

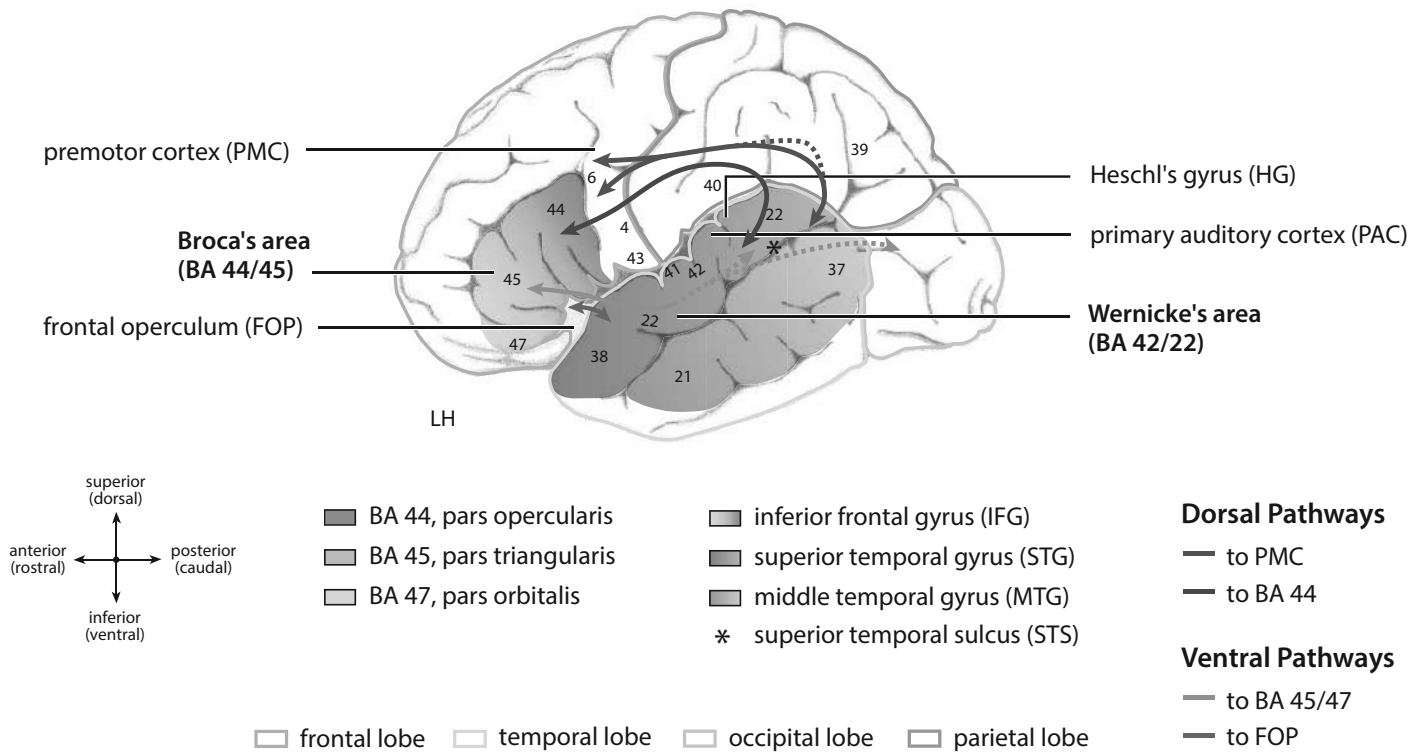
## Language as a Brain System

The brain itself is a very complex system, and the description of the relation between language functions and the brain remains a big challenge. The brain consists of gray matter and white matter. The gray matter is composed of about 100 billion neuronal cells that are interconnected via trillions of synapses. Each neuron has a number of connections via which it receives signals from other neurons (these are the dendrites), and it also has connections via which it forward signals to other neurons (these are the axons). The axons come into contact with other neurons via synapses at which the transmission of the signals is realized by neurotransmitters. The white matter, in contrast, contains only few neuronal cells, being composed of fiber bundles connecting adjacent brain regions by short-range fiber bundles, or connecting more distant parts of the brain by long-range fiber bundles that guarantee communication between these. In their mature state, these fiber bundles are surrounded by myelin, which serves as insulation and enables rapid propagation of the signal. Both the gray and the white matter are the basis for all cognitive abilities, including language.

