

38 Key Issues and Future Directions: The Neural Architecture for Language

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An adequate understanding of the human capacity for language requires a merging of constraints from functional accounts (the cognitive architecture) and from specifications of the neural infrastructure that supports it (the neural architecture). This part focuses mainly on the latter. Which aspects of brain organization have made our species language-ready? Which building blocks of brain organization are especially critical for the cognitive computations that are involved in speaking, listening, reading, and related language skills? Clearly, language is a multicomponent system, minimally involving levels of phonology, syntax, and semantics (Hagoort, 2005, 2013; Jackendoff, 2002). Each of these components might need to recruit the contribution of a different set of neuronal circuits. The degree to which brain areas and brain networks are specialized for aspects of language is an issue of debate. Another unresolved issue is which level of brain organization is most critical for supporting cognitive computations.

Palomero-Gallagher and Zilles (chapter 33) argue that insights into cytoarchitecture and receptor architecture are crucial prerequisites for our understanding of the neurobiological basis of language. They discuss these architectural features in quite some detail for the language-relevant areas. In addition, these authors argue that especially the receptor fingerprints represent the molecular default organization of the regionally specific local information processing in each cortical area. Neurochemically, related cortical areas may participate in the same functional system. Interestingly, the left hemisphere receptor fingerprints revealed a tight clustering of all language-relevant areas.

Another central aspect of brain organization is its organization of distinct building blocks into networks, forming structural and functional systems extending across the brain. This is the focus of the contribution of Przeździecki, Haak, Beckmann, and Bartsch (chapter 34). They discuss current descriptions of structural and functional organization between distinct areas that

form the “language connectome” and further argue that neurobiological models of language ought to be validated on empirical data, considering the mesoscopic variations in brain connectivity patterns as well as more macroscopic connectivity and the topographic organization thereof. The observed level of coactivity across different language-relevant parts of the brain provide an important set of benchmark boundary conditions for investigating the complexity of interactions within the language system.

Listening and speaking are the evolutionary primordial speech and language skills. Although tightly linked, they link differently to the underlying neural infrastructure. For listening, it is conceivable that in the human brain the circuitry devoted to auditory perception is optimized to ensure efficient and robust analysis of the complex speech signals (Formisano, chapter 35). The online analysis of an incoming speech signal requires the simultaneous analysis of spectral and temporal components at multiple scales. As Formisano reviews, not only in higher-level auditory cortex but also in early auditory areas neuronal populations are fine-tuned to the characteristic properties of speech. The absence of these tuning characteristics in the auditory cortex of the macaque monkey suggests that human auditory areas express some unique features that are likely acquired through lifelong learning and have emerged as a critical step in the evolution of speech and language.

Likewise, for speaking, the motor cortex seems to have developed a speech-ready organization (Bianchi & Simonyan, chapter 36). Speaking is one of the most complicated motor acts we perform, requiring the coordinated activity of more than 100 respiratory, laryngeal, and orofacial muscles. This necessitates a degree of motor control unmatched by any other motor system in the body. The laryngeal motor cortex (LMC) is a key component of the motor system for supporting speech. Compared to the macaque brain, the human LMC establishes a nearly sevenfold increased connectivity

with the somatosensory and inferior parietal cortex, putatively to enable sensorimotor integration needed for speech production. An additional reorganization of LMC in the course of hominin evolution is the establishment of direct connections with laryngeal motor neurons in the brain stem. In short, both auditory and motor cortices have undergone important adaptations to realize a neural architecture that is speech- and language-ready.

Despite these sizeable brain adaptations to requirements of speech and language, there remains an important riddle for our understanding of the mapping relation between the cognitive and the neural architecture for language. This is discussed chapter 37 by Bedny and MacSweeney about the changes in the neural architecture in individuals that are born blind or deaf. Their contribution suggests that there is more than one neuronal solution to the computational challenges of language. For instance, the visual cortex of the congenitally blind is sensitive to the grammatical and lexical properties of linguistic stimuli, which *prima facie* have quite different computational requirements than the visual input in the seeing brain. This brings us back to the issue of what are the computational degrees of freedom over variations in the underlying neural architecture.

