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## On the organization of the perisylvian cortex: Insights from the electrophysiology of language Comment on "Towards a Computational Comparative Neuroprimatology: Framing the language-ready brain" by M.A. Arbib

Comment

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The Mirror System Hypothesis (MSH) on the evolution of the language-ready brain draws upon the parallel dorsal-ventral stream architecture for vision [1]. The dorsal "how" stream provides a mapping of parietally-mediated *affordances* onto the motor system (supporting preshape), whereas the ventral "what" stream engages in object recognition and visual scene analysis (supporting pantomime and verbal description). Arbib attempts to integrate this MSH perspective with a recent conceptual dorsal-ventral stream model of auditory language comprehension [5] (henceforth, the B&S model). In the B&S model, the dorsal stream engages in *time-dependent* combinatorial processing, which subserves syntactic structuring and linkage to action, whereas the ventral stream performs *time-independent* unification of conceptual schemata. These streams are integrated in the left Inferior Frontal Gyrus (IIFG), which is assumed to subserve cognitive control, and no linguistic processing functions. Arbib criticizes the B&S model on two grounds: (i) the time-independent as syntactic processing), and (ii) the absence of linguistic processing in the IIFG (reconciling syntactic and semantic representations is very much linguistic processing proper). Here, we provide further support for these two points of criticism on the basis of insights from the electrophysiology of language. In the course of our argument, we also sketch the contours of an alternative model that may prove better suited for integration with the MSH.

The B&S model is effectively a cortical instantiation of the extended Argument Dependency Model (eADM) [3,4]. The eADM posits a cascaded architecture, in which an algorithmic-driven processing stream ( $\sim$  the dorsal stream in the B&S model) works in parallel to a plausibility processing stream ( $\sim$  the ventral stream). The former serves to assign thematic roles to incoming noun phrases based on "prominence" information (e.g., animacy, case marking, and linear word order) and to link these to the argument structures of incoming verbs, whereas the latter determines the most plausible combination of the arguments and the verb in a sentence, while ignoring (linear, hence

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time-dependent) surface structure. The outcomes of the two streams are integrated in a generalized mapping step ( $\sim$  IIFG function in the B&S model). Crucially, the eADM explicitly links processing in these different streams to Event-Related brain Potential (ERP) components. Of interest to the present argument is that the eADM postulates that difficulty in plausibility processing modulates the amplitude of the N400 component, whereas difficulty in integrating the outcome of this stream with that of the algorithmic-driven stream modulates P600 amplitude. The eADM shares this mapping with a number of other prominent multi-stream models, all of which have been motivated to explain so-called 'Semantic P600'-effects [13,21,14,11]. Crucially, it has been argued that none of these models can account for the full spectrum of these findings [7]. By contrast, the single-stream Retrieval-Integration (RI) model, in which syntactic and semantic processing is more integrated, does account for the data at hand [7,8] (see [6], for explicit computational support). These insights from the electrophysiology of language question the validity of a plausibility heuristic (or structure-independent semantic analyzer) (see also [19]), and thereby a conceptualization of the ventral stream as reflecting time-independent semantic processing. This supports Arbib's first point of criticism.

On the RI model, N400 amplitude does not reflect any compositional semantic processing, but rather the contextualized retrieval of the conceptual knowledge associated with an incoming word from memory (cf. [15,16,20]). P600 amplitude, in turn, does reflect compositional semantic processing: it indexes the integration of the meaning of an incoming word with the unfolding utterance interpretation. Cortically, the retrieval processes underlying the N400 are mediated by the left posterior Middle Temporal Gyrus (lpMTG; Brodmann Area 21), whereas the integrative processes underlying the P600 are mediated in the IIFG (BA 44/45/47) [8]. Hence, in contrast to the B&S model, on which the IIFG does not reflect any linguistic processing functions, the RI model posits the IIFG as the core computational epicenter for compositional semantic processing. Importantly, this view on the IIFG unifies a number of conflicting hypotheses on the role of this area (see [10,17], for reviews) by subsuming syntactic, semantic, as well as working-memory related, and control processes (see [8], for discussion on how the complex architecture of the IIFG could support such a diverse spectrum of functions). This view (which seems consistent with the MSH perspective on Broca's area) thus *subsumes*, but does not *limit* IIFG function to cognitive control. Indeed, it is unclear how the data that motivated this subsumption-based account, especially the data implying the IIFG in combinatorial semantic processing (e.g., see the evidence reviewed in [11]), could be reconciled with a *cognitive control*-only view on this region. This supports Arbib's second point of criticism.

As for the dorsal-ventral stream distinction, the RI model effectively assumes a reverberating circuit between the retrieval (lpTMG) and integration (IIFG) epicenters, requiring bidirectional connectivity between these regions. The dorsal and ventral pathways, and their respective sub-pathways (see [9]), support such a reverberating circuit between temporal and frontal regions (see [2], for a speculative proposal). However, it remains an open question which (sub)pathways are involved in bottom-up (lpMTG  $\rightarrow$  IIFG), and which are involved in top-down (IIFG  $\rightarrow$ lpMTG) computations. As of yet, the literature shows little consensus on the functional roles of the dorsal and ventral streams (e.g., [12,18,22,9,2,5]). At best, there appears to be some agreement on the involvement of the ventral stream in form to meaning mapping [12,9,5], supporting a bottom-up role for this pathway (consistent with the MSH). As for the dorsal stream, it has been suggested that one of its sub-pathways may be involved in delivering top-down predictions from the frontal to the temporal lobe [9]. However, others have proposed a precise mirror image of this dorsal-ventral stream distinction [2].

