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A HIERARCHY OF DEVELOPMENTAL CONTINGENCIES: A REVIEW OF PURVES AND LICHTMAN'S PRINCIPLES OF NEURAL DEVELOPMENT[1]

ROBERT R. PROVINE

UNIVERSITY OF MARYLAND BALTIMORE COUNTY

Neuroscience has become one of the most productive, influential, and popular scientific disciplines of the 1980s. Indeed, neuroscience may now occupy the position once held by molecular biology during its "golden age" in the 1950s. It is no coincidence that the major unanswered questions and powerful analytic procedures of neuroscience have attracted such leading figures of the molecular revolution in biology as Crick, Edelman, Nirenberg, Benzer, Brenner, Leventhal, and Stent, several of whom are Nobel laureates. These distinguished individuals have been joined by a multitude of eager recruits from psychology, biology, physiology, computer science, chemistry, psychiatry, anatomy, and other disciplines who recognize that such broad and difficult problems as the mechanisms of memory, visual perception, and schizophrenia transcend disciplines and are unlikely to yield to traditional approaches.

A major trend within neuroscience is the increased role played by developmental analyses. This is a recent recognition of one of the most extraordinary properties of the nervous system, its capacity for self-assembly. During the last two decades, the study of neurogenesis has been transformed from a narrow specialization within developmental biology into developmental neuroscience, a research specialty pursued by hundreds of investigators from different backgrounds. The vigor and maturity of developmental neuroscience were recognized in 1986 by the award of the Nobel Prize to Rita Levi-Montalcini and Stanley Cohen for their discovery of the nerve growth factor (NGF), a protein necessary for the development and maintenance of nerve cells.

Some areas of behavioral science have been slow to incorporate findings and concepts of developmental neuroscience, in part because it is perceived to be a nativistic discipline that is irrelevant or even antagonistic to the empiricistic agenda of their disciplines (Provine, in press). For example, stimulus-response developmental theorists or contemporary cognitivists may have difficulty dealing with the following facts: (a) Early embryonic movement is probably the product of *spontaneous* (nonevoked) discharges originating within the spinal cord (i.e., embryos "spond" before they "respond" and the brain seems relatively uninvolved in this activity). (b) An important if not principal role of embryonic movement may be to *sculpt* the joints and to contribute to the development and maintenance of muscles. (c) Many areas of the central nervous system show *motor precocity,* the tendency to establish their efferents before they receive their afferents. This maturational sequence obviously limits early sensory influences on neurogenesis. Such findings may be overlooked or ignored by developmentalists who are theoretically inspired by remnants of British empiricism or who attempt to extrapolate from the postnatal to the prenatal period.

Developmental psychology would have a different, and certainly broader, agenda if its priorities were derived more directly from the description of developing organisms (Provine, in press). Developmentalists have long understood that embryos are not simply smaller, unformed versions of the adult, but they have often failed to take the logical next step of appreciating the unique features and specializations of embryos, some of which are

[1]Purves, D., & Lichtman, J. W. (1985). *Principles of neural development.* Sunderland, MA: Sinauer. 433 pp., including glossary, bibliography, and index.

For reprints, write the author at the Department of Psychology, University of Maryland Baltimore County, Catonsville, Maryland 21228.

structural and functional adaptations to the prenatal environment and the demands of the developmental process (Oppenheim, 1981). The prenatal and postnatal forms of an organism, or even embryos at different developmental stages, are often so different in structure and function that were it not for the thread of developmental continuity, they would seem to be members of different species (Provine, in press). The present emphasis on the uniqueness of embryological processes is not an argument for the irrelevance of early development for the business of psychology. It is an attempt to draw attention to the historical neglect of the theory, techniques, and facts of embryology.