The brain's functioning, however, is not yet completely understood. This holds for all different neural levels, from the single neurons and the communication between them up to the level of local circuits and the level of macrocircuits at which neuronal ensembles or even entire brain regions communicate. But our knowledge about the brain has increased considerably over the past centuries and decades, allowing us to provide a first description of the neural language network. Today we are able to bring together data from different neuroscientific levels of the language-related brain regions ranging from the cellular and molecular level, to neural circuits, and up to the systems level represented by larger neural networks consisting of distant brain regions. All these levels of analyses should lead to a physiologically integrative view on language in the human brain.

### A Brief History of the Language-Brain Relationship

Historically,<sup>4</sup> Franz Gall (1758–1828) was the first to suggest a relation between cognitive functions and particular brain regions, and he postulated that language is located in the left frontal lobe. In 1836 Marc Dax presented a talk and, based on his observations that lesions of the left hemisphere lead to language impairments, suggested an involvement of the left hemisphere for language (Dax, 1836). The first documented empirical proof that language is indeed represented in particular parts of the brain was a clinical case in the late nineteenth century. This first famous case was a patient of the French scientist Paul Broca. The patient was described to suffer from a severe deficit in language production as he was only able to utter the syllable *tan*. Broca described the language behavior of this patient well, but in order to report a language-brain relationship, the neurologists at that time had to wait until the patient died and a brain autopsy was conducted. During autopsy, neurologists



**Figure 0.1**

Neuroanatomy of language. Anatomical and cytoarchitectonic details of the left hemisphere (LH). Top: The different lobes (frontal, temporal, parietal, occipital) are marked by colored borders. Major language-relevant gyri (inferior frontal gyrus (IFG), superior temporal gyrus (STG), middle temporal gyrus (MTG)) are color-coded, superior temporal sulcus (STS) located between STG and MTG is marked by an asterisk. Numbers indicate language-relevant Brodmann areas (BA) that Brodmann (1909) defined on the basis of cytoarchitectonic characteristics. The coordinate labels (see bottom left) superior (dorsal)/inferior (ventral) indicate the position of the gyrus within a lobe (e.g., superior temporal gyrus) or within a BA (e.g., superior BA 44). The horizontal coordinate labels anterior (rostral)/posterior (caudal) indicate the position within a gyrus (e.g., anterior superior temporal gyrus). Broca's area consists of the pars opercularis (BA 44) and the pars triangularis (BA 45). Located anterior to Broca's area is the pars orbitalis (BA 47). The frontal operculum (FOP) is located ventrally and medially to BA 44, BA 45. The premotor cortex (PMC) is located in BA 6. Wernicke's area is defined as BA 42 and BA 22. The primary auditory cortex (PAC) and Heschl's gyrus (HG) are located in a lateral to medial orientation in the temporal lobe. White matter fiber tracts, i.e., the dorsal and ventral pathways connecting the language-relevant brain regions are indicated by color-coded arrows (see bottom right). Reprinted from Friederici (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, 91 (4): 1357–1392.

located the brain lesion of “Monsieur *Tan*” in the left inferior frontal gyrus, today called Broca's area (Broca, 1861) (see figure 0.1). Some years later, Carl Wernicke from Breslau described a number of patients who were characterized by a deficit in language comprehension (Wernicke, 1874). These patients were found to have lesions in the left temporal cortex, today called Wernicke's area (see figure 0.1). Based on these descriptions, Broca's area was seen to support language production, and Wernicke's area was taken to support language comprehension. These brain lesions were caused by a stroke—in these cases an ischemic stroke in which a blood vessel carrying blood to a particular brain area is blocked,

leading to death of neuronal cells in the respective area. Later these language deficits were called Broca's and Wernicke's aphasia.

Initially, the respective language deficits were categorized on the basis of the patient's language output and comprehension during clinical observations. Patients with a primarily deficit language output often spoke in a telegraphic style leaving out all the function words, such that sentences sounded like a telegram as if grammar was gone. This symptom was called agrammatism (Pick, 1913). In contrast, patients who mainly appeared to have a comprehension deficit as described by Wernicke were shown to produce sentences that were not easy to understand for others. These patients often produce utterances in which constituents are incorrectly crossed or unfinished. For example, consider the following utterance in German and its literal English translation: *und ich nehme auch an dass das mit dem Sprechen oder was sonst überall, also das da, das ist es, sonst anders als die Beine so was hat ich keine* / and I suppose also that this with the speaking or what else overall, this one, this is it, different to the legs that one I did not have. This symptom was called paragrammatism (Kleist, 1914; Jakobsen, 1956).

