Book Reviews

Accommodations of the Nervous System

Body and Brain. A Trophic Theory of Neural Connections. DALE PURVES. Harvard University Press, Cambridge, MA, 1988. viii, 231 pp., illus. $35.

Renewed interest in the biological consequences of change in body size and form has resulted in a profound alteration in the way biologists view behavioral, ecological, and physiological processes. Neurobiologists, with the exception of a small group interested in brain-body allometry, generally ignore body size and view the nervous system as the controller of the body rather than as an organ system that is itself greatly affected by changes in body size and form. In this short, well-written monograph, rich in detail, Purves reveals that both the number and the form of neurons composing vertebrate nervous systems are far more labile than has been generally believed and that patterns of neural connections are subject to ongoing chemical regulation throughout life by interactions with the target cells they contact.

This trophic theory of neural connections is predicated on the observation that the number of neurons does not change in proportion to change in body size, which alters the number of target cells, whether epithelial, gland, or muscle, that must be innervated. Therefore change in neural connections is likely selected for, along with change in body size and form, to prevent loss of or inappropriate neural function.

In the first chapter, Purves argues that both the number and the connections of neurons are, in fact, regulated throughout life, in part by molecular signals that arise from neural targets. In subsequent chapters, he documents the coordination of number of neurons and target size, consequences of body scaling for dendritic patterns and axonal connections, regulation of pathway formation and synaptogenesis during development, plasticity of neural number and connections in mature organisms, the molecular basis of trophic factors, and, finally, the effects of neural activity on trophic factors. Each topic is introduced logically and with a minimum of technical terms, although the glossary will still be appreciated by many readers. Careful brief explanations are followed by examples that are sufficient to allow the nonspecialist to follow the argument and intriguing enough to delight the initiated. Equally important, Purves presents a balanced treatment, citing many examples that could be interpreted to counter his arguments as well as noting where research is needed to corroborate or amend his ideas.

The trophic theory has profound implications for our understanding of neural development and plasticity, long-term information storage involved in learning and memory, and neural evolution. Purves frequently notes these implications throughout the text and reinforces this theme with an important last chapter emphasizing them.

The topics Purves covers and the implications he notes, often only tantalizingly, are so numerous that a full-length review could be written on each of the four areas impacted by his theory. However, I will consider only three aspects of the implications of the trophic theory for neural evolution, which is my own special interest and the least explored topic in this exciting monograph.

Purves correctly notes that the number of neurons does not change in proportion to change in body size but does scale with such change in an orderly way. Interspecifically, brain size in vertebrates and presumably number of neurons scale with an allometric slope of approximately 0.75. The biological basis of this scaling is unclear, and different causal factors have been proposed: body surfaces determining brain size, metabolic rates limiting brain size, and reproductive or even life history strategies limiting brain size. Purves only notes some of these factors in a figure legend (fig. 2.5) and does not explore the causes of neural scaling or indicate that a second important aspect of change in brain size and, presumably, neural number is changes intercept with vertebrate radiation. The brains of most sharks, birds, and mammals are larger for their body sizes than are brains in other vertebrate groups. Though there is no reason to believe that trophic interactions are fundamentally different for big-brained vertebrates, these differences suggest interesting questions regarding the number of neurons allocated to targets and their maintenance.

Purves has, on the other hand, broken new ground regarding neural form in phylogeny by noting that the packing density of nerve cells decreases in bigger animals, with a concomitant increase in the length of dendritic branching, and that the complexity of dendritic arbors appears to be correlated with the complexity of inputs. In noting that geometrically simple neurons are innervated by few or even a single input and neurons with complex arbors by numerous differential inputs, Purves provides reason to believe that changes in body size have profound effects on neural complexity and function. Though a number of researchers have recently explored the consequences of decreasing body size on the design of neural systems, the effects of increasing body size have generally been neglected. Such effects have the potential, however, of providing additional reasons why selection might favor large body size.

Other phylogenetic topics of particular importance that are explored by Purves are the nature of aberrant projections in development and the implications of the trophic theory regarding regressive theories (parcellation and neural Darwinism) of neural connectivity. The observation that the central projections of many brain regions exhibit wider distribution in late embryonic and early postnatal life than in adulthood has been difficult to explain. The trophic theory suggests that an initial exuberance of projections may serve diverse purposes that include the establishment of quantitatively appropriate innervation of individual target cells, but it does not explain transient pathways to "wrong targets" (that is, targets that do not receive such inputs in the adult). Two explanations are possible: transient connections involve behavioral or trophic functions that change in the course of ontogeny, or transient connections are vestiges of phylogenetically older connections. There is currently insufficient evidence to allow us to discriminate between these possibilities.

Several regressive theories of neural connectivity share the notion that an initial set of neural connections is generated early in development and is ultimately reduced to more restricted connections, owing primarily to competition. Purves presents a more balanced view and argues that development involves a prolonged creation (and elimination) of connections, a reordering that continues in many cases in the adult. From this perspective, connectivity patterns are never complete, and regression of some connections and elaboration of others are an inevitable consequence of neural adjustment in both ontogeny and phylogeny.

I would have been delighted to see these and other phylogenetic topics explored in detail in a separate chapter, and I suspect that other readers will have their own candidates for further elaboration in this exciting work. In any case, the book should be required reading for any student of the nervous system in its broader biological context.

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