



Comment

Adaptations to vision-for-action in primate brain evolution:
Comment on “Towards a Computational Comparative
Neuroprimatology: Framing the language-ready brain”
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As Arbib [1] notes, the two-streams hypothesis [5] has provided a powerful explanatory framework for understanding visual processing. The inferotemporal ventral stream recognizes objects and agents – “what” one is seeing. The dorsal “how” or “where” stream through parietal cortex processes motion, spatial location, and visuo-proprioceptive relationships – “vision for action.” Hickock and Poeppel’s [3] extension of this model to the auditory system raises the question of deeper, multi- or supra-sensory themes in dorsal vs. ventral processing. Petrides and Pandya [10] postulate that the evolution of language may have been influenced by the fact that the dorsal stream terminates in posterior Broca’s area (BA44) while the ventral stream terminates in anterior Broca’s area (BA45). In an intriguing potential parallel, a recent ALE metaanalysis of 54 fMRI studies found that semantic processing is located more anteriorly and superiorly than syntactic processing in Broca’s area [13]. But clearly, macaques do not have language, nor other likely pre- or co-adaptations to language, such as complex imitation and tool use. What changed in the brain that enabled these functions to evolve?

Early conceptualizations of the two-streams hypothesis focused on similarities between monkey and human brain organization. At the time, there simply was not a way to study considerable numbers of healthy, living nonhuman primate and human brains in a directly comparative manner. More recently, though, advancements in neuroimaging have made this possible, and now mounting evidence points toward both functional and structural elaboration of the human dorsal stream.

Relative to macaques, humans show unique responsivity to 3D-form-from-motion stimuli in the intraparietal sulcus [16], unique responsivity for observed tool use in the anterior supramarginal gyrus [11], and reduced prefrontal activation during the observation of objects [2]. Relative to chimpanzees, humans show similar co-activation between executed action and both transitive and intransitive observed action, in homologues to macaque mirror regions, but a differential distribution of activation during grasping observation, with chimp activation being largely prefrontally-focused and human activation showing increases in occipitotemporal and parietal cortex [7]. Interestingly, the finding

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of increased parietal activation during human manual action observation agrees with Gasser et al.'s [4] modeling study which suggests that increased proprioceptive input could facilitate the ontogenetic ritualization of manual gestures. These differences in activation may be causally related to differences in connectivity, which have been identified with diffusion tensor imaging. This includes elaboration of dorsal language connections via the arcuate fasciculus [12]; elaboration of dorsal action-perception pathways through the middle longitudinal fasciculus and superior longitudinal fasciculus, but relative conservation of ventral connections through the extreme capsule [6]; and extension of the third branch of the superior longitudinal fasciculus into anterior Broca's region, particularly in the right hemisphere [9].

Arbib asks what these connectivity differences mean: new connections between modules, strengthening of existing connections, or actual processing differences? While the underlying cellular mechanisms await further experimental investigation, the systems-level neuroimaging evidence above suggests that the answer is, "All of the above." On a general, theoretical level, tight inter-relationships seem probable between the organization of white matter connections and the type of processing carried out by gray matter regions. Changes in one seem likely to drive changes in the other, both at the level of experience-dependent plasticity within an individual, and of adaptive change across generations. On a more specific level, my colleagues and I have proposed that adaptations to action observation networks may be related to the evolution of social learning. Chimpanzees show a bias toward reproducing "what" an observed action accomplishes (emulation), while humans are biased toward reproducing "how" an observed action is carried out (imitation); monkeys are not known to imitate. Thus, monkeys' and chimpanzees' relative preponderance of ventral, temporal-frontal circuitry might correspond to their bias toward reproducing mainly action goals. In contrast, humans' elaboration of dorsal, temporal-parietal and parietal-frontal circuitry might support increased our bias toward reproducing specific methods. In particular, the extension of SLFIII into BA45 might provide a point of greater intersection between dorsal and ventral streams, supporting increased integration of hierarchical conceptualizations of action goals with concrete kinematic, proprioceptive, and spatial details – a function which would be increasingly important during the evolution of behaviors where hierarchical action goals are causally dependent on kinematics, as they are in stone toolmaking. And indeed, activation in BA45 differentiates between Oldowan toolmaking, which involves only simple successive flake removal, and Acheulean toolmaking, which requires nested hierarchical strategic plan [14,15]. Moreover, acquisition of Paleolithic stone toolmaking skills in modern humans causes white and gray matter changes in regions in and around the superior longitudinal fasciculus, including right BA45 [8].

Notably, the computational models developed by Arbib and colleagues are ideally suited to address the functional relevance of organizational changes within action circuitry. What happens when one alters the weight or organization of connections between nodes? Does this cause processing changes? Do those processing changes parallel what we see in experimental comparative neuroscience? Social learning and cultural evolution have been modeled at the population level. Would it be possible to create a population of MNS models and examine how variation in circuit organization plays out across interacting individuals? Arbib's substantial past work, combined with his call for a "computational comparative neuroprimatology," serves as a jumping-off point for empirical questions like these which could continue to expand our understanding of the evolution of the abilities that differentiate us from our primate relatives.

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References

- [1] Arbib MA. *Phys Life Rev* 2016;16:1–54. <http://dx.doi.org/10.1016/j.pprev.2015.09.003> [in this issue].
- [2] Denys K, et al. *J Cogn Neurosci* 2004;16(9):1505–16.
- [3] Hickok G, Poeppel D. *Trends Cogn Sci* 2000;4(4):131–8.
- [4] Gasser B, et al. *Neuroinformatics* 2014;12(1):93–109.
- [5] Goodale MA, Milner AD. *Trends Neurosci* 1992;15(1):20–5.
- [6] Hecht EE, et al. *Cereb Cortex* 2013;23(5):1014–24.
- [7] Hecht EE, et al. *J Neurosci* 2013;33(35):14117–34.
- [8] Hecht EE, et al. *Brain Struct Funct* 2015;220(4):2315–31.
- [9] Hecht EE, et al. *NeuroImage* 2015;108:124–37.
- [10] Petrides M, Pandya DN. *PLoS Biol* 2009;7(8):e1000170.
- [11] Peeters R, et al. *J Neurosci* 2009;29(37):11523–39.
- [12] Rilling JK, et al. *Nat Neurosci* 2008;11(4):426–8.

- [13] Rodd JM, et al. *Brain Lang* 2015;141:89–102.
- [14] Stout D, et al. *Philos Trans R Soc Lond B* 2008;363:1939–49.
- [15] Stout D, et al. *Eur J Neurosci* 2011;33(7):1328–38.
- [16] Vanduffel W, et al. *Science* 2002;298(5592):413–5.