Granger R. (2006). Behavioral & Brain Sci 29:17-18

The Evolution of Computation in Brain Circuitry
[excerpt from review of Striedter 2005]

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Abstract:

The attempt to derive mental function from brain structure is highly constrained by study of the allometric changes among brain components with evolution. In particular, even if homologous structures in different species produce similar computations, they may be constituents of larger systems (e.g., cortical-subcortical loops) that exhibit different composite operations as a function of relative size and connectivity in different-sized brains. The resulting evolutionary constraints set useful and specific conditions on candidate hypotheses of brain circuit computation.

As reptilian precursors of avian wings presumably had utility in their own right (e.g., speed, swimming, jumping) before they made the evolutionary transition to full-fledged instruments of flight (e.g., Dial 2003; Zhao 2004), so phylogenetic changes among brain areas are studied for their differing contributions to mental function as homologous structures become successively engaged in evolving circuit designs. Human brain has by far the largest brain-body ratio, and by far the largest ratio of telencephalon to remaining brain components; it is also the structure that uniquely yields complex language, extensive manufacture of artifacts, scientific investigation, and elaborate economic, social and political constructs. Whether this fount of unique species-specific behaviors arises from correspondingly unique circuitry, absent from non-human brains, or strictly from humans' unprecedented telencephalic enlargement of that circuitry, is a hotly debated question (see, e.g., Preuss 2000; Striedter 2005).

Mammalian cortico-striatal loops, in particular, enlarge allometrically and alter in configuration as brain size grows, becoming the system architecture that accounts for the vast majority of territory in human brain (schematically illustrated in Figure 1). The figure highlights three of the primary changes that occur with allometric growth from small-brained (a) to large-brained (b) mammals: 1) the growth of longitudinal fasciculi connecting anterior and posterior cortical regions (AC, PC); 2) a shift in targets of the pallidal (P) output stage, from descending motor nuclei (dashed box) to the thalamo-cortical circuitry that provided its striatal (S) inputs, "closing" the loop (gray "card"); 3) anterior cortex "invasion" of motor targets formerly innervated by pallidum (Nudo and Masterson, 1990). To the extent that cortical, thalamic, striatal, and pallidal circuitry compute similarly in small and large brains, they must be able to contribute to the range of different configurations in which they find themselves embedded; for instance, the basal ganglia's outputs must presumably be intelligible both to motor nuclei and to thalamocortical circuitry (Granger et al., 2004; 2005).

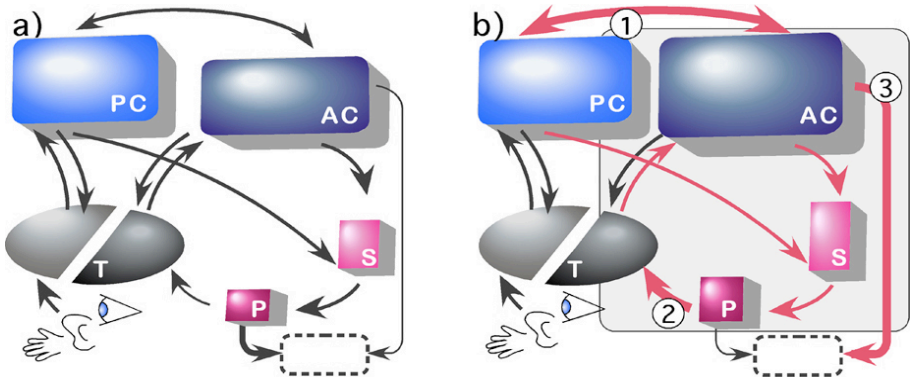

Figure 1. Allometric changes in primary components of telencephalon. The anatomical connection pathways among posterior and anterior neocortex (PC, AC), striatum (S), and pallidum (P) are shown for small-brained (a) and large-brained (b) mammals. Sensory inputs (vision, audition, touch) arrive at thalamus (T); projection loops connect thalamus with cortex and cortex to striatum to pallidum and back to thalamus; both pallidal and motor cortex efferents target brainstem motor nuclei (dashed box). (a) In small-brained mammals, primary output from pallidum is to motor systems; primary output of anterior cortex is to striatum. (b) Prominent allometric connection changes in large-brained mammals: (1) Substantial growth occurs in projections between anterior and posterior cortical regions (fasciculi). (2) Pallidal outputs increasingly target thalamus, completing the large cortico-striatal-thalamo-cortical loops. (3) Anterior cortical projections to motor targets grow large (pyramidal tract).