An appreciation of the history of embryology gives a sense of the dynamics of the developmental process that transcends the particular problem or organ system being studied. For example, history instructs that early development is not genetically determined or nativistic in the sense understood by many behavioral scientists. In a classic experiment published in 1892, Driesch demonstrated that each of the first two blastomeres (the two cells derived from the first cleavage of the zygote) were totipotent, being able to form a complete organism. This crucial experiment resolved the centuries-old debate between the preformationists and epigeneticists in favor of the epigeneticists. (Preformationists believe that the developmental fate of a cell is fixed from the time of fertilization or even before. For preformationists, development is a process of growth. Epigeneticists believe that the fate of a cell is established gradually during development by the influence of nongenetic factors. For epigeneticists, development is primarily a process of differentiation.) However, the dispatch of preformationism created the problem of discovering the actual determinants of development, a search that continues to the present day. Contemporary developmentalists realize that the vertebrate embryo is not a mosaic of predetermined cell lineages. Instead, the embryo is a complex and harmonious constellation of cells whose developmental fate is coordinated, and in some cases determined, by a hierarchy of relationships with adjacent cells, the relative weightings of which shift with age. Indeed, a text in developmental biology is a catalogue of such intracellular and intercellular contingencies. These contingencies act as a system of checks and balances that prevent the biological catastrophes that would result from strict preformation. Without them, the many cells that get displaced during the numerous migrations of development would express their genotypes in inappropriate locations. Embryonic tissue is very democratic, but the majority rules. The displaced cells are outvoted by the resident majority that alters the developmental fate of the wayward cells to accord with their new address. This example illustrates that even the fate of individual cells is not "genetically determined" in the commonly understood sense. The genes do not and cannot encode structure directly; they can only orchestrate the developmental process. This fact suggests another reason for studying developmental neuroscience: Natural selection must somehow alter the developmental process to bring about structural and behavioral evolution. Ontogeny is the key to phylogeny.

Developmental studies are largely responsible for our current perspective that even the mature nervous system is composed of plastic neurons that are responsive structurally and functionally to both presynaptic and postsynaptic influences. The plasticity of the embryonic nervous system is well known. For example, about 40% of motoneurons die during normal development because they do not make contact with their normal muscular targets during a critical period of development. The fate of a particular neuron is not predetermined. There seems to be a kind of natural selection operating at the level of individual motoneurons; those that lose out in the competition for receptor sites perish. (Cases of developmental cell death are common in other organ systems. For example, the naturally occurring death of cells in the interdigital spaces is responsible for the emergence of discrete fingers and toes from their paddle-like primordia.) Less dramatic instances of neural plasticity remain after birth. For example, if a given neuron is deprived of its normal source of input, adjacent nerve fibers may move in and form novel synapses at the site of the vacancy. Even at the level of synapses, newly created parking spaces seldom remain empty. Changes in the density of synapses and dendritic branching as a result of sensory deprivation and enhancement are other, better known, examples of neuronal plasticity at postnatal stages. These are only a few of what has become a long list of examples.

This dynamic perspective of neural structure and function is now a necessary component of all contemporary accounts of neural development, evolution, and learning (e.g., Edelman, 1987). The day of the computer as a reasonable metaphor for the nervous system is now past, or at least severely limited. The hardware of the computer must be able to model the wetware of the nervous system. The ultimate test for future models of the brain may be their capacity to account for ontogeny and phylogeny, in addition to their ability to mimic mature function. In ways we are only beginning to realize, these processes may be inseparable.

The experimental analysis of behavior should have little difficulty in incorporating the concepts and findings of developmental neuroscience. Being a contingency-governed science (Provine, 1984b), behavior analysis has been able to adapt and evolve. Furthermore, it provides organizational principles that help to integrate and clarify some apparently disparate phenomena at the behavioral, physiological, and structural levels. Skinner showed the way in two insightful articles, "Selection By Consequences" (Skinner, 1981) and "The Phylogeny and Ontogeny of Behavior" (Skinner, 1966). He suggested that a variety of natural phenomena, ranging from the natural selection of morphology across generations to the shaping of a behavioral response during the lifetime of the individual, are all influenced by contingencies that help species and organisms adapt to a changing environment. Although Breland and Breland (1961) suggest otherwise in a much publicized paper (but see Skinner, 1984, p. 506), Skinner's perspective opens behavior analysis to discoveries such as "species typical" behavior that may be ignored or resisted by some S-R learning theorists who attend exclusively to influences that act during the life of the individual. In regard to "pattern-generating circuits" in motor systems, or "feature detectors" in sensory systems (Provine, 1984a), Skinner (1984, p. 507) comments, "That a given species is predisposed by its genetic history to see particular stimuli in preference to others or to behave in particular ways in preference to others are facts of the same sort. A different kind of selection has been at work."