1. The Neuroanatomical Stance

Among experts in the field of neuroanatomy and neurophysiology there are, in broad strokes, two opposing views (cf. Hagoort, 2018). This we will illustrate at the example of the role of cytoarchitectonics. A prime example of the contribution of neuroanatomy is the famous map by Korbinian Brodmann (1869–1918). This map consisted originally of 52 different areas, usually referred to by expressions such as BA44 for Brodmann area 44. The labeling of the Brodmann areas was determined by the order in which Brodmann went through the brain, analyzing one area after the other. Brodmann's classification is based on the cytoarchitectonics of the brain, which refers to the structure, form, and position of the cells in the six layers of the cortex, the quantification of which was done by Brodmann based on a small number of postmortem brains. These were sectioned into slices of 5- to 10-micron thickness that underwent Nissl staining and were then inspected under the microscope. In this way, the distribution of different cell types across cortical layers and brain areas could be determined. Even today, Brodmann's map, published in 1905, is seen as a hallmark achievement in the history of neuroscience. Brodmann's work reveals that the composition of the six cortical layers, both in terms of cell types and cell numbers, varies substantially

across the brain. The primary visual cortex, for instance, has about twice as many neurons per cortical column as other brain areas (Amaral, 2000). In recent times, the work of Brodmann and others from the classical era of neuroanatomy has been substantially modernized by Zilles, Amunts, and colleagues (see Palomero-Gallagher & Zilles, chapter 33 of this volume).

Importantly, the classical view among neuroanatomists is that these architectural differences in brain structure are indicative of functional differences, and, conversely, that functional differences demand differences in architecture (Bartels & Zeki, 2005; Brodmann, 1905; Vogt & Vogt, 1919; Von Economo & Koskinas, 1925). Following the classical view, through different ways of characterizing brain structure (i.e., cyto-, myelo-, and receptorarchitectonics; Amunts & Zilles, 2015; Zilles & Palomero-Gallagher, 2001), brain areas can be identified, for which differences in structural characteristics imply functional differences. From this view, it follows that one should look for the structural features that determine why a particular brain area can support, for instance, morphological decomposition or syntactic encoding.

In contrast to the classical view in neuroanatomy, more recent accounts have argued that, from a computational perspective, different brain areas are very similar. For instance, Douglas and Martin (2004) argued that “the same basic laminar and tangential organization of the excitatory neurons of the neocortex, the spiny neurons, is evident wherever it has been sought. The inhibitory neurons similarly show a characteristic morphology and patterns of connections throughout the cortex ... all things considered, many crucial aspects of morphology, laminar distribution, and synaptic targets are very well conserved between areas and between species” (p. 439; see also Douglas & Martin, 2018). Bastos et al. (2012) therefore spoke of a canonical microcircuit that has the same computational organization across all of the neocortex, despite the cytoarchitectonic differences that can be observed between, for instance, the sensory and motor cortexes. Functional differences between brain areas arise in this perspective mainly due to variability of the input signals in forming functional specializations. The functional contribution of a particular piece of cortex might thus primarily not be determined by heterogeneity of brain tissue, but rather by the way in which its functional characteristics are shaped by the afferent connections.

2. Key Issues and Future Directions

The two opposing views discussed in section 1 have consequences for how one envisions to identify the

relevant neural building block for cognitive computations. At the same time, functional and structural neuroimaging studies can provide some relevant insights into this matter. Importantly, a number of remarkable manifestations of neural plasticity have been reported in recent years. For instance, Amedi, Raz, Pianka, Malach, and Zohary (2003) reported on congenitally blind subjects with increased activation in primary visual cortex (V1) during a verbal memory task. Moreover, the stronger the activation in V1, the better the memory performance. If the structural properties of V1 had been exclusively decisive for its functional capacities, then it would be hard to see how the same neurons that in subjects with intact vision support basic visual processing could be recruited in the blind for verbal memory, assuming that major cytoarchitectonic features of visual cortex are not shaped by the specifics of the sensory experience. Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, and Saxe (2011; see Bedny & MacSweeney, chapter 37) reported language processing in the occipital cortex of congenitally blind individuals. This even includes high-level language function such as the computation of sentence-level combinatorial structure. These findings demonstrate that the cytoarchitectonic constraints for specifications of cognitive function are rather loose. Presumably, the patterns of connectivity between areas and ensuing differences in inputs are a more relevant functional parameter than the differences between the cytoarchitectonic details of specific cortical areas. For another part of brain, Bola et al. (2017) reported that in deaf humans the high-level auditory cortex gets involved in vision. Based on these and similar findings, Bedny (2017, p. 637) concluded that “human cortices are cognitively pluripotent, that is, capable of assuming a wide range of cognitive functions. Specialization is driven by input during development, which is constrained by connectivity and experience.”

