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The neuroanatomic and neurophysiological infrastructure for speech and language

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New tools and new ideas have changed how we think about the neurobiological foundations of speech and language processing. This perspective focuses on two areas of progress. First, focusing on spatial organization in the human brain, the revised functional anatomy for speech and language is discussed. The complexity of the network organization undermines the well-regarded classical model and suggests looking for more granular computational primitives, motivated both by linguistic theory and neural circuitry. Second, focusing on recent work on temporal organization, a potential role of cortical oscillations for speech processing is outlined. Such an implementational-level mechanism suggests one way to deal with the computational challenge of segmenting natural speech.

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Introduction

Experimental research on the neurobiological foundations of speech and language processing has taken considerable strides in the last decade, due in part to advances in the methods available to study the human brain (improved resolution of recording techniques) and in part to more theoretically motivated research that builds on crucial distinctions provided by the results of linguistics, cognitive psychology and computer science (improved ‘conceptual resolution’). As the neurobiology of language matures, the units of analysis continue to change and become increasingly refined: from (i) broad (and somewhat pre-theoretical) categories such as ‘production’ versus ‘perception/comprehension’ to (ii) sub-routines of language processing such as phonology, lexical

processing, syntax, semantics, and so on, to (iii) ever more fine-grained representations and computational primitives argued to underpin the different subroutines of language, such as concatenation, linearization, among others.

In all areas of language processing, noteworthy new perspectives have been developed (reviewed, among many others, for example, in [1–3], with special emphasis on speech, linguistic structure-building, and the sensorimotor basis of speech/language, respectively). Notwithstanding the novel approaches, many of the substantive challenges are only now becoming clear. The number and arrangement of the cortical and subcortical regions underpinning speech and language processing demonstrate that the system is considerably more complex and distributed; the age of Broca’s and Wernicke’s areas and the era of left-hemisphere imperialism are over. Here I focus on a two issues that are redefining the research agenda, pointing towards a *computational neurobiology of language* [4], a research direction that emphasizes the representational and computational primitives that form the basis of speech and language.

There are, of course, many ways to illustrate the progress that has been made, highlighting new ideas and directions. One approach would be to review the different aspects or levels of language processing that have been examined in new neuroscientific experimentation, that is, phonetics, phonology [5,6], lexical access [7–10], lexical semantics [11], syntax [12,13], compositional semantics [14,15], discourse representation [16,17]; moreover, the interaction of the linguistic computational system with other domains has been investigated in interesting ways, including how language processing interfaces with attention [18], memory [19], emotion [20], cognitive control [21], predictive coding [22–24], and even aesthetics [25]. A different approach is taken here, focusing first on the revised spatial map of brain and language; then, narrowing to one functional problem, a new ‘temporal view’ is discussed to illustrate a linking hypothesis between the computational requirements of speech perception and the neurobiological infrastructure that may provide a neural substrate.

The new functional anatomy: maps of regions, streams, and hemispheres

Our understanding of the anatomic foundations of language processing has changed dramatically in the last 10 years, ranging from the biggest to the most local levels.