As components of telencephalon grow allometrically with brain size, how do the resulting interactions confer new computational capabilities to larger assemblies? This property is far from universal; many algorithms scale poorly with size, and even those that scale linearly or better do not typically acquire the power to solve new kinds of problems as they grow larger. Laminar organization of neocortex (and, possibly, of avian wulst) may have enabled it to scale to large size without incurring prohibitive space complexity (wiring) costs, but the larger question of added function remains open. It is intriguing to note that grammars are structures that can carry out abstract string processing operations, and grammatical engines exhibit capabilities that enlarge with the size of the grammatical database on which they operate; i.e., as the grammatical rule database grows, grammar systems acquire new capabilities, despite performing the same set of functions on this larger database. This is forwarded as a framework within which to think about the quandary: if thalamo-cortico-striatal circuitry constructs, by its nature, nested sequences of clusters of sequences of clusters, etc., as has been proposed (Rodriguez et al., 2004; Granger et al., 2004; Granger 2005), these data structures, comprising a specified form of "sensorimotor grammar," provide a candidate explanation for the challenging phenomenon of new behavioral abilities emerging as telencephalic brain structures phylogenetically proliferate.

A long-simmering question of brain evolution has recently been brought to a boil: birds and mammals both have species with very large brain-body ratios, each based on quite different telencephalic expansions (cortex in mammals; dorsal ventricular ridge in birds), but the homological relations have been unclear. Recent relevant findings have focused on the avian song system. In particular, lesions to the lateral magnocellular nucleus of the anterior nidopallium (LMAN) eliminate generative variability whereas stimulating LMAN increases variability (Olveczky et al., 2005) as a young zebra finch learns to produce the song "taught" by his father. The question of possible mammalian homologues naturally

arises, but none has yet been proposed. On predominantly computational grounds, an otherwise unlikely candidate emerges: tonically active neurons (TANs) comprise only about 5% of mammalian basal ganglia but project broadly and diffusely to striatal matrisomes and receive inhibitory input from striosomes (Aosaki et al., 1995; Shimo and Hikosaka 2001; Yamada et al., 2004). In modeling studies (see Granger 2004, 2005), nonspecific excitatory TAN activity disrupts matrix responses to a given cortical input, causing small, near-random variations. If cortico-striatal LTP in striosomes corresponds to accretion of statistical "predictions" of dopaminergic rewards that have followed a particular learned matrix response to a cortical input (see, e.g., Schultz 1998; 2002), then striosomal inhibition of TANs will increase as reward efficacy of a particular response is learned. The resulting model behavior resembles exploratory variability of action during learning, that diminishes as learning succeeds over trials. If so, TAN damage should selectively impede (and stimulation should increase) early behavioral variability in exploration-based learning; and blocking striosomal inhibition of TANs should prevent the reduction in variability, impeding such learning.

The literature suggests that TANs and LMAN are unlikely to be homologically related, as the former is presumed to be cholinergic (Aosaki et al., 1995; Bennett and Wilson, 1999; Koos and Tepper 2002), as well as acting via substance P and neurokinins A and B; whereas the latter is glutamatergic (Livingston and Mooney, 1997; Stark and Perkel, 1999), though it is worth noting that LMAN has repeatedly been reported to exhibit at least sparse cholinergic labeling (Ryan and Arnold, 1981; Watson et al., 1988; Zuschratter and Scheich, 1990; Ball et al., 1990; Sakaguchi and Saito, 1991; Sadananda 2004) and tyrosine hydroxylase immunoreactivity (Bottjer 1993); that NMDA (such as the receptor targets of LMAN) evokes ACh release at least in mammalian striatum (Kemel et al., 2002); and that LMAN's target nucleus RA is differentially responsive to ACh during the sensitive period of song learning (Sakaguchi 1995), raising the possibility that future findings may identify further points of comparison between these avian and mammalian mechanisms.

Acknowledgments:

The work described here was supported in part by grants from the Offie of Naval Research and from the Defense Advanced Research Projects Agency.

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