Skinner suggests further that the selection for heritable behavioral or structural traits is a phylogenic analogue of response acquisition. There are also phylogenic analogues of the extinction of structure and/or behavior, such as the legs of the whale (Skinner, 1984, p. 508) and the loss of wing-flapping behavior and apparatus of flightless birds (Provine, 1984b). Skinner's hierarchy of contingencies can be expanded easily to incorporate data concerning neural development. Consider, for example, the previously discussed competition between motoneurons for a finite number of receptor sites on muscle and the lethal consequences of being unable to find them. This process is both an example of a developmental contingency and the basis for a rapid and precise mechanism for neurobehavioral evolution (Provine, 1984b). Behavior analysts may enjoy searching for the various behavior-analytic themes in developmental neuroscience.

The best introduction to developmental neuroscience, by far, is the *Principles of Neural Development* by Purves and Lichtman (1985). It is the discipline's only current, comprehensive textbook, although the earlier but now dated editions of *Developmental Neurobiology* by Jacobson (1970, 1978) and *The Formation of Nerve Connections* by Gaze (1970) deserve recognition as heroic efforts to integrate a scattered and complex literature fraught with puzzling age-specific and species-specific effects. The developmental literature has become more settled in recent years, general principles have started to emerge, and some of the false leads of the past have fallen by the wayside. The time is right for a review and synthesis, and the neurobehavioral community should be grateful that Purves and Lichtman took time from their active research careers to provide one. Their book makes a difficult literature accessible and will encourage nonspecialists to offer courses on developmental neuroscience. Until now, students learned about neural development at the feet of researchers who often had narrow, system-specific interests, and the rare courses that were offered were usually small seminars that were based on reading lists of journal articles. Outsiders might wonder what all of the excitement is about. The appearance of the Purves and Lichtman text signals the emergence of general principles and agreement about significant research that mark the maturity of the discipline.

The text begins with a brief summary of the history of general experimental embryology before moving on to the specifics of neurogenesis. This is an important starting point because it may be the only exposure the typical student in the behavioral sciences gets to embryological thought and theory. For this reason, the author begins his course in developmental neuroscience with an extensive section on the history of developmental thought in biology and psychology. A useful supplemental source of historical material is Gould's (1977) scholarly *Ontogeny and Phylogeny,* which describes past theoretical positions and controversies and provides an antidote to the tendency to regard as fools the proponents of such discarded theories as preformation. The history of embryology is an especially rich source of centuries of thinking about ontogeny that complements and extends that of the younger science of psychology. For example, the previously noted preformation/epigenesis debate in embryology provides an interesting context in which to consider the somewhat similar but still contested nativist/empiricist debate in psychology. Purves and Lichtman add a nice historical touch in the series of brief biological sketches of past and present masters of developmental neuroscience presented in "boxes" throughout the book. They are a reminder that scientific research is a human endeavor.

After this brief summary, the text moves through early development, neuronal differentiation, organizing principles, neuronal migration, nerve fiber outgrowth, naturally occurring neuron death, trophic factors, synapse formation, effects of the experimental rearrangement of connections, maintenance and modifiability of synapses, the development of behavior, and a short concluding presentation of "principles." The last chapter deserves special consideration because there are only 11 principles, and they represent a synthesis; they are not simply a summary of the text. (The comments following some of the principles listed below are those of this reviewer.)

"1.) Neural development, like development generally, depends on genetic and epigenetic influences" (p. 357). Development is influenced by both the highly determined, relatively direct effect of gene expression and the more probabilistic consequence of environmental factors such as cell position.

"2.) The fate of cells becomes progressively restricted" (p. 357).