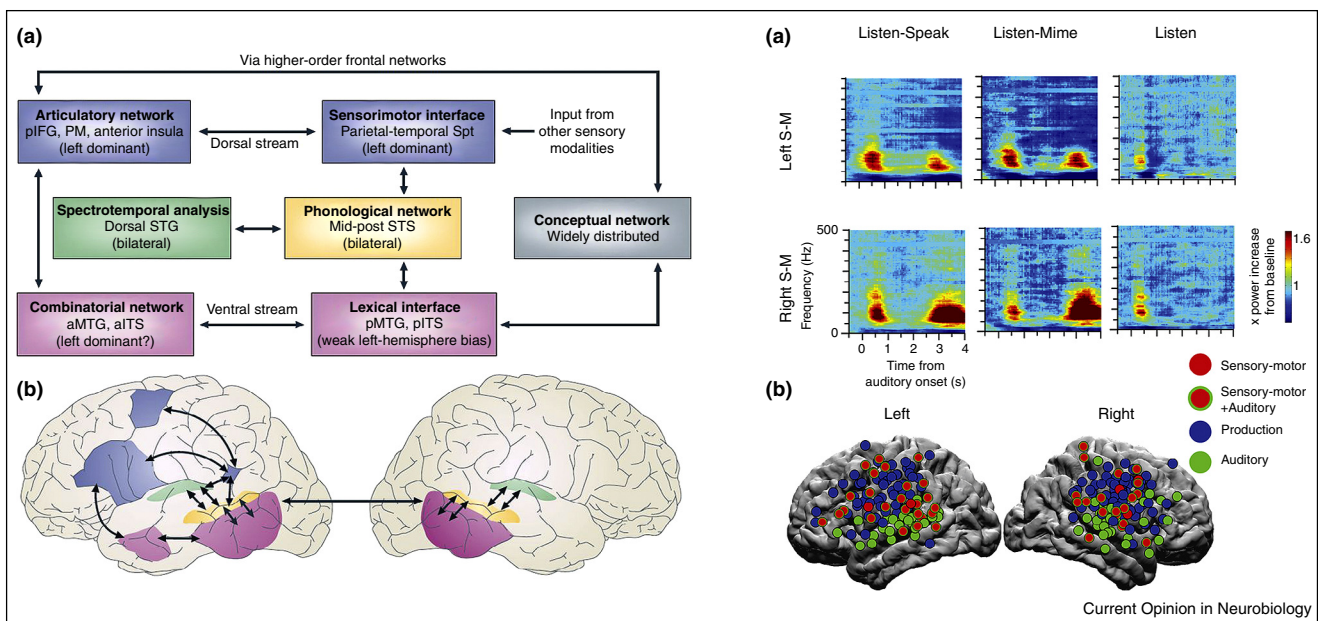
One might call this the *maps problem* [26], that is, the challenge to define the best possible spatial map that describes the anatomic substrate [27–29]. The older, ‘classical’ view and its limitations are discussed further in Hagoort, this volume, where a contrasting dynamic network view of local function is described.

(a) Starting at the most coarse level, consider the role of hemispheric asymmetry. Historically, the lateralization of language processing to the ‘dominant hemisphere’ has been one of the principal defining features. It was uncontroversial that language processing is strongly lateralized. However, a more nuanced and theoretically informed view of language processing, breaking down the processes into constituent operations, has revealed that lateralization patterns are complex and subtle—and that not all language processing components are lateralized. For example, when examining the cortical regions mediating speech perception and lexical level comprehension, lesion [30,31], imaging [32–34], and electrophysiological data [35,36] demonstrate convincingly that both left and right superior temporal cortical regions are implicated. Indeed, the operations mapping from input signals (e.g. sound) to lexical-level meaning, argued to be part of ventral stream processing (see **b**, below) appear to be robustly bilateral, as illustrated in **Figure 1a** (bottom panel).

By contrast, it is typically argued that the structures and operations underlying production, for example, are lateralized. As illustrated in **Figure 1a**, *one* of the dorsal stream projections, suggested to underpin the sensory-motor mapping necessary for perception-production alignment, is depicted as fully lateralized. However, new data acquired in pre-surgical epilepsy patients using electrocorticography (ECog) seriously challenge even this generalization [37]. It is shown based on a range of tasks requiring sensory (sound)-to-motor (articulatory) transformation that the dorsal stream structures that provide the basis for this mapping are clearly bilateral as well (**Figure 1b**). Other, non-speech dorsal stream functions, for example operations that are part of grammatical relations, may be supported by other dorsal stream projections, and their lateralization pattern has not been fully established, although there appears to be a fair degree of lateralization to the dominant hemisphere (see [2] and Hagoort, this volume).

Various other imaging and physiology experiments on other aspects of language [38,23] also invite the interpretation that lateralization patterns are more complex than anticipated. Cumulatively, in other words, the language-ready brain (to use a phrase of Hagoort, this volume) appears to execute many of its subroutines bilaterally,

Figure 1



(a) Dual stream model [1]. (b) Note the bilateral arrangement of the ventral stream network (mapping from sound to meaning) and the lateralized dorsal stream projections (mapping to articulation). (b) Bilateral processing of sensory-motor transformations for speech, from [37]. (c) Spectrograms for three tasks: A ‘Listen-Speak’ task: subjects heard a word and after a short delay had to repeat it; A ‘Listen-Mime’ task: subjects heard a word and after the same short delay had to move their articulators without vocalizing; ‘Listen’ task: subjects listened passively to a word. Sensory-motor (S-M) responses are seen in example electrodes in both the left (top row) and right (bottom row) hemispheres as demonstrated by a high gamma neural response (70–90+ Hz) present both when the subject listened to a word and when they repeated/mimed it. (d) Population average brains with active electrodes demonstrate that S-M processes occur bilaterally (red). Electrodes that responded to the passive listen condition are also noted with green outlines (red with green outlines).

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