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Language in Our Brain

The Origins of a Uniquely Human Capacity

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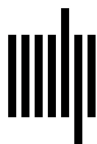
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The Neural Basis of Language

Language is an integral part of our daily life. We use it effortlessly, and when doing so, we usually think about what we want to say rather than how to say it in a grammatically correct way. Thus we use language quite automatically. The intriguing question is what puts us humans in the position to learn and use language the way we do. I started out in the beginning of the book by saying that this is due to an innate language faculty. Over the course of the book it became clear that the language system is a complex system.

In the natural sciences complex phenomena and systems are usually broken down to their basic elements or operations in order to make them approachable. These basic elements—once identified—can be put together and thereby explain a complex system. In chemistry, for example, we are dealing with different basic elements that can be reduced further to a number of atoms, but which can also bind together with other elements to build more complex structures. In this book I have taken a similar approach by breaking the complex language system into its elements and basic operations: these are the lexical elements and the syntactic rules. For the domain of syntax that approach works well due to a clearly formulated linguistic theory that defines a most basic computation, namely Merge (Chomsky, 1995b). This computation was localized in the brain with a high consistency across individuals. For the domain of lexical and sentential semantics this is more difficult, partly due to the indeterminacy of a word's meaning caused by the fact that a word has many mental associations that differ from individual to individual. Linguistic theory can describe the semantic relation between a noun and a verb by means of selectional restrictions in a given language that holds for all individuals using this language, but is not in the position to describe the associations at a cross-individual level, as these may differ substantially from person to person. Given this it is not surprising that the localization of these processes in the brain shows more inter-individual variance.

I also stated that language is a uniquely human trait characterized by the ability to generate and process hierarchically structured syntactic sequences that differentiate us from non-human primates. A comparison with our phylogenetically close relatives, therefore, could provide some insight into what this difference is based upon. Such a comparison can be conducted at different levels: the behavioral level, the brain level, or the genetic level.

With respect to the genetic level, we know that the genetic difference between human and non-human primates is less than 2 percent, but so far we do not know which genetic aspect is responsible for the language faculty. It has been proposed that *FOXP2* is a gene that plays a major role in speech and language because the mutation of this gene was identified in a family with speech and language problems (Fisher, Lai, and Monaco, 2003), although they were more speech-related rather than language problems as such. The view, however, has also been challenged for several reasons. One reason is that *FOXP2* can also be found in non-human primates, mice, birds, and fish, thus in animals that do not speak (Scharff and Petri, 2011). A second reason is the finding that *FOXP2* as such regulates a large number of other genes and thereby the coding of proteins—a relevant aspect in detailed genetic analyses. Novel methods of genetic analyses can inform us about the time trajectory of human evolution and thereby possibly the emergence of language. Using such analyses it could be shown that the *FOXP2* codes a particular protein in the Neanderthals that is the same protein as in the modern human but different from that in the chimpanzee (Krause et al., 2007, Prüfer et al., 2014). These findings suggest that the genetic basis for language was laid down early during evolution—after the separation from the chimpanzee, but before the emergence of the Neanderthals—about 300,000 to 400,000 years ago.¹

Today geneticists agree that the language faculty can not be traced down to a single gene, but rather to a number of related genes that jointly contribute to neural pathways that are important for normal brain maturation and possibly the development of language. With respect to brain development it is known that genetic programs help to guide neuronal differentiation, migration, and connectivity during development, together with experience-dependent contribution of the environment (Fisher and Vernes, 2015). These results provide evidence for a relation between genes and brain development in general, but they do not speak directly to the genetics of language. Most recently it has been shown that a specific gene controls the number of gyri in a particular brain region that includes Broca's area (Bae et al., 2014). Using a combined genetics and brain imaging approach, these researchers examined 1000 individuals with respect to their cortical folding. They found five individuals of three different families that suffered intellectual and language difficulties but had no motor disability. The genetic analysis revealed abnormalities to mutations in the regulatory region of the *GPR6* gene; *GPR6* encodes a protein that functions in neuronal guidance and thereby cortical maturation. This study is the first to show a relation between genetics, brain structure of Broca's area, and language behavior. It is a promising case showing how a tripartite relation between genetics-brain-behavior can help to determine the biological basis of language.

