



OXFORD LIBRARY OF NEUROSCIENCE

Editor-in-Chief GORDON M. SHEPHERD

Oxford Handbook of Developmental Behavioral Neuroscience

Edited by

Mark S. Blumberg

John H. Freeman

Scott R. Robinson

OXFORD
UNIVERSITY PRESS

2010

Introduction: A New Frontier for Developmental Behavioral Neuroscience

Mark S. Blumberg, John H. Freeman, and Scott R. Robinson

As editors of this volume, we wrestled with alternative titles to capture what we felt was a theoretically connected but highly interdisciplinary field of science. Previous edited volumes that have addressed related content areas were published over a 15-year span beginning in the mid-1980s under the label of “developmental psychobiology” (e.g., Blass, 1986, 1988, 2001; Krasnegor, Blass, Hofer, & Smotherman, 1987; Shair, Hofer, & Barr, 1991). Although all three of the editors of the present volume have longstanding ties to the field of developmental psychobiology (DP) and its parent society (the International Society for Developmental Psychobiology), we also view our work as part of a larger community of researchers in behavioral neuroscience, comparative psychology, developmental science, and evolutionary biology. This volume is aimed at this larger research community concerned with empirical and theoretical issues about behavioral and neural development.

DP has traditionally concerned itself with investigations of the biological bases of behavior and how they change during development. The rich tradition of DP is seen in the many advances it has provided to our understanding of behavior and behavioral development. Moreover, DP has been distinguished by its adherence to an epigenetic perspective, that is, a perspective that embraces all contributions to individual development, from the molecular to the social. DP remains a productive and innovative discipline, but it now faces new challenges posed by rapid advances and the advent of powerful technologies in molecular biology, neuroscience, and evolutionary biology. These challenges, however, are also opportunities. Thus, our goal for this volume is twofold: (1) to communicate the central research perspectives of DP to a wider community interested in behavioral and neural development and

(2) to highlight current opportunities to advance our understanding of behavioral and neural development through enhanced interactions between DP and its sister disciplines.

In 1975, in his influential book *Sociobiology: The New Synthesis*, E. O. Wilson famously looked forward to the year 2000 when, he predicted, the various subdisciplines of behavioral biology could be represented by a figure in the shape of a barbell—the narrow shaft representing the dwindling domain of the whole organism (i.e., ethology and comparative psychology) and the two bulging orbs at each end comprising the burgeoning fields of sociobiology and neurophysiology. Wilson’s prediction that the study of the whole organism would be “cannibalized” by population and reductionistic approaches seemed, to many behavioral researchers over the last quarter century, to be relentlessly fulfilled. But ultimately, the “death of the organism” has proven greatly exaggerated. On the contrary, we are witnessing a resurgence of interest in a diversity of mechanisms—especially developmental mechanisms—that contribute to the form and function of the organism. Most importantly (for this volume), the behavior of whole organisms has emerged as a central product and causal influence of developmental change.

Wilson’s view of the future from his 1975 perch reflected two biological themes—cell theory and evolutionary theory—that were central to the rise of modern biology in the nineteenth century and which were greatly refined and expanded in their influence in the twentieth century. By the mid-twentieth century, these two perspectives culminated in the rise of the Modern Synthesis, the discovery of DNA, and the success of the molecular