Until the late 1970s and early 1980s, neurologists were not able to look into a patient's brain in vivo. Only with the advent of new imaging techniques did the possibility emerge to describe the relation between language behavior and brain lesion in a living patient. Together with the advancement in neuroimaging methods, crucial developments in linguistic and psycholinguistic theorizing occurred. This led to a revision of the classical view of Broca's area being responsible for language production, and Wernicke's area being responsible for comprehension.

This classical view of the function of Broca's area and Wernicke's area was revised when more fine-grained tests based on linguistic and psycholinguistic theories were applied, and the outcome of those tests required a functional redefinition of these brain regions (Zurif, Caramazza, and Myerson, 1972; Caramazza and Zurif, 1976). It was found that Broca's aphasics not only had problems in language production—they spoke in an agrammatic telegraphic style leaving out all function words—but they also demonstrated problems in language comprehension when confronted with grammatically complex constructions whose comprehension depended on function words. These were, for example, passive sentences—*The boy was pushed by the girl*—which were misinterpreted when only processing the content words *boy pushed girl*. The observation led to the view that Broca's area subserves grammatical processes during both production and comprehension. A similar shift in functional interpretation took place with respect to Wernicke's area. The finding that Wernicke's patients not only showed deficits in comprehending the meaning of utterances, but also displayed problems in word selection during production, led to the view that the temporal cortex where Wernicke's area is located supports lexical-semantic processes. Thus, it was linguistic and psycholinguistic theorizing that brought on new insights into the language-brain relationship. These studies provided first indications that

different subcomponents of language, such as the grammar and the lexicon, might have different localizations in the brain.

With the development of new neuroscientific methods in the late twentieth century, the relation between language and the brain could be observed in living persons while processing language. Today the language network can be described to consist of a number of cortical regions in the left and the right hemisphere. These interact in time under the involvement of some subcortical structures that are not specific for language but may serve as a relational system between the language network and its sensory input systems (e.g., auditory cortex for auditory language and visual cortex for sign language) and its output systems (e.g., motor cortex for articulation and for signing). In this book I primarily focus on the cortical regions of the neural language network, which I will discuss with respect to their particular language function in the adult brain and the developing brain.

### **A Brief Neuroanatomy of Language**

In order to map the language network in the human brain, we need a coordinate system that subdivides the brain into relevant parts and applies labels to these parts. Unfortunately, different neuroanatomical coordinate systems and labels have been and still are used nowadays. Therefore, I will present them all here. One way to describe the neuroanatomical location of a given function in the brain is to name the different gyri in the cortex: inferior frontal gyrus in the frontal lobe or superior temporal gyrus and middle temporal gyrus in the temporal lobe (see figure 0.1). This model represents the anatomical details of the left hemisphere, the dominant hemisphere for language.<sup>5</sup>

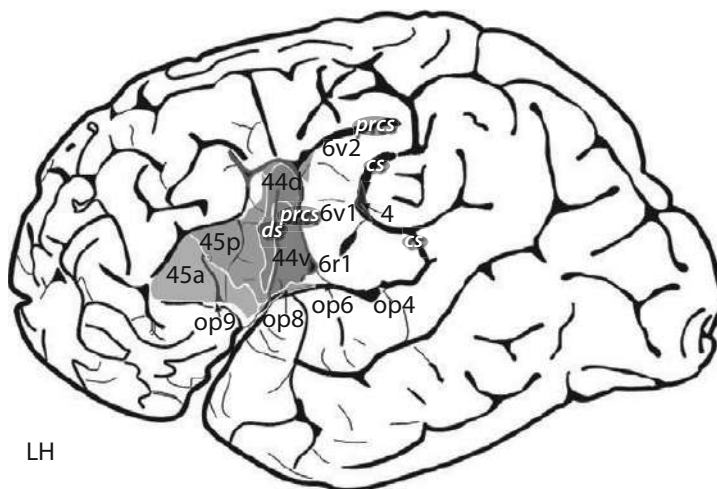
The brain regions that have been known for more than a century to be centers of language processing are Broca's area and Wernicke's area in the left hemisphere. These two brain regions have been described with respect to their neuroanatomical microstructure at the cytoarchitectonic level and more recently also at the neuroreceptorarchitectonic level. These microstructural analyses allow the parcellation of larger cortical areas, which is much more finely grained than any lesion-based functional parcellation, since brain lesions usually cover larger parts of cortical tissue.

