Developmental psychobiology comes of age

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Developmental Neuropsychobiology

Edited by William T. Greenough and Janice M. Juraska. 1986, Academic Press. 485 pp. Cloth, \$64.50. Paper, \$33.50.

Handbook of Behavioral Neurobiology: Vol. 8. Developmental Psychobiology and Developmental Neurobiology

Edited by Elliot M. Blass. 1986, Plenum. 328 pp. \$55.00.

The field of developmental psychobiology can be defined as the branch of physiological psychology concerned with the study of developing organisms. However, just as physiological psychology has been all but swallowed by the all-encompassing field of neuroscience, most of developmental psychobiology has been absorbed by developmental neuroscience. In both cases, the explosion of neuroanatomical, neurophysiological, neuropharmacological, and cell-biological techniques in the last two decades has allowed researchers to identify and pose questions about new problems, as well as to ask more focused questions about old problems. Greenough and Juraska attempt to convey the greater sophistication that characterizes modern research in developmental psychobiology by titling their volume *Developmental Neuropsychobiology*; Blass takes a similar tack, titling his volume *Developmental Psychobiology and Developmental Neurobiology*. Both volumes are dramatic proof of the enormous conceptual and technical advances that have evolutionized, if not revolutionized, the field of developmental psychobiology.

Two features distinguish developmental psychobiology from other developmental neurosciences: first, the goal is to understand developmental processes as they relate to *behavior*; second, research in developmental psychobiology is driven mainly by theory, whereas that in many of the other developmental neurosciences is driven by empiricism. In general, the contents of both books possess these distinguishing features of developmental psychobiology and provide ample evidence of theoretical richness and vitality within the field. Both of these volumes serve well as introductions to some of the major problems in developmental psychobiology, and although developmental psychobiologists will find much of the material very familiar, there are a few surprises for everyone.

However, the two books clearly reflect the slightly different loci occupied by Blass and by Greenough and Juraska within the field. The book edited by Blass focuses more heavily on sensory and behavioral problems than does Greenough and Juraska's volume, which places greater emphasis on cellular and intercellular mechanisms in brain development. In their preface, Greenough and Juraska lament the fact that investigators studying basic neural processes—the developmental neurobiologists—are professionally segregated from those studying basic behavioral processes—the developmental psychobiologists. Although this is true, I suspect that this results in part from the diverse interests of investigators within developmental neuroscience; one can attend only a few of the increasing number of specialty meetings. Nevertheless, their point is well taken. The stated purpose of this book, to provide cross-fertilization between those whose interests are primarily neural and those whose interests are primarily behavioral, is an important one.

Blass also remarks that developmental psychobiology and developmental neurobiology "have often followed parallel tracks," but that recent developments should make increased interaction particularly rewarding to researchers in both fields. It is therefore curious that Blass has chosen to address problems at the interface between developmental psychobiology and behavioral ecology in a separate volume. Despite this, most of the chapters in Volume 8 deal rather directly with questions of behavior. Although Blass suggests that the emphasis of the book is on the developing organism as an adaptation to a niche as well as a precursor to adulthood, this theme is not consistently maintained by the authors.

Developmental Neuropsychobiology

One of the impressive features of this volume is its consistency of style and continuity between chapters. Although each chapter stands alone, Greenough and Juraska have chosen a coherent set of contributors and put their writings together so that they flow well. The general organization of the book is from early to late, molecular to molar, and simple to complex. The first four chapters deal with basic embryological mechanisms. How do cells know where they are, when they are, and what to do? From there, the book moves on to two chapters describing how the internal environment modulates the development of the central nervous system (CNS). The next two chapters describe more molar aspects of development of the brain and behavior, providing a transition to

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the next section, which contains several chapters on external influences on the development of the brain and behavior, with particular emphasis on the visual system. The volume concludes with two chapters on the development of complex behaviors; these chapters are, as one would expect, the least neurally oriented.

The first chapter, by Dennis Summerbell and Lawrence S. Honig, describes mechanisms governing pattern formation and differentiation. I found this chapter, which describes the developing limb bud of the chick as a model system, very interesting. However, it is somewhat disappointing in a few respects. First, and this criticism is not unique to this chapter or to this volume, there is little sense of history in the introduction. I had difficulty accepting the fact that Hans Spemann is not even mentioned. Second, given that the remainder of the book focuses on the nervous system, I would have liked to see more reference to development of the nervous system. For example, a brief discussion of clonal analyses of the nervous system being used by Marcus Jacobson and his colleagues to delineate development of the African clawed frog, *Xenopus laevis*, would have been welcome. By and large, however, the chapter succeeds in illustrating the genetic and cellular interactions that shape development.

