

the onset of limb movement and motoneuron death and the almost total preservation of motoneurons by curare-produced paralysis (Oppenheim & Nunez 1982; Pittman & Oppenheim 1978).

The key role of prefrontal cortex structure and function

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Abstract: The tension between focusing on species similarities versus species differences (phylogenetic versus adaptationist approaches) recurs in discussions about the nature of neural connectivity and organization following brain expansion. Whereas Striedter suggests a primary role for response inhibition, other possibilities include dense recurrent connectivity loops. Computer simulations and brain imaging technologies are crucial in better understanding actual neuronal connectivity patterns.

Striedter's (2005) book represents an important synthesis of ideas and approaches to brain evolution across different levels, with general constraints and evolutionary principles clearly related to neural structures and functions throughout the chapters. It also includes an excellent review of the history of comparative neurobiology (Ch. 2) that concludes by noting the existence of a "tug-of-war between those who emphasize species differences in brain organization and those who dwell on similarities" (p. 50). It is useful to realize that this tug-of-war is being waged today on fields beyond just neuroscience. More generally, these contrasting views are often referred to as the *phylogenetic approach* (emphasizing the continuity and similarities across species) and the *adaptationist approach* (emphasizing the adaptive specializations within each species).

These contrasting views play out at several levels, on many topics, across the behavioral sciences. Most recognize and accept the phylogenetic view of species (ironically, the most controversial aspect of evolutionary theory in the nineteenth century); research with model animals such as pigeons, rats, and apes demands at least an implicit phylogenetic view. On the other hand, the adaptationist view, sometimes labeled as "evolutionary psychology," is currently quite controversial and prone to both adamant support and vigorous opposition (e.g., Rose & Rose 2000; Tooby & Cosmides 1992).

Tension between phylogenetic and adaptationist approaches recurs within Striedter's argument for the importance of absolute brain size. It is an important insight that increases in absolute brain size have implication for patterns of connectivity and organization in general (i.e., more widely connected regions, decreases in average connection density, and more structural and functional modularity as a consequence). Yet there are unaddressed issues within these general implications. How was the brain parsed into modular aspects in the course of evolution? Was it cut like a cake with a chainsaw: random, messy, and in random bits? Or was it like the fissioning of cells, families, and academic departments: the parts already functionally relevant to each other were maintained (relatively higher connection densities), whereas the connections across these parts were reduced? This is precisely the sort of adaptationist question that has been relatively neglected, and is a key to stronger linkages between neuroscience and psychology.

Striedter addresses the core issue of what is special about human brains (Ch. 9), and emphasizes the importance of the enlargement of the lateral prefrontal cortex and its various associated regions, which seems to be well motivated due to the involvement of the

prefrontal cortex in high-level cognitive control, selective attention, working memory, and planning, as well as standard intelligence tests, as shown by neuroimaging studies (see Duncan 2001; Miller & Cohen 2001). This chapter also suggests that "response inhibition" plays a major role in enabling the human prefrontal cortex to mediate the production of novel solutions to behavioral problems, but we submit that the nature of the neural mechanisms and architectures supporting flexibility of human behavior and cognition is not yet so clearly specified.

It is also possible that (alternatively or additionally) dense recurrent connectivity loops in the lateral prefrontal cortex enable the formation of stable reverberatory states in working memory, planning, goal representation, and effect anticipation. These active neural representations would "go beyond the stimulus given," and mediate context-sensitive input-output associations, based on a representation of the task context (Duncan 2001; Miller & Cohen 2001). Response inhibition and top-down control of input-output associations would therefore be achieved by means of these stable states in competition (via mutual inhibition) with bottom-up context-independent associations (e.g., impulsive responses). Feedback connections from dorsolateral prefrontal cortex to posterior cortical areas would mediate control of unimodal and multimodal representational states in perception and memory retrieval. In this view, more stable states emerging in the lateral prefrontal cortex via extensive recurrent loops would dominate more transient representations in the brain encoding for current stimuli, responses, and their closer associates. For example, sustained working memory (delay) activity in the lateral prefrontal cortex is immune to interference, whereas delay activity in the inferotemporal cortex is vulnerable to task-irrelevant interfering distracters (Miller et al. 1996). In other words, we share Striedter's view about the crucial role of the enlargement of dorsolateral prefrontal cortex in increasing the flexibility of human behavior and cognition, but we propose that the emergence of convergent recurrent loops within the dorsolateral prefrontal cortex and between the dorsolateral prefrontal cortex and posterior cortical areas (as well as premotor areas) was to mediate this increase in functional flexibility. Another possibility is that the human dorsolateral cortex has evolved to support massive adaptive coding of its neuronal populations (Duncan 2001), combining inputs and outputs in novel context-dependent bindings, in an ongoing dialog with relatively-specialized modules in posterior cortical areas and premotor cortex.

Computer simulations are likely to play a crucial role in shedding light on how different kinds of neuronal connectivity patterns can lead to optimal function-related neuronal coherence within and between brain regions, with special reference to the orchestrating role of the dorsolateral prefrontal cortex. Striedter (Ch. 7) clearly considers the importance of small-world networks, of which the visual cortex can be regarded as an example, and related theoretical studies. Other large-scale simulations (Tononi & Edelman 1998; Tononi et al. 1996) have emphasized the importance of recurrent or re-entrant connectivity systems in binding of neural representations and the emergence of consciousness. The dorsolateral prefrontal area may play a crucial role in coordinating neural synchrony and multi-regional cooperative signaling in the brain (see Ch. 9) in a task-dependent fashion, and in encoding action contexts, because of the high number of convergent re-entrant circuits coding multiple modalities and synapses mediating maintenance of stable activation patterns, such as NMDA-synapses (Wang 1999).

Relating structure to function by means of EEG/MEG (combined with high spatial resolution fMRI) and single-cell recording studies, as well as large-scale computer simulation and neuropsychological evidence, may provide a crucial contribution to clarify the role of the dorsolateral prefrontal cortex in making humans superior to other animals in cognition and flexible behavior. Chapter 9 of Striedter's book can be regarded as a good starting point for this challenge.