The initial and still valid parcellation is the *cytoarchitectonic* description of the cortical structure, and was provided in 1909 by Korbian Brodmann (Brodmann, 1909). He only gave it for the left hemisphere because it took him many years to present this analysis, as he was looking at the cortex millimeter by millimeter under the microscope. He analyzed the six layers of the cortex with respect to the type of neurons and their density. As a result, he identified cytoarchitectonically different regions, which he numbered, and are known today as Brodmann areas (BA) (see figure 0.1). This numbering is still used to indicate the location of a functional activity in the brain. Based on the cytoarchitectonic analysis by Brodmann, Broca's area, for example, was subdivided into a more posterior part (BA 44) and a more anterior part (BA 45). This cytoarchitectonic subdivision of Broca's area into two subparts was later confirmed by objective cytoarchitectonic analyses (Amunts et al.,

1999). The subdivision into BA 44 and BA 45 coincides with the neuroanatomical separation into pars opercularis and pars triangularis, respectively. Wernicke's area is located in the temporal cortex and refers to BA 42/22. Cytoarchitecturally, BA 22 has been differentiated from the primary and secondary auditory cortex (BA 41, 42) and the inferiorly located middle temporal gyrus (Brodmann, 1909).

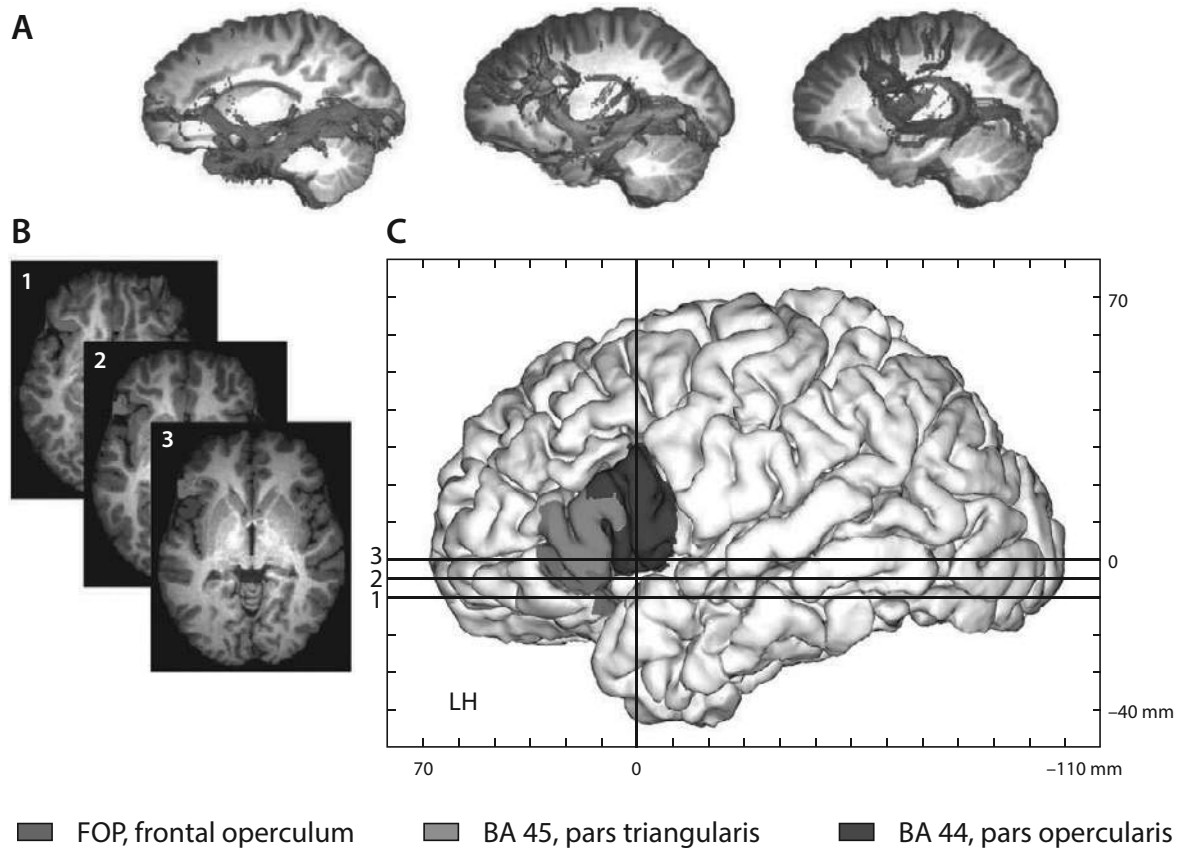
In the twenty-first century, novel methods of parcellating different brain regions have been developed. One method is *receptorarchitectonic* parcellation and the other method is connectivity-based parcellation. The receptorarchitectonic analysis takes into consideration the type and density of neurotransmitters in a given region (Zilles and Amunts, 2009; Amunts et al., 2010;). Neurotransmitters are biochemicals that transfer signals between neurons and thereby transport information from one neuron to the next. The receptorarchitectonic analysis also indicates a global distinction between BA 44 and BA 45, an even more fine-grained differentiation within each of these areas, and, moreover, a distinction between lateral area 45 and 44 and the more ventral-medial area, the frontal operculum (Amunts et al., 2010; for details see legend of figure 0.2).