In the second chapter, Paul Letourneau describes mechanisms by which the nervous system begins to wire itself up. The focus of this chapter is, quite appropriately, on mechanisms of neurite outgrowth and the role of the growth cone. And although the chapter is as up-to-date as possible, Letourneau has taken care to season it with history in proper doses. For example, he briefly describes the checkered history of the theory of neurobiotaxis, and then describes recent experiments that restore its viability and suggest possible mechanisms by which electrical fields could affect behavior of the growth cone. In short, this chapter is a thoughtful, well-written treatment of an important topic in developmental neurobiology.

John Edwards's chapter on development of insect nervous systems aroused mixed feelings, not dissimilar to those aroused by Summerbell and Honig's chapter. This is important work, but its relevance to the focus of the rest of the volume is not clear enough. Edwards begins his chapter by asking "Are insects relevant?" Unfortunately, he does not present a strong case for their relevance. Instead, he rails against the linear view of evolution, in which extant creatures are placed on a "lower-higher" continuum, with vertebrates above insects. His argument would have been much more compelling had he mentioned the important and specific roles that research on invertebrates has played in our understanding of, for example, cell fate, mechanisms of pattern generation, axonal pathfinding, neurophysiology, and cellular bases of learning and memory. The main part of the chapter, however, is concerned with how the nervous system of insects gets wired up, and is an excellent extension of Letourneau's discussion of in vitro studies of neurite outgrowth.

Raymond Lund and Fen-Lei Chang discuss development of the visual system, focusing on cellular interactions and the development of anatomical order, rather than on the effects of experience on function. As does Edwards's chapter, this chapter provides a nice illustration of forces shaping the nervous system in vivo.

The next two chapters describe the complex and multifarious roles played by secretory products. Jean Lauder and Helmut Krebs discuss the unconventional, nontransmission, trophic roles of neurotransmitters in the development of the nervous system. They go on to discuss regulation of CNS development by more traditional humoral substances, including thyroid and corticosteroid hormones, and their interactions with neurotransmitters. Given the enormous amount of information presented in this chapter, one should not criticize omissions. Nonetheless, it is unfortunate that there is no discussion of the role of opiates in development of the brain and behavior, especially considering the current and rapidly growing interest in that topic. Dominique Toran-Allerand goes beyond the well-known story on the role of sex hormones in the differentiation of the brain into "male" and "female" forms. One could criticize her for not discussing "organizational" and "activational" effects, or for not describing dimorphic areas of the brain and their relationship to behavior, but reviews of those topics abound. Instead, Toran-Allerand offers a thoughtful discussion of experiments that suggest mechanisms by which hormones alter neural maturation, including the effects of androgens and estrogens both in vivo and in vitro. The only omission obvious to me is the work of Breedlove and Arnold on the nucleus bulbocavernosus of the spinal cord. Those are important studies because they demonstrate that sex hormones can alter CNS anatomy indirectly, by preventing degeneration of a peripheral target, rather than by direct action on the CNS tissue.

At this point, the tenor of the volume shifts as Robert Provine discusses the ontogeny of motor systems. He provides a brief and welcome historical introduction to the problem, but the next part of the chapter seems a little disjointed, as Provine's discussion jumps from one behavior in one species to a different behavior in a different species with little warning, transition, or apparent goal. It would have been nice if the discussion had been more tightly wound around particular theoretical issues. True to the neuroembryological tradition, Provine includes prenatal and prehatching behavior in his discussion and focuses on the ontogeny of fundamental and relatively simple behaviors.

The ancient (by neuroscience standards) notion of increasing size and functional importance of rostral CNS structures (encephalization) during development receives full treatment in Dennis Stelzner's chapter. One might take issue with Stelzner's apparently linear view of evolution, in which encephalization increases in "higher" organisms, but this is a minor point made only as an introductory remark. The bulk of the chapter deals with encephali-

zation as an ontogenetic phenomenon, and here Stelzner is on solid ground. To support his thesis, he draws on evidence from neurochemical, neuroanatomical, electrophysiological, and behavioral studies of intact and lesioned animals. An important point made by Stelzner is that encephalization does not represent an absolute order of neural maturation along the neuraxis. Rather, functionally related systems must mature throughout the neuraxis so that coordination of function is not compromised during development; as the cortex matures and its axons invade the spinal cord, spinal mechanisms that interact with those invading fibers must also undergo further maturation. The nervous system is not a "lump of clay," and encephalization is not simply the addition of "more lumps of clay" to the rostral end, as has often been implied.