In this book I claimed that the structural language network is genetically predetermined. Under this hypothesis one would expect to find genetic-brain-language relations most likely with respect to the brain-structural parameters. The study by Bae et al. (2014) provides support for the assumption that language emerged during evolution in a genetically yet to be defined step that left its traces in the human brain.

The remaining discussion and the view proposed here will, therefore, be restricted to the brain-behavior level. In the next section I will bring together evidence from the different research areas I discussed in the previous chapters. I will try to provide an integrative view of the language network by taking into account empirical data from human and non-human primates across the various neuroscientific levels.

8.1 An Integrative View of the Language Network

The integrative view of the neural basis of the language network that I propose here will not primarily concern the integration of syntax and semantics within the human language system, but will rather try to integrate language-relevant data across two biologically relevant dimensions: a neurophysiological dimension and an evolutionary dimension. The neurophysiological dimension will focus on the human brain and try to identify within the human brain to what extent particular brain structures for language are characterized by specific parameters at different neurophysiological levels from the neuron to large-scale neural networks. The evolutionary dimension will compare the human and the non-human primates and consider the changes of brain structure and function between primates with the goal of determining possible differences crucial for language. The formulation of such a view, however, must remain incomplete at this point in time, since the required data base is still sparse, but the available data do provide interesting information in particular for the domain of syntax.

With respect to the neurophysiological dimension, I have focused the discussion in this book on the core language system and its representation in the human brain, directing my efforts toward a consideration of the neural basis of language at the functional and macrostructural level, and moreover, across the different levels of neuroscientific analyses—from the neuron up to the large-scale network.

Here I will aggregate the topics discussed in prior chapters. Starting at the system level, I have described the different language functions such as phonology, syntax, and semantics and localized these in the brain. More importantly I have described the dynamics of functional interplay between the different subsystems within the neural network in time and identified the white matter brain structure that could guarantee this interplay. We saw that the general language network could, moreover, be characterized as a specific network at the molecular level based on the participating regions' neurotransmitter similarity. This provides a strong signal that language function and brain structure stand in a certain dependency relation.

In this book I have argued that syntax is at the core of human language, as it provides the rules and computational mechanisms that determine the relation between words in a sentence. In chapter 1, I identified a left-hemispheric fronto-temporal network for language and a particular neural network for syntax. This specific network guarantees (a) the syntactic binding of two words (or elements) into phrasal units, based on an operation called

Merge and, moreover, (b) the syntactic binding of phrasal units into sentences based on the multiple, recursive application of Merge. Within this network the posterior portion of Broca's area together with the adjacent frontal operculum represent a local circuit subserving the basic syntactic computation of Merge. The posterior portion of Broca's area (BA 44) as part of the core language network is connected to the posterior superior temporal cortex via a particular white matter fiber tract, the arcuate fasciculus (see figure 0.1). The two brain regions together with the connection between them represent a long-range circuit which supports the assignment of syntactic and thematic relations of phrasal units within a sentence. The two brain regions, and in particular the fiber tract connecting them, have been shown to be crucial for the development of syntactic abilities and possibly for the human faculty of language. This means that parts of the gray matter together with a part of the white matter appear to be the neurobiological basis of the unique human faculty of language.

However, the description of the neural network with its functional gray and white matter parts remains incomplete unless we add information about the temporal dynamics within the network. After all, language processing takes place in time. Electrophysiological measures, which allow us to register brain activation millisecond by millisecond, have provided information about the temporal course of phonological, syntactic, and semantic processes—but only with a coarse brain localization of these dynamics, except for the few instances where intracranial recordings were used. These intracranial recordings provided interesting results on word processing but so far only concerned single neurons in one brain region and neglected the rest of the network. Thus there is room for speculations of how different parts of the language network code, share, and integrate pieces of information. I briefly touched upon this issue and speculated the information exchange between different brain regions may be possible by so-called *mirror neural ensembles* that encode and decode information in the sending and receiving brain regions, respectively.