"3.) The lineage of specific cell types in many simple animals is largely preordained, whereas in complex animals the fate of individual cells is more flexible" (p. 357). This principle is consistent with the greater difficulty in modifying the behavior of simple than complex organisms.

"4.) An important component of the epigenetic influences on differentiation is cell position" (p. 358). The structure and function of a neuron are influenced by its cellular neighborhood.

"5.) Neuronal precursors, and subsequently neuronal processes, move according to directional cues in their local environment" (p. 359). Embryonic neurons often migrate considerable distances through the cellular matrix of the embryo before reaching their final destination. These neurons then send out dendrites and axons that sometimes grow great distances before forming synapses. This migration and fiber outgrowth are guided by chemical and structural landmarks.

"6.) As vertebrate neurons mature, they acquire obligatory trophic dependencies" (p. 359). A trophic agent is a substance necessary for the maintenance or survival of a tissue or cell. Neurons become dependent on chemicals from neurons or other targets of innervation and show withdrawal symptoms if they are deprived of them.

"7.) Vertebrate nerve terminals compete with one another for trophic support" (p. 360). This is another example of selection operating within a neural context.

"8.) The patterns of neuronal connections established during development also depend on recognition between presynaptic and postsynaptic cells" (p. 360). The synaptic connections between neurons and their targets are the highly specific consequence of matching of yet to be understood presynaptic and postsynaptic factors.

"9.) Patterns of neural connections are maintained in an equilibrium throughout life" (p. 361). Neuronal structure is not "hardwired"; it adjusts to perturbations throughout life.

"10.) Neuronal malleability tends to persist in more complex animals" (p. 362). This neurological principle has a behavioral analogue. You may be able to teach an old dog but not an old cockroach new tricks.

"11.) The sphere of influences acting on the nervous system continually enlarges during development" (p. 362). This last principle concerns the continuity between the embryological realm and the primarily postnatal world of the behavioral sciences. During development, the critical milieu of a neuron expands from the intraneuronal contents and immediate cellular neighborhood to include extraorganismic sensory or social influences after birth.

The inclusion of a brief penultimate chapter on the development of behavior is a significant gesture. Although a wide variety of researchers now study the developing nervous system, experimental embryologists of the past were trained in an anatomical tradition that tended to ignore behavior or treat it as a curious epiphenomenon of the nervous system. Purves and Lichtman are a pleasant exception. In the introduction to the chapter on behavior, they comment that "The reductionist approach of most early chapters tends to obscure the fact that the goal of neural development is appropriate behavior" (p. 329). Instructors of courses in the behavioral sciences will probably want to expand the breadth and depth of topic coverage beyond the brief treatments of instinctual behavior, imprinting, bird song, and visual deprivation presented in this chapter. But, if too much expansion, integration, and predigestion of the material in this and other chapters are done to accommodate the behaviorist, the highbred vigor that is a strength of the interdisciplinary approach may be jeopardized. Readers should sample from a full menu and decide for themselves what is relevant, useful, or novel.

The author of this review has had good results in using the Purves and Lichtman book to teach three courses in developmental neuroscience. The students have been senior undergraduates and graduate students in psychology and biology, some with minimal experience in biology. Students with introductory biology backgrounds can perform well because the detail of the material has a leveling influence; even biologists with developmental backgrounds have little exposure to the specifics of neuroembryology. Although the instructor might choose to abbreviate or consolidate some chapters and expand others such as the behavior chapter, only the third chapter on pattern and positional information was generally unsuccessful—insufficient data were given to allow nonexperts to follow the presentation. The book includes a useful glossary. Too often, authors provide examples of phenomena such as specificity, regulation, morphogenetic field, or contact guidance, but never define them. The references are comprehensive, well chosen, and up to date, and the illustrations are numerous and clear.

The *Principles of Neural Development* is an exceptional book that belongs on the shelves of all students and researchers concerned with the mechanisms of behavior. In the near future, an understanding of neural development will no longer be an esoteric specialty but will become part of the core knowledge expected of all behavioral scientists.

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