The next four chapters review the literature on the development of sensory systems. Three of them discuss aspects of maturation in the visual system, and although the focus differs from chapter to chapter, they can be discussed together. Wolf Singer focuses his discussion on mechanisms that underlie experience-dependent modifications of the visual system; Ronald Booth, Elsi Vassdal, and Marilyn Schneck focus on anatomical changes in the visual system, particularly in the lateral geniculate nucleus; and Richard Tees addresses the problem of visual function following selective deprivation. In general, I felt that there were simply too many pages devoted to the retinogeniculostriate system, despite the fact that the mammalian visual cortex is arguably the best-understood vertebrate sensory system in terms of its development and underlying mechanisms of maturation. The chapter by Booth et al. was little more than a catalog of anatomical results following various experimental manipulations, and was very dry and sometimes tedious to read. The chapters by Singer and Tees were better, but Tees's review of the literature on the development of visual perception also reverted to the shopping-list-of-results approach, reducing the sense of excitement. Perhaps the best of this lot is Singer's chapter, in which "permissive gating" of input to the cortex by the diencephalon is proposed to play a major role in specific modifications of the visual cortex. If these three chapters had been condensed into a single chapter, little important information would have been lost and other elegant examples of complementary research on the visual system could have been included. For example, a chapter on the optic tectum/superior colliculus—which could have been written by any number of authors, including Martha Constantine-Paton on the frog, Gerald Schneider on the hamster, or Eric Knudsen on the barn owl—would have provided some balance, a different perspective, and a focus on related and yet different problems.

The fourth chapter on sensory development, by Ben Clopton, covers the nonvisual systems: auditory, somatosensory, and olfactory. His treatment of each system is a fairly dry, straightforward description of maturational events. His description of the auditory system includes both central and peripheral aspects of development,

whereas his description of the somatosensory system focuses on the cortical barrel fields of the vibrissae of rodents. There is little discussion of functional implications anywhere, which may leave the reader asking "So what?"

The final four chapters address more complex interactions between the developing mammal and its environment. William Greenough discusses the effect of environmental complexity on synaptogenesis and neurite growth in the cortex. He offers the interesting idea that "expected" ontogenetic experiences act to winnow the number of synapses in associated neural systems, which were overproduced in anticipation of those events. Conversely, incorporation of information from "unanticipated" events stimulates the production of new synapses. Unfortunately, he fails to explain how one determines, independently of its effects on the nervous system, whether an event is anticipated or not. For example, patterned visual stimulation is presented as an example of anticipated events, whereas environmental complexity is presented as an example of unanticipated events. Since the natural environment of the rat is more complex than the experimental "complex" environments, it is not clear in what way the latter complex environments are unanticipated. Similarly, his argument that a Hebb-Williams maze is an unexpected event seems weak, because the complex systems of trails followed by rats in their natural habitats are not unlike Hebb-Williams mazes.

Janice Juraska, in the briefest chapter in the book, offers an interesting and refreshing look at environmental factors that contribute to sex differences in animals and differences in the ways in which the CNSs of males and females respond to the same environmental events.

Elliott Blass discusses the role of olfaction in various nest-related behaviors of the rat. Unfortunately, the chapter appears to have been written hurriedly, because it contains many awkward sentences and grammatical gaffes. A model of behavioral conditioning in the developing neonate is presented at the end of the chapter, but is not adequately explained.

Jeffrey Alberts evaluates the importance of mother-infant interactions, from the perspectives of both the infant and the parent. This chapter is a delight to read, and is well-organized in short, logical sections. The first two major divisions of this chapter introduce concepts of mother-infant interactions and of the developing organism. These lead to the major theoretical contribution of this chapter, a section in which five different models of parent-offspring interactions are presented, along with supporting evidence for each. Alberts does not argue for the correctness or best fit of a particular model; the models are simply introduced to stimulate the reader to think about parent-offspring interactions in new and different ways, and they do that very effectively. Perhaps better than any other in this volume, this chapter conveys the excitement that characterizes current work in developmental psychobiology; it is a fitting conclusion to the book.

Best chapters: Alberts, Juraska, Letourneau, Singer, Stelzner, Toran-Allerand.

Developmental Psychobiology and Developmental Neurobiology

This book does not seem to be strung quite as tightly as Greenough and Juraska's volume. There is less continuity, and the chapters differ considerably in style, length, and content. Whereas the whole of Greenough and Juraska's book may be greater than the sum of its parts, this volume must stand on the strengths of the individual contributions.

The first chapter of the book, like Summerbell and Honig's chapter in Greenough and Juraska's volume, is intended to introduce fundamental concepts from embryology. However, Ronald Oppenheim and Lanny Haverkamp focus on neural and behavioral questions, and therefore this chapter is slightly more intimately related to the rest of the book. Their discussion revolves around experiments utilizing tissue grafts and manipulations of sensory and motor experience in the study of early development. A major and important point made by these authors is that development begins before birth or hatching, and that developmental psychobiologists would do well to increase their knowledge and understanding of embryological issues and theories.