In the remainder of this section I will recapitulate what we know about the relevant parts of the language network functionally and structurally at the different neuroscientific levels within the human brain. I will start with the larger fronto-temporal language network in the adult human brain and then zoom into particular parts that can be backtracked through different neuroscientific levels down to their neuroanatomical detail and, moreover, can be followed back in phylogeny.

The Language Network in Our Brain

The human language network constitutes areas in the inferior frontal gyrus and in the temporal cortex that are connected by white matter fiber tracts. This larger network holds responsibility for the processing of language. Within this larger network, distinct brain areas and specific sub-networks support the processing of the sound of words, their meanings, and their relations in phrases and sentences as well as the melodic parameters of these entities.

The sound of language concerns the word forms and the melodic parameters, words, phrases, and sentences. Words are composed of different phonemes that are initially processed in the primary and secondary auditory cortex located in the middle portion of the superior temporal cortex. Regions in the posterior portion, as well as in the anterior portion of the superior temporal cortex, are responsible for the processing of the phonological language-specific information. These latter regions are connected to the primary auditory cortex by short-range fiber bundles guaranteeing the transmission of the information from the lower level-processing region of the auditory system to the next level of phonological processing.

Once the phonological word form is identified the next processing levels and their respective neural networks become active. It is assumed that the system initially uses syntactic word category information to build up phrase structure online. This process appears to involve two steps: a first step during which adjacent elements are identified and a second step during which a local syntactic is hierarchically built. The first step involves the anterior superior temporal gyrus and the frontal operculum connected via a ventrally located fiber tract called uncinata fasciculus, color-coded in red in figure 8.1. The second step during which the syntactic hierarchy is built involves the posterior portion of Broca's area (BA 44). Processing of the syntactic relation in a sentence involves a network consisting of Broca's area (BA 44) and the posterior superior temporal gyrus/sulcus. These two brain regions are connected via a dorsally located fiber tract called the arcuate fasciculus, color-coded in purple in figure 8.1. Lexical-semantic information of words stored in the middle temporal gyrus is accessed through the anterior portion of Broca's area (BA 45/BA 47). These two brain regions are connected via a ventrally located fiber pathway with the abbreviation inferior fronto-occipital fasciculus (IFOF), color-coded in orange in figure 8.1. The posterior superior temporal gyrus/sulcus is assumed to serve as a region where syntactic and thematic information are integrated. The right hemisphere comes into play when prosodic information is processed and the corpus callosum (as the fiber bundle connecting the two hemispheres) supports the interaction between syntactic information processed in the left hemisphere and prosodic information processed in the right hemisphere.

The white matter fiber tract connections are the basis of the information transfer from one region to the next and the cooperation between them. This cooperation has been demonstrated by functional connectivity results and oscillatory measures, both of which reflect the joint activation of these regions.

During language perception semantic and syntactic information processed in different brain regions and subsystems have to be integrated to achieve comprehension. At this point the question arises about which brain area is responsible for the integration of syntactic and semantic information. I discussed the posterior temporal cortex as the major region of integration, based on the results that we observe activation in this region when both semantic and syntactic information in natural sentences has to be processed, but not when processing syntactic sequences without any semantic information. A similar activation

