning songbirds [[3]](#_bookmark11) ([Box 1](#_bookmark5)). 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]](#_bookmark10). Although there are some individual differences in the capacity to acquire language, there are as yet no firmly established group differences ([Box 2](#_bookmark5)). 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 19th 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 IndoEuropean languages [[4]](#_bookmark12). This view inspired Darwin himself to note parallels between language and species family trees ([[5]](#_bookmark17), p. 422423). 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]](#_bookmark18). For example, the frequency of word use seems to follow a clear pattern of descent with modification, mirroring Darwinian natural selection [[9]](#_bookmark22). Other researchers [[10]](#_bookmark23), following the seminal work of CavalliSforza [[11]](#_bookmark25), 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.

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](#_bookmark5)).

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]](#_bookmark29). It follows that human language is grounded on a particular computational mechanism, realized neurally, that yields an infinite array of structured expressions.

Each expression is assigned an interpretation at two interfaces, as depicted in [Figure 1](#_bookmark6), which envisions an abstract system block diagram for the language faculty. The first interface appears at the left side of [Figure 1](#_bookmark6), a sensorymotor 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 conceptualintentional interface, depicted on the righthand side of [Figure 1](#_bookmark6), connects these same mental expressions to semanticpragmatic 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]](#_bookmark30).

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]](#_bookmark31):

(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:

1. language(and human)specific components (often called universal grammar [[16,17]](#_bookmark33)); (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,

temporal cortex (STC) in addition to BA 44 as part of Brocas area, to which it is connected via the arcuate fascicle (AF) and parts of the superior longitudinal fascicle (SLF) ([Figure 2](#_bookmark7)).

The finding that the processing of natural syntactically complex sentences involves the posterior STC in addition to Brocas area, in particular BA 44 [[40,41]](#_bookmark21), whereas the processing of artificial grammar sequences only involves Brocas area [[28]](#_bookmark13), suggests that within this network BA 44 supports complex structurebuilding, 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]](#_bookmark24). 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]](#_bookmark24) or not intact [[43]](#_bookmark26), 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]](#_bookmark28). 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]](#_bookmark32) ([Figure 3](#_bookmark8)). In adults this pathway is involved in oral repetition of speech [[29]](#_bookmark13) and in infants this sensorytomotor mapping circuit appears to support phonologybased language learning demonstrated in infants during their first months of life [[48,49]](#_bookmark34). Thus, although this pathway allows the detection of phonologicallycoded 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 auditorybased phonological learning during early infancy [[48,50]](#_bookmark34)  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]](#_bookmark21), appears to be necessary to process syntactically complex sentences [[51]](#_bookmark37).

*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]](#_bookmark40)), but only few of these studies considered the fact that lexicalsemantic and conceptualsemantic aspects during word processing are not easily distinguishable. Within this context, the anterior temporal cortex has been discussed as a region that represents semanticconceptual 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]](#_bookmark41).