John Fentress and Peter McLeod approach the question of development of motor patterns in development from an ethological perspective. Although these authors raise some important questions with respect to the neural control of movement, the bulk of the chapter focuses on the rules that govern the development of behavioral sequences and on the development of social behavior. As a result of its emphasis on molar aspects of behavior, it is considerably less neurally oriented than is the equivalent chapter by Provine in Greenough and Juraska's volume. However, it is also a much more ambitious chapter than Provine's; Fentress and McLeod discuss behavior of animals ranging from insects to primates, and from the simplest reflexes to communication.

Timothy Moran provides a succinct review of the literature on suckling in infant rats that has accumulated during the last 15 years. He discusses current interpretations of data that suggest that suckling and feeding are independent systems, the former being an adaptation to infancy and the latter being a precursor to adult-like feeding. Huddling behavior, like suckling, is a nest-related behavior of infants that is of considerable importance to the neonate (see Alberts's chapter in Greenough and Juraska). However, Moran's treatment in this chapter of research on huddling is brief and out of place, sandwiched as it is between discussions of suckling and the development of independent ingestion.

Sarah Bottjer and Arthur Arnold review the voluminous literature on birdsong. This chapter is particularly clear and is one of the most thought-provoking chapters in the volume. Different aspects of song acquisition, the roles played by different parts of the song circuitry, and a critical look at some of the conclusions drawn from earlier

work are all highlights of this chapter. Numerous important theoretical issues are raised, and the authors close the chapter with a nice comparison between research on vocal learning in humans and research on song learning in birds.

The next three chapters focus on development of sensory systems. Perhaps reflecting a difference in the research interests of the editors, there is a greater emphasis on chemical senses in Blass's volume than in Greenough and Juraska's volume. Patricia Pederson, Charles Greer, and Gordon Shepherd provide a nice overview of the development of the olfactory system in rodents. They discuss embryological development of different elements and pathways in the system and the emergence of function. Perhaps the most interesting and unusual feature of this chapter is the discussion of the modified glomerular complex, which lies between the main and accessory olfactory bulbs, appears to mature relatively early, and may be involved in processing olfactory stimuli that are of particular importance to the neonate. Charlotte Mistretta and Robert Bradley provide a relatively straightforward review of neurophysiological studies of the development of gustation. They focus on changes in sensitivity to different taste stimuli during ontogeny and relate this to the "ontogeny" of individual taste cells. This chapter is clearly written and easy to understand, although it seems that the authors fail to distinguish responses of taste cells, as revealed by electrophysiology, from responses of whole animals, as revealed behaviorally. The chapter on the ontogeny of vision, written by Helmut Hirsch, suffers from the same problems as the chapters on development of the visual system in Greenough and Juraska's volume. Copious amounts of data are presented, with little conceptual integration until the chapter summary. In the absence of broader organizing concepts, it is virtually impossible for one not working in this specialty to assimilate this information as rapidly as it is presented, which makes this chapter somewhat tedious to read and reduces comprehension and interest.

The chapter by Michael Leon on the development of thermoregulation is noteworthy because it does what no other chapter in either book does: It addresses comparative as well as developmental aspects of the problem, from pythons and birds to the more typically discussed mammals. Although the discussion of the organization and maturation of the neural controls of thermoregulation is scanty, this is easily forgiven, because, much like Alberts's chapter in Greenough and Juraska's volume, this chapter conveys a sense of excitement and wonder.

Best chapters: Bottjer and Arnold, Fentress and McLeod, Leon, Oppenheim and Haverkamp.

Summary and Future Prospects

Both of these books contain many fine chapters, and both provide a fair perspective (although the two are quite different) on current issues and research in developmen-

tal psychobiology. I think it is appropriate that there is not a single author who contributed to both volumes (although Blass was an author in one and editor of the other), a fact clearly resulting from the different perspectives of the editors and the diversity of the field. Greenough and Juraska's volume is likely to be more valuable to those whose primary interest is in forces that shape the developing nervous system, whereas Blass's volume is more useful to those whose primary interest is in the development of mechanisms of behavior.

Neither book, however, provides a clear indication of the future direction of the field. If I were to hazard a guess, it would be that the greatest gains in understanding mechanisms of behavioral development will be made by

those who study naturally occurring behaviors and their neurological underpinnings. If so, we may have yet another subdiscipline of developmental neuroscience: developmental neuroethology. Clearly, research into the development of the control of birdsong best exemplifies this approach, but the chapters on motor development by Provine and by Fentress and McLeod, on suckling and huddling by Moran, on mother-infant interactions by Alberts, and on thermoregulation by Leon may also suggest a trend in that direction. It seems to me that the developmental neuroethological approach should also further the goals set out by Greenough and Juraska and by Blass, enabling neurobiologists and psychobiologists to develop still closer ties over an increasing number of bridges.