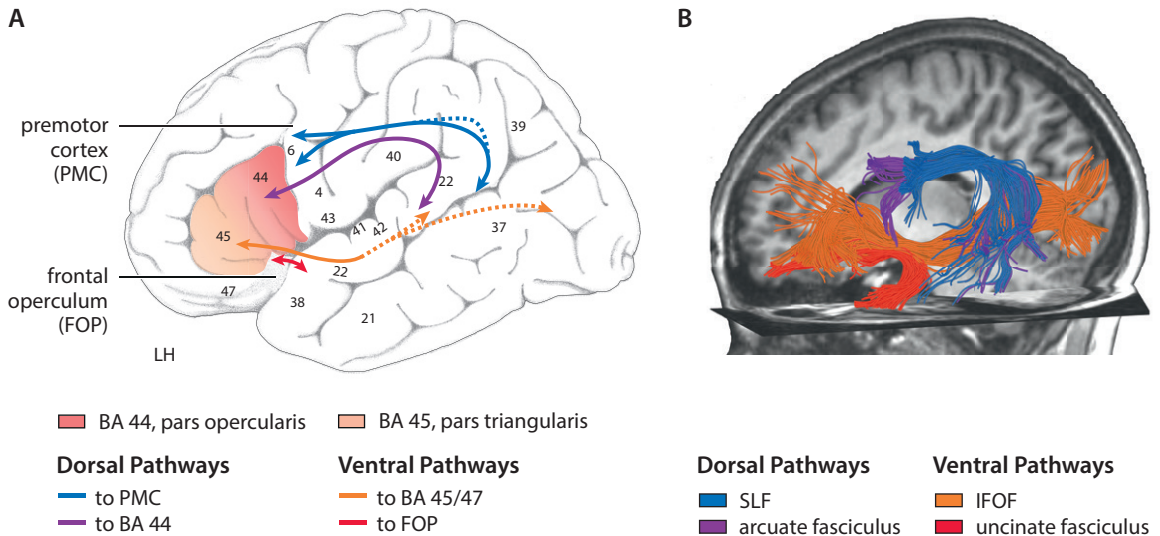


Figure 8.1

Core language fiber tracts in the human brain. (A) Systematic view; (B) anatomical view. There are two dorsally located pathways and two ventrally located pathways. The dorsal pathway connecting the dorsal premotor cortex (PMC) with the posterior temporal cortex [the posterior superior temporal gyrus and sulcus (pSTG/STS)] involves the superior longitudinal fasciculus (SLF) (depicted in light blue); the dorsal pathway connecting Brodmann area (BA) 44 with the posterior STG involves the arcuate fasciculus (depicted in purple). The ventral pathway connecting the inferior frontal cortex—that is, BA 45/47 and others—with the temporal cortex involves the inferior fronto-occipital fasciculus (IFOF) (depicted in orange); the ventral pathway connecting the anterior inferior frontal cortex—that is, frontal operculum (FOP) with the anterior superior temporal gyrus (aSTG) involves the uncinata fasciculus (depicted in red). Adapted from Friederici and Gierhan (2013). The language network. *Current Opinion in Neurobiology*, 23 (2): 250–254, with permission from Elsevier.

pattern depending on the presence of semantic information, however, was also found for BA 45 in the inferior frontal gyrus (Goucha and Friederici, 2015). This leaves the option open that BA 45 may also play a role in syntactic-semantic integration. And indeed the larger region of the inferior frontal cortex has been proposed as the integration region by Hagoort (2005). Here I suggest that if the inferior frontal cortex is involved in integration processes, it may rather be BA 45 in particular, given the data by Goucha and Friederici (2015), which revealed an involvement of BA 45 together with BA 44 for the processing of syntactically structured sequences as long as minimal semantic information was present therein. BA 45 can qualify as an integration area not only on the basis of the functional data, but, moreover, on the basis of receptorarchitectonic data (Amunts et al., 2010). These data indicate a subdivision of BA 45 into two subregions: a posterior part (45p) and an anterior part (45a) (see the introduction, figure 0.2). The posterior part of BA 45 (45p) is adjacent to BA 44, known to be a syntax-relevant area, and is sometimes seen to be active together with BA 44 (at least when minimal semantic information is still present

in the stimulus material). The anterior part of BA 45 (45a) is adjacent to BA 47 and often seen active together with 47 when semantic information is processed. The two subparts of BA 45, the anterior part (45a) and the posterior part (45p), may thus provide a possible basis for integration processes in addition to the posterior temporal cortex. It remains to be determined whether the posterior temporal cortex and BA 45 serve different subfunctions of integration or whether they perform integration jointly.