The *connectivity-based* parcellation approach refers to an analysis that differentiates cortical areas on the basis of their white-matter fiber connections to other areas in the brain (Johansen-Berg, 2004; Anwender, Tittgemeyer, von Cramon, Friederici, and Knösche, 2007). With the use of connectivity-based parcellation analysis, Broca's area has also been divided into BA 44 and BA 45, both of which are separated from the more ventrally



**Figure 0.2**

Receptorarchitectonic parcellation of left IFG. Receptorarchitectonic differences of areas within the inferior frontal gyrus (IFG) analyzed in post mortem brain. Extent of delineated areas projected to the lateral surface of an individual left hemisphere (LH) of a post mortem brain. Different receptor binding sites were studied. The color coding indicates receptorarchitectonically defined borders. Area 44 can be subdivided into 44d (dorsal) and 44v (ventral). Area 45 can be subdivided receptorarchitectonically into an anterior (45a) and a posterior (45p) part. Area 6 can be subdivided into three subparts. Other abbreviations: op, Operculum (numbering indicates different subparts); prcs, precentral sulcus; cs, central sulcus. Reprinted from Amunts et al. (2010). Broca's region: novel organizational principles and multiple receptor mapping. *PLoS Biology*, 8: e1000489.



**Figure 0.3**

Structural connectivity-based parcellation of left IFG. Parcellation of the inferior frontal gyrus (IFG) based on the areas' connectivity of the white matter fiber tracts. (A) Parcellation results for the inferior frontal gyrus into three clusters for the group average, pars opercularis, BA 44 (purple); pars triangularis, BA 45 (orange); and frontal operculum, FOP (red). (B) Delineates these areas for one participant in three different axial levels on the Talairach-scaled cortical surfaces of the left hemisphere (LH). (C) Shows the location of the axial slices at three different levels that equidistantly cut through the parcellated areas; locations of axial slices are indicated by solid horizontal lines (numbered 1–3). Note the intersubject variability with respect to differences in shape and size of both areas, but the invariable principle order of the three clusters. Adapted from Anwander et al. (2007). Connectivity-based parcellation of Broca's area. *Cerebral Cortex*, 17 (4): 816–825, by permission of Oxford University Press.

located frontal operculum (Anwander et al., 2007; figure 0.3). Using a connectivity-based approach, BA 22 in the superior temporal gyrus can be parcellated into three subareas (Raettig, Kotz, Anwander, von Cramon, and Friederici, submitted). Based on this approach the superior temporal gyrus and the superior temporal sulcus can be subdivided into three parts: a posterior, middle, and anterior subpart.

The combined data from different analyses provide a strong empirical basis for the view that particular brain regions can be separated from each other at different neuroscientific levels: at the lower levels on the basis of cyto- or receptorarchitectonic parameters, and at higher levels on the basis of structural connectivity. As we will see, these separations at

the different neuroscientific levels are most relevant for the differentiation of functional subcomponents in the cognitive language system.

