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Prerequisites for an evolutionary stance on the neurobiology of language

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The neurobiology of language has to specify the cognitive architecture of complex language functions such as speaking and comprehending language, and, in addition, how these functions are mapped onto the underlying anatomical and physiological building blocks of the brain (the neural architecture). Here it is argued that the constraints provided by the classical anatomical measures (cytoarchitectonics and myeloarchitectonics) are in our current understanding only very loose constraints for detailed specifications of cognitive functions, including language learning and language processing. However, measures of the computational features of brain tissue might provide stronger constraints. For understanding cognitive specialization, for the time being we thus have to put our cards on measures of functional instead of structural neuroanatomy. The implication for an evolutionary stance on the neurobiology of language is that in a cross-species comparative perspective one needs to identify the factors that gave rise to the properties of the canonical microcircuits in the neocortex, and to the large scale network organization that created the language-readiness of the human brain.

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Dobzhanski's famous claim [1] that nothing makes sense in biology except in the light of evolution does not hold necessarily for the neurobiology of higher cognitive functions such as language. No doubt both brain and language are the product of an evolutionary history. But for the current state of the art in the neurobiology of language, the insights from evolutionary accounts on the origin of language are not (yet) precise enough to be of tremendous help. Moreover, there is a very long and complex to-do list for the neurobiologists with an interest in language that can guide the research agenda without a clear role for constraints from evolutionary biology. Although Dobzhanski's claim is undoubtedly correct in the ontological sense, for the time being its epistemological status is less clear. I will illustrate this for alternative views on the neuroanatomical basis of language-relevant computations.

The research agenda of the neurobiology of language has at least three key issues that need to be addressed. The first one is a decomposition of the tripartite architecture of language [2] in its core components. This entails a detailed specification of the building blocks of the system for speech sounds, the lexical building blocks, the combinatorial machinery of syntax and semantics, etcetera. The second requirement is a detailed characterization of the neural infrastructure at multiple levels. Minimally this entails detailed information about cytoarchitectonic, myeloarchitectonic and receptorarchitectonic properties of brain areas [3], fiber pathways, large scale network properties, neurophysiological mechanisms (e.g. brain oscillations in different frequency bands), the computational properties of the columnar organization of the six-layered neocortex [4], the laminar organization of feedforward and feedback connections [5], the temporo-spatial patterns of brain activation [6], etcetera. Finally, one needs to take a stance on the mapping relation between the cognitive architecture and the neural architecture [7•]. For instance, at what level of granularity should one seek the natural kind relations between brain and language. This could go from 'Neuron X + Y represent the final consonant in the word CAT', to 'creating a situational model is based on the contribution of the right frontal cortex', all the way up to the textbook wisdom that 'language is subserved by the left hemisphere'. All these issues are complex and keep many researchers busy in their daily research life. In my reading of the literature, evolutionary considerations do not play a role (or only minimally so) in answering these issues on the to-do list of the average cognitive neuroscientist.

One reason that evolutionary considerations do not play a central role in the neurobiology of language is undoubtedly that for higher cognitive functions the evidence is not straightforward, and hence many accounts have the characteristic of just-so stories [8]. Of course, this does not invalidate the relevance of Tinbergen's four questions: the proximate causes (mechanism and ontogeny), and the ultimate causes (adaptive value and phylogeny) [9]. However, in order to stand a chance of making progress on the evolutionary question (the ultimate causes), we might need to take a stance on which features of the neural machinery and its ontogeny (the proximal causes) are considered to be more key than others for the search of evolutionary precursors. In the remainder I will illustrate this for the endo-phenotype, namely the anatomy of the human brain (all features of the brain are equal but some are more equal than others).

The neuroanatomical stance

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 BA 44 for Brodmann Area 44. The numbers of the Brodmann Areas were determined by the order in which Brodmann went through the brain, analysing 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. Quantification was done by Brodmann on post-mortem brains. These were sectioned into slices of 5–10 μm 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, that was published in 1909, is seen as a hallmark in the history of neuroscience. Brodmann's work reveals that the composition of the six cortical layers, in terms of cell types, varies across the brain. Also cell numbers can vary. The primary visual cortex, for instance, has about twice as many neurons per cortical column as other brain areas [10].

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 [11–14]. Following the classical view, through different ways of characterizing brain structure (i.e. cytoarchitectonics, myeloarchitectonics and receptor-architectonics; [15,3]), brain areas can be identified for which differences in structural characteristics imply functional differences. From this view it follows that one should thus 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 [16••] argue 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 [17]). Bastos *et al.* [4] therefore speak of a canonical microcircuit that has the same computational organization across all of neocortex, despite the cytoarchitectonic differences that can be observed between, for instance, sensory and motor cortex. Functional differences between brain areas are 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 input.

Neuroimaging studies provide support for this view. A number of remarkable forms of neural plasticity have been reported in recent years. For instance, Amedi *et al.* [18] report that they found in congenitally blind subjects 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 decisive for its functional capacities, then it would be hard to see how the same neurons that in seeing people support vision could be recruited in the blind for verbal memory. Bedny *et al.* [19] report 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 input and the patterns of connectivity between areas are a more relevant functional parameter than the differences between the cytoarchitectonic details of different cortical areas. Bola *et al.* [20] report that in deaf humans the high-level auditory cortex gets involved in vision. Hence, Bedny [21••] concludes 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.' (p. 637).

All this does not imply that I 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. However, the issue here is that these building blocks enter into processes of functional specialisation. My claim is that the exact nature of these functional specialisations are more easily inferred from an analysis of