The Syntactic Network in Our Brain

In this subsection I concentrate on the syntactic network for two reasons. First, I argued that syntax is the core of the human language capacity. Second, there is ample evidence showing that non-human animals such as non-human primates and dogs can learn the meaning of words and frozen phrases but cannot learn syntax.

When decomposing the human language network at the different neuroscientific levels, it seems that those brain structures involved in the human specific ability to process syntax have specific characteristics at the neurostructural and neurofunctional level. There are two structures, relevant for syntactic processes: first is BA 44, the posterior portion of Broca's area in the inferior frontal gyrus; and second is the fiber tract connecting this area to the posterior temporal cortex, namely the arcuate fasciculus. This network has been identified to support the processing of complex syntax in humans. So what are the specifics of these brain structures?

Broca's area. Within the syntactic network involving BA 44 in Broca's area and the posterior superior temporal gyrus, BA 44 plays a special role. BA 44 is responsible for the generation of hierarchical syntactic structures, and accordingly has particular characteristics at the neurophysiological level. This area is different from other brain regions in many respects, both at the functional and various neurostructural levels.

At the cytoarchitectonic level, as one of the lowest structural levels, BA 44 differs from other regions in the frontal cortex in the granularity of the six layers of the cortex (Amunts et al., 1999), with BA 44 showing more pyramidal neurons in certain layers (dysgranular structure) than the more posteriorly located premotor cortex (BA 6) (agranular structure), but fewer of these neurons than the fully granular cortex of BA 45 (granular structure) (Brodmann, 1909). Moreover, in human adults BA 44 has been demonstrated to be larger in the language-dominant left hemisphere compared to the right hemisphere. This asymmetry has been related to the human language faculty, in particular as a similar difference in the cytoarchitectonics of the left and right hemisphere is not present in chimpanzees (Schenker et al., 2010). Thus BA 44 in the left hemisphere, compared to its right hemispheric homolog, appears to be specifically large in adult humans.

At the microstructural histological level it has been shown that BA 44's dendritic structure is more elaborate than that of the adjacent motor cortex and its right hemispheric homolog (Scheibel, 1984). Dendrites guarantee the information transfer between neurons

and are thus relevant for those processes represented in the particular area. BA 44's intricate dendritic structure has been discussed as being related to the particularly complex functional processes this region supports—that is, language or more specifically, syntax. In the adult human brain we see a clear functional difference between BA 44 and the adjacent motor cortex, as indicated by local field potentials as measured by electrocorticography: while BA 44 is involved in speech planning, the motor cortex supports the motor act of speaking (Flinker et al., 2015). Thus BA 44 in the human left hemisphere is specific, since it has a more dense dendritic structure than adjacent brain regions or its homolog in the right hemisphere.

As one of the lowest functionally relevant levels we can consider the level of the neurotransmitters that were analyzed for the larger language network (Zilles, Bacha-Trams, Palomero-Gallagher, Amunts, and Friederici, 2014), and for Broca's area in the inferior frontal cortex in particular (Amunts et al., 2010). These analyses revealed (a) that BA 44 as the posterior portion of Broca's area can be differentiated from BA 45 as the anterior portion of Broca's area, (b) that area 44 can be subdivided receptorarchitectonically into a dorsal and a ventral part, and (c) that BA 44 can be separated from the frontal operculum located more ventrally. These neuroreceptorarchitectonic differentiations can be nicely mapped onto the functional language data at the systems level. Let's consider the data point by point.