The brain regions that constitute the major parts of the functional language network in the left hemisphere—in particular Broca’s area and Wernicke’s area—are displayed and color-coded in figure 0.1. These regions subserve the processing of words and sentences across all languages in the world. Homolog areas in the right hemisphere (not displayed in figure 0.1) are also part of the language network and subserve the processing of prosodic information, such as a sentence’s melody. The different brain regions in the network are connected by fiber bundles, which provide pathways that guarantee information transmission from one region to the other (schematically indicated by the colored arrows in figure 0.1). These pathways exist within each hemisphere and connect frontal and temporal language regions, and, moreover, there are fiber bundles that connect the left and right hemispheres allowing information transfer between the two hemispheres.

From this short description it already becomes clear that the relation between language and the brain is a complex one, in particular when considering that the different parts of the network have to work in real-time to make language processing possible.

### **Language and the Brain: The Story to Be Told**

My goal in this book is to provide a coherent view on the relation between language and the brain based on the multifold empirical data coming from different research fields: electrophysiological and functional neuroimaging data of the adult language system, neuroscientific data of the developmental language system, and data on the brain structure and its maturation in humans as well as in non-human primates.

I have organized these data in four larger parts at the end of which I define the anatomical model outlined in figure 0.1 with respect to language functions. In part I (chapters 1 and 2) I describe the basic language functions and their brain basis from auditory input to sentence comprehension, both with respect to “where” and “when” different subprocesses take place. I dissect the complex language system into its subparts and then put the bits and pieces together again to provide then a functional neuroanatomical model of language comprehension. I follow chapter 1 with an excursion (chapter 2) that goes beyond the issue of language comprehension. I provide empirical data in support of the view that there is a common knowledge base for language comprehension and production. Moreover, I briefly discuss aspects of communication that are not part of the core language system. In part II (chapters 3 and 4) I provide the description of the language networks connecting the different language-relevant brain region, both structurally and functionally. Here I delineate the spatial and temporal characteristics of and within the neural language network. I will propose a dynamic neural language circuit describing the interaction of the language-relevant areas in the adult brain. In part III (chapters 5 and 6) I discuss the brain basis of language acquisition, looking into language development during early childhood and into aspects of second language learning. Here we will learn about the neurobiological

conditions of language development. A neurocognitive model of the ontogeny of language capturing these data is proposed. In part IV (chapters 7 and 8), first I tackle questions about the evolution of language and the possible underlying neural constraints, and then bring together the material covered in the different chapters. At the end I propose an integrative view on the neural basis of the core language system.

As the book unfolds I hope to guide the reader through a rich database for language and the brain by starting with a purely functional model which is then developed into a neurocognitive model becoming ever more complex as additional data are discussed. We will see that the different language-relevant brain regions alone cannot explain language, but that the information exchange between these supported by white matter fiber tracts is crucial, both in language development and evolution.

In order to ease the recognition of language-relevant brain regions and the pathways across the figures representing variations of the model presented in figure 0.1, I have kept the colors constant. Moreover, I have also adapted the colors of the figures coming from different published papers for coherence.



# I

The miracle of language often occurs to us only when language does not function anymore, such as after brain damage, or when language acquisition becomes really tedious, such as when learning a second language. In everyday language, however, we never think about the efficiency of the language system that allows us to produce and understand complex sentences in milliseconds. We just use it. Within a very short time frame we process the sound of language, the meaning of words, and the syntactic structure of an utterance.

Psycholinguistic models assume that these processes, which are concerned with different information types, take place in different subsystems that work together in time in a partly cascadic and partly parallel manner. During language comprehension this means that once the acoustic information is perceived, the different subprocesses dealing with phonological, syntactic, and semantic information have to be performed. These processes constitute what is called the “core language system” (Berwick, Friederici, Chomsky, and Bolhuis, 2013; see also Fedorenko and Thompson-Schill, 2014). Comprehension during interpersonal communication, however, may also involve situational and emotional aspects that are not considered part of the core language system since these, as we will see, can act independently of language.

Chapter 1 focuses on the cognitive structure of these different processes during language comprehension and their respective neural basis. An excursion (chapter 2) has two purposes. It will discuss a common knowledge base of syntactic rules and words for language comprehension and language production. Moreover, it will briefly touch upon aspects of communication that go beyond the core language system.