Response to Bornkessel-Schlesewsky *et al.* – towards a nonhuman primate model of language?

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In a recent Opinion article, Bornkessel-Schlesewsky *et al.* [1] make the interesting proposal that the basic computational mechanisms necessary for language processing are implemented in the nonhuman primate brain. According to the authors, neural differences between human and nonhuman primates are quantitative but not qualitative in nature. Both species share a ventral stream underlying auditory object recognition and combination, and a dorsal stream underlying sequence processing. The cross-stream interaction is assumed to be crucial for human language to emerge. The observed cross-species differences in language are based on the prefrontal cortex (PFC) that allows the integration of information from both streams only in humans.

We agree with Bornkessel-Schlesewsky *et al.* that language, in common with other cognitive functions, is grounded on basic physiological principles [2]. We furthermore acknowledge that the nonhuman primate prefrontal cortex supports symbolic manipulation abilities that can be seen as precursors to the syntactically guided structuring of signs in humans [3]. However, we emphasize that some important data not discussed by Bornkessel-Schlesewsky *et al.* strongly support the view that there are clear qualitative, and not merely quantitative, differences between the species with respect to both the intrinsic functional connectivity of frontal and temporal cortices, and their direct structural connection via a dorsal white matter fiber tract. Moreover, we should point out that the exact nature of the claimed interaction between streams postulated by the authors awaits specification at both the functional and structural levels, and remains to be proven empirically.

Comparative diffusion-weighted magnetic resonance imaging studies reveal that the brain of the macaque (*Macaca mulatta*) is comparable to the human (*Homo sapiens sapiens*) brain with respect to its macrostructural architecture of dorsal and ventral white matter fiber tracts related to language processing in humans [4]. Notably, the macaque brain exhibits a direct long-distance connection from the homologous region of the human Brodmann area 44 (BA44) to the posterior superior temporal cortex (pSTC) via the arcuate fasciculus, which is associated with higher-order syntactic and thematic computations in the human brain [5]. The observation that the diffusion probability of this structural connection differs qualitatively, not only quantitatively [4], was decisively complemented by a recent resting-state fMRI study comparing the intrinsic functional connectivity of the dorsal pathway between species [6]. Crucially, while BA44 is intrinsically connected to the pSTC in the human brain, this direct functional connection is absent in the macaque brain, which only shows a link between BA44 and the inferior parietal cortex. This finding suggests that the dorsal language network of *Homo sapiens sapiens* shows not only structural but also functional properties that have not emerged in the nonhuman primate brain. Future studies involving human primates will be necessary to clarify if this dorsal fronto-temporal functional connection is specific to the phylogenesis of *Homo sapiens sapiens* or is an evolutionary achievement shared with other hominids.

The argument of Bornkessel-Schlesewsky *et al*. that cross-stream interaction is the only and necessary condition for the emergence of language is exclusively based on previous conceptual work discussing the heuristic plausibility of this notion, and not on empirical data directly supporting it. Furthermore, it remains unclear how the authors' view that there are differences in the structure and function of the PFC, enabling feedback and crosstalk between streams in human, but not in nonhuman primates, is compatible with the claim that there are no qualitative neurocomputational differences between species.

In summary, we argue that pronounced disparities with respect to the structural and functional connectivity of inferior frontal and superior temporal cortices compromise the idea that the nonhuman primate brain provides an accurate animal model of human language. The attempt of Bornkessel-Schlesewsky *et al.* to introduce such a model remains conceptually underspecified and empirically not well supported.

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References

1 Bornkessel-Schlesewsky, I. *et al.* (2015) Neurobiological roots of language in primate audition: common computational properties. *Trends Cogn. Sci.* 19, 142–150

2 Friederici, A.D. and Singer, W. (2015) Grounding language processing on basic neurophysiological principles. *Trends Cogn. Sci.* 19, 329–338

3 Nieder, A. (2009) Prefrontal cortex and the evolution of symbolic reference. *Curr. Opin. Neurobiol.* 19, 99–108

4 Rilling, J.K. *et al.* (2008) The evolution of the arcuate fasciculus revealed with comparative DTI. *Nat. Neurosci.* 11, 426–428

5 Skeide, M.A. *et al.* (2015) Brain functional and structural predictors of language performance. *Cereb. Cortex* Published online March 13, 2015. http://dx.doi.org/10.1093/cercor/bhv042

6 Neubert, F.X. *et al.* (2014) Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex. *Neuron* 81, 700–713

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