- (a₁) BA 44 is cytoarchitectonically (Amunts et al., 1999) and receptorarchitectonically (Amunts et al., 2010) different from BA 45.
- (a₂) BA 44 is responsible for syntactic processes and functionally separate from BA 45 responsible for semantic, propositional processes (Friederici, 2002; Goucha and Friederici, 2015).
- (b₁) Receptorarchitectonic analyses suggest a subdivision of BA 44 into a dorsal and a ventral part (Amunts et al., 2010).
- (b₂) Neuroimaging data found the dorsal part to be involved in phonological processes and the ventral part to be involved in syntactic processes (Hagoort, 2005).
- (c₁) The ventral part of BA 44 is receptorarchitectonically different from the adjacent frontal operculum (Amunts et al., 2010).
- (c₂) The ventral part of BA 44 can functionally be separated from the frontal operculum (Zaccarella and Friederici, 2015a).

These data indicate that at the receptorarchitectonic level BA 44 can clearly be differentiated from its adjacent regions, both from the more anterior located BA 45 and from the more ventro-medially located frontal operculum.

Thus in sum, the structural and molecular analyses reveal a number of parameters that differentiate BA 44 in Broca's area from adjacent areas in the left inferior frontal gyrus.

These differences map onto specific functions in the language network and may therefore be crucial for the language faculty.

The dorsal language pathway. Within the larger left hemispheric language network the subnetwork that specifically supports the ability to process human syntax involves BA 44 in the inferior frontal gyrus and the posterior temporal gyrus connected via a dorsally located fiber tract, in particular the arcuate fasciculus (figure 8.1).

At the macrostructural level we can relate the degree of white matter fiber density functionally to syntactic behavior, and we see that the degree of maturity of the arcuate fasciculus during development, in particular its myelination, predicts syntactic performance (Skeide, Brauer, and Friederici, 2016). This structure-function relation is furthermore supported by the report that the decrease in integrity of this dorsal pathway during progressive aphasia correlates with a decrease in syntactic performance (Wilson et al., 2011). This classical language network involving Broca's area and the posterior temporal cortex with its dorsal and ventral pathways is universally present in all human brains, but the strength of some of the fiber tracts in the language pathways is modulated by the particular language learned (Goucha, Anwander, and Friederici, 2015).

At the level of functional connectivity, BA 44 in Broca's area and the posterior superior temporal gyrus show a high functional cooperation during sentence processing (den Ouden et al., 2012; Makuuchi and Friederici, 2013). This connectivity between these two areas increases with age during childhood; moreover, correlational analyses with sentence comprehension tests revealed that the connectivity between these areas becomes increasingly relevant for sentence processing between ages 5 and 6 years (Xiao, Friederici, Margulies, and Brauer, 2016b).

Studies using oscillatory measures found a high synchronicity between left frontal and left parietal and temporal brain regions when processing the syntactic structure of phrases and sentences (Ding, Melloni, Zhang, Tian, and Poeppel, 2015; Meyer, Grigutsch, Schmuck, Gaston, and Friederici, 2015). These data suggest that neural ensembles in the left frontal region and neuronal ensembles in the left posterior regions are active coherently during sentence processing. It appears that the neuronal ensembles in the respective brain regions work together online.

In sum these data point toward a distinct structural connectivity between BA 44 in Broca's area and the posterior temporal cortex via the dorsal pathway and a strong functional connectivity between these regions. The functional relevance of the dorsal pathway for the processing of syntactic hierarchies has been demonstrated clearly in several studies.

The Language Network across Phylogeny and Ontogeny

Finally, when considering the language network across ontogeny and phylogeny we may learn more about the specifics of the neurobiology underlying the human faculty of syntax. The simple view is that non-human primates and young infants, in contrast to human

adults, do not have the capacity of language nor syntax in particular. What is the difference in their respective structural networks? The available data suggest that the networks differ with respect to area BA 44 and, moreover, with respect to the dorsal fiber tract connecting BA 44 and the posterior superior temporal cortex.

