

# Introduction

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AN ADEQUATE neurobiological model of our uniquely human language faculty has to meet the following two requirements: (1) it should decompose complex language skills such as speaking and listening into the contributing types of knowledge and processing steps (the cognitive architecture); (2) it should specify how these are instantiated in, and supported by, the organization of the human brain (the neural architecture; Hagoort, 2013). Until not too long ago, the neurobiological model that dominated the field was the Wernicke-Lichtheim-Geschwind (WLG) model (Levitt, 2013). In this model, the human language faculty was situated in the left perisylvian cortex, with a strict division of labor between the frontal and temporal regions. Wernicke's area in left temporal cortex was assumed to subservise the comprehension of speech, whereas Broca's area in left inferior frontal cortex was claimed to subservise language production. The arcuate fasciculus connected these two areas. Although Broca's area, Wernicke's area, and adjacent cortex are still considered to be key nodes in the language network, the distribution of labor between these regions is different than was claimed in the WLG model. Lesions in Broca's region are long since known to impair not only language production but also language comprehension, whereas lesions in Wernicke's region also affect language production.

More recently, neuroimaging studies provided further evidence that the classical view on the role of these regions is no longer tenable. For example, central aspects of language production and comprehension are subserved by shared neural circuitry (Segaert, Menenti, Weber, Petersson, & Hagoort, 2012). Moreover, the classical model focused on single-word processing, whereas

a neurobiological account of language processing in its full extent should also take into account what goes on beyond production and comprehension of single words. As a consequence of the mounting evidence against the classical WLG model, in recent years alternative neurobiological models for language have been proposed. In addition, due to new innovative ways of measuring the living human brain in healthy participants, such as diffusion tractography, novel ideas about the architecture of the language cortex arose (Catani et al., 2005; Catani et al., 2013).

This section of the current volume summarizes some exciting developments that characterize the progress in the field since the previous version of this handbook.

One important development relates to the neuroanatomical characteristics of the language-ready brain. Language-relevant cortex is mapped out in much more detail than before. Relevant areas such as Broca's area and Wernicke's area are further parcellated in terms of their cytoarchitectonic and receptorarchitectonic properties (Amunts et al., 2010). Furthermore, diffusion tractography studies have provided a much more extended view on the major connections between language-relevant areas, above and beyond the arcuate fasciculus (see chapter 52 by Amunts & Catani). This infrastructure supports a system that is characterized by an amazing pace.

One of the central aspects of understanding language is the speed at which it occurs. We can produce and easily recognize three to five words per second. Mainly based on electrophysiological evidence (ERPs), there is nowadays firm and quite detailed evidence that fast comprehension is, in part, achieved by predictions that are made continuously during the updating of the input representation. Quite detailed evidence is available that these predictions happen at different levels, all the way from the event schemas and syntactic characteristics of lexical items such as their grammatical gender to the actual words that might follow (see chapter 55 by Kutas, Urbach, & Federmeier).

The role of prediction and most other features of language processing is based on studies of only a handful of—mostly Indo-European—languages. Classically, the neurobiology of language has focused on core features of language such as words and syntax, with an eye on those properties that are universally shared among the many languages in the world. However, a central feature of human languages is the remarkable variation between them. Our capacity for language is deeply rooted in our biological makeup. We all share the capacity to acquire language within the first few years of life, without any formalized teaching program. Despite its complexity, we master our native language

well before we can lace our shoes or perform simple calculations. This is all based on the universal availability of a language-ready brain. At the same time, there seems to be no other cognitive system in humans that shows as much variability as language. Language comes in very different forms, at all levels of organization. The more than 6,000 languages still in existence today vary widely in their sound repertoires, their grammatical structures, or the meaning that the lexical items code for. For instance, some languages have a sound repertoire of only a dozen phonemes, whereas others have more than a hundred; some languages require every sentence to be tensed, others require every referent to be specified for visibility/invisibility. Further, sign languages are expressed by movements of hands and face, whereas spoken languages are expressed by movements of the vocal tract. How the specific characteristic of any particular language modulates the organization and recruitment of the underlying neurobiological infrastructure is still a largely open question. It is clear that cross-language comparisons are needed. One example is provided in chapter 54 by Marslen-Wilson, Bozic, and Tyler. They provide evidence for the domain of word formation, where language families vary substantially in inflectional and derivational morphology. Another domain is sign language. The language of the deaf is expressed in a very different format than speech (see chapter 56 by Emmorey and Özyürek). These differences are shown to create variations on a common theme in the neurobiology of language.

The common theme is codetermined by the intrinsic constraints that the brain brings to bear for any given cognitive task. In effect, the brain is a Kantian machine (Dehaene & Brannon, 2010). The consequence of this idea is that reading and speaking might have developed in a way that adapts their structural features optimally to intrinsic brain organization (Christiansen & Chater, 2008; Christiansen & Müller, chapter 58, this volume; Dehaene & Cohen, 2007). One novel and exciting idea is that speech might have adapted itself to the intrinsic rhythms of the brain. This sheds new light on language evolution and on how central structural characteristics of speech (phonemes, syllables, prosodic contours) might be shaped by the characteristics of intrinsic brain rhythms (delta, theta, gamma; see chapter 53 by Ghazanfar and Poeppel). The lesson here is that key features of human speech might have adapted themselves to the organization of the brain, rather than, or in addition to, the reverse scenario.

So far, what has been discussed is the machinery to encode and decode verbal utterances. However, in communicative settings, the coded meaning of these utterances is very often not the same as the intended message.

For instance, the statement “It is hot here” produced in the right context will often be interpreted as a request for action; for example, to open the window or turn on the air conditioner. In communication, the listener tries to infer the intention behind the utterance. What is understood is often unsaid but requires making inferences. This step from coded meaning to what is often called speaker meaning involves the theory of mind, or ToM, network (see chapter 57 by Hagoort and Levinson). To understand the use of language in its full extent, we need to understand what neurobiological systems, in addition to those representing a lexicon and syntax, are needed to determine the communicative value of language. This has become part of the research agenda in recent years. It shows clearly that any account that claims language comprehension can be fully explained by a mirror neuron system will fail.

Language has often been claimed to enable thinking at a level of abstraction unmatched by conceptual processes in other species. However, just as in the case of language, an adequate understanding of thinking requires decomposition in its core constituents. Our thinking, abstract as it may be, as well as the choice of our linguistic expressions are deeply connected to neural mechanisms of voluntary choice. The basic outlines of the human and monkey systems for making decisions begin to emerge (see chapter 59 by Glimcher).

Language and thinking are among the most complex functions the human mind commands. Its neurobiological infrastructure is still understood only very partially. It is beyond the scope of this section to do full

justice to the progress that nevertheless has been made. In recent years new theoretical orientations have been developed and novel topics have appeared on the research agenda, all indicating that we are faced with a field on the move.

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