All this does not imply that one should deny the great importance of cytoarchitectonic structures for human cognition. Clearly, without these basic building blocks of the brain, cognition would not be possible. Without different types of neurons, glia, and axons, the cognitive machinery would not work. Nevertheless, the issue here is that these building blocks enter into processes of functional specialization and segregation. It might be that the exact nature of these functional specializations are more easily inferred from an analysis of input/output and connectivity than by looking at the detailed cytoarchitectonic characteristics.

The conundrum that remains for this view is what to do with the concept of a brain area. How should one define borders independently of cytoarchitecture? One

solution is to specify brain areas themselves in functional instead of structural terms. An example is parcellations based on resting-state functional MRI (e.g., Zhang et al., 2015; see Eickhoff, Thirion, Varoquaux, & Bzdok, 2015, for an overview). Alternative options are a parcellation of cerebral cortex on the basis of a multimodal combination of structural and functional measures (Glasser et al., 2016). Connectivity-based parcellations are predicated on the assumption of a correspondence between a cortical brain area and its connectivity fingerprint, as derived by diffusion-weighted MRI and resting-state functional MRI (Eickhoff et al., 2015). In either case, however, current approaches for characterizing elementary building blocks of computation will require further advances in imaging methodology to capture the rich functional variations across different parts of the brain. These provide further constraints in terms of the necessity to capture both functional variation within brain areas as well as functional multiplicity. The former refers to the fact that evidence from sensory cortices suggest a multiscale hierarchical functional organization while the latter acknowledges the possibility that the same patch of cortex can exhibit multiple modes of organization simultaneously. For instance, V1 can be probed for orientation selectivity as well as for foveal versus high eccentricity, giving rise to multiple modes of area description. Indeed, recent work suggests that various areas of interest might be characterized by multiple modes of organization, with overlapping topographically organized modes of connectivity (Haak, Marquand, & Beckmann, 2018), further challenging the concept of a brain area with piecewise homogeneous and unitary structure.

What are the consequences for accounts of language learning and language processing? We don't think that at the moment there is much evidence for the claim that all hinges on whether a particular activation is found in, say, BA44 rather than BA45. Patterns of activity have been shown to vary depending on the precise experimental context (see Przeździk et al., chapter 34, figure 34.2). An approach based on reversed inferences from structural anatomy or functional activation to cognitive function seems in the light of our current knowledge, not well-constrained enough. It is functional anatomy that counts, and that might provide stronger constraints than structural anatomy for specifications of the different forms of human cognition. This implies that for an evolutionary perspective on the neural architecture for language, we should look at patterns of associations and dissociations in measures of brain activity, and do comparative studies of, for example, tractography in different species (e.g., Rilling et al., 2008; Rilling & van den Heuvel, 2018). The differences

in the arrangements of network elements in the nervous system among related species might be key to understanding the evolutionary origins of language and other cognitive functions (Petersen & Sporns, 2015). The network topologies might provide more direct insights into the neural instantiations of cognitive functions than of the classical anatomical measures (Xiang, Fonteijn, Norris, & Hagoort, 2010). In the words of Park and Friston (2013, p. 7), “Function may deviate from structure to exhibit dynamic and contextualized behavior. Such divergence of function from structure is perhaps the most intriguing property of the brain.”

3. Conclusion

A cognitive neuroscience approach to language takes information and constraints from different levels of analysis into consideration, in the service of a full account of the neurobiology of language. The assumption hereby is that these different levels become mutually informative and can be connected in a transparent way. At the same time, not all constraints have the same impact. Here it is argued that the constraints provided by the classical anatomical measures (cyto- and myeloarchitectonics) are—in our current understanding—not very tight constraints for detailed specifications of cognitive functions, including language learning and language processing. Maybe, measures of the computational features of brain tissue might provide stronger constraints. For understanding cognitive specialization, future research should pay close attention to measures of functional and structural connectivity.

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