Broca's area. We have seen that the cytoarchitectonic structure of BA 44 and its relative expression in the left and the right hemisphere is different in human adults and non-human primates. The cytoarchitectonic analysis for Broca's area including BA 44 shows a clear leftward asymmetry in human adults (Amunts, Schleicher, Ditterich, and Zilles, 2003), but not in chimpanzees (Schenker et al., 2010). In humans, the leftward asymmetry is not present early in life, but then follows a function-related developmental trajectory.

During human development we can observe an interesting differentiation between BA 44 known to support syntactic processes and BA 45 known to support semantic processes. While BA 45 shows this asymmetry by the age of 5 years, BA 44 only demonstrates this asymmetry by the age of 11 years (Amunts et al., 2003). These data mirror the functional development trajectory of both semantics and syntax at the behavioral (Friederici, 1983), the electrophysiological level (Strotseva-Feinschmidt, Schipke, Gunter, Friederici, and Brauer, submitted). At the brain imaging level the specificity of BA 44 for syntactic processes only develops in late childhood, and that prior to this BA 45 is also recruited (Skeide, Brauer, and Friederici, 2014), indicating a late emergence of the full syntactic language ability. The mature BA 44 then shows a clear specificity for syntax and appears to be indicative for the structural and functional difference observed between human adults compared to infants and monkeys and may thus be crucial for the faculty of language.

The dorsal language pathway. We have learned that BA 44 and the posterior superior temporal gyrus are connected by a dorsal fiber tract (the arcuate fasciculus), which together represent the syntactic network in the adult human. At this point we may ask whether there is a parallel between its emergence during phylogeny and ontogeny. Comparisons reveal that this fiber tract in human adults differs from both human infants (Perani et al., 2011) and non-human primates (Rilling et al., 2008). This dorsal pathway is very weak in macaques and chimpanzees (who do not have language) but strong in adult humans (who master language) (Rilling et al., 2008). Moreover, the arcuate fasciculus is very weak and poorly myelinated in newborns (who do not yet master language) (Perani et al., 2011). These data indicate that when myelin of the arcuate fasciculus is low, the syntax function is poor. This conclusion is supported by a result demonstrating that its increasing strength correlates directly with the increasing ability to process complex syntactic structures (Skeide et al., 2016). This fiber tract may thus be one of the reasons for the difference in the language ability in human adults compared to the prelinguistic infant and the monkey.

In conclusion these phylogenetic and ontogenetic data provide compelling evidence for the specific role of BA 44 and the arcuate fasciculus connecting BA 44 and the posterior superior temporal cortex for the language faculty. These brain structures may have emerged to subserve the human capacity to process syntax. This fiber tract could be seen as the missing link that has to evolve in order to make the full human language capacity possible.

8.2 Epilogue: Homo Loquens—More than Just Words

Humans differ from non-human primates in their ability to build syntactic structures. This statement has set the scene for our assessment of language in this book. Many sections of *Language in Our Brain* have focused on syntax, and yet our feeling—when considering language—may rather tend to favor semantics and meaning as the most important aspects of language. We do, after all, want to communicate meaning. In order to do so, however, we need syntax to combine words into phrases and sentences.

We use words to refer to objects and mental entities and to refer to actions and mental states, but we need syntax to determine the thematic relation between the words in a sentence. Syntax allows to express logical relations (e.g., the if-then relation: if he does X then Y will happen) and it permits us to formulate believes of ourselves and of others (e.g., I think he believes that ...).

Language is what enables us to plan the future together with others, and to learn from the past through narratives. Language forms the basis of our social and cultural interaction not only in the “here and now,” but most importantly also in the “there and then.”

This evolutionary step is realized in a brain that—as far as we know—underwent only minor, although important changes compared to our closest relatives. I have argued that the syntactic specificity of Broca’s area, in particular its posterior part, namely BA 44 and its connection to the temporal cortex granting the interplay between these two regions, is what accounts for one of these changes. From an evolutionary perspective it remains an open question whether humans develop language to cover those needs and whether the emergence of language determined the homo loquens as a cultural being.

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