In sum, insights from the electrophysiology of language do not support a conceptualization of the ventral stream as subserving time-independent semantic processing. Moreover, it seems difficult to reconcile a *cognitive control*-only role for the IIFG with the data at hand, especially the data that imply the IIFG in combinatorial semantic processing (see [11]). We have argued that these insights support Arbib's criticism of the B&S model, and we have briefly sketched the contours of an alternative model, the RI model, [7,8], which posits a reverberating circuit between temporal (memory) and frontal (semantic integration) areas. It remains to be seen what the precise roles are that the dorsal and ventral streams play in this circuit, and hence, if and how the MSH and the RI model can be integrated. It may be precisely here where a synthesis between a computational neurolinguistics and a computational comparative neuroprimatology is the way forward.

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## References

- [1] Arbib MA. Towards a computational comparative neuroprimatology: framing the language-ready brain. Phys Life Rev 2016;16:1–54. http://dx.doi.org/10.1016/j.plrev.2015.09.003 [in this issue].
- [2] Baggio G, Hagoort P. The balance between memory and unification in semantics: a dynamic account of the N400. Lang Cogn Processes 2011;26:1338–67.
- [3] Bornkessel I, Schlesewsky M. The extended argument dependency model: a neurocognitive approach to sentence comprehension across languages. Psychol Rev 2006;113(4):787–821.
- [4] Bornkessel-Schlesewsky I, Schlesewsky M. An alternative perspective on semantic P600 effects in language comprehension. Brains Res Rev 2008;59(1):55–73.
- [5] Bornkessel-Schlesewsky I, Schlesewsky M. Reconciling time, space and function: a new dorsal-ventral stream model of sentence comprehension. Brain Lang 2013;125(1):60–76.
- [6] Brouwer H. The electrophysiology of language comprehension: a neurocomputational model. PhD thesis. University of Groningen; 2014.
- [7] Brouwer H, Fitz H, Hoeks JCJ. Getting real about semantic illusions: rethinking the functional role of the P600 in language comprehension. Brain Res 2012;1446:127–43.
- [8] Brouwer H, Hoeks JCJ. A time and place for language comprehension: mapping the N400 and the P600 to a minimal cortical network. Front Human Neurosci 2013;7:758.
- [9] Friederici AD. The cortical language circuit: from auditory perception to sentence comprehension. Trends Cogn Sci 2012;16(5):262-8.
- [10] Grodzinsky Y, Santi A. The battle for Broca's region. Trends Cogn Sci 2008;12(12):474-80.
- [11] Hagoort P, Baggio G, Willems RM. Semantic unification. In: Gazzaniga MS, editor. The cognitive neurosciences. 4th edition. MIT Press; 2009. p. 819–36.
- [12] Hickok G, Poeppel D. The cortical organization of speech processing. Nat Rev Neurosci 2007;8(5):393-402.
- [13] Kim A, Osterhout L. The independence of combinatory semantic processing: evidence from event-related potentials. J Mem Lang 2005;52(2):205–25.
- [14] Kuperberg GR. Neural mechanisms of language comprehension: challenges to syntax. Brain Res 2007;1146:23–49.
- [15] Kutas M, Federmeier KD. Electrophysiology reveals semantic memory use in language comprehension. Trends Cogn Sci 2000;4(12):463–70.
- [16] Lau EF, Phillips C, Poeppel D. A cortical network for semantics: (de)constructing the N400. Nat Rev Neurosci 2008;9(12):920–33.
- [17] Rogalsky C, Hickok G. The role of Broca's area in sentence comprehension. J Cogn Neurosci 2011;23(7):1664–80.
- [18] Saur D, Kreher BW, Schnell S, Kümmerer D, Kellmeyer P, Vry M, et al. Ventral and dorsal pathways for language. Proc Natl Acad Sci 2008;105(46):18035–40.
- [19] Stroud CMA, Phillips C. Examining the evidence for an independent semantic analyzer: an ERP study in Spanish. Brain Lang 2011;120(2):108–26.
- [20] van Berkum JJA. The 'neuropragmatics' of simple utterance comprehension: an ERP review. In: Sauerland U, Yatsushiro K, editors. Semantics and pragmatics: from experiment to theory. Basingstoke: Palgrave Macmillan; 2009. p. 276–316.
- [21] van Herten M, Chwilla DJ, Kolk HHJ. When heuristics clash with parsing routines: ERP evidence for conflict monitoring in sentence perception. J Cogn Neurosci 2006;18(7):1181–97.
- [22] Weiller C, Musso M, Rijntjes M, Saur D. Please don't underestimate the ventral pathway in language. Trends Cogn Sci 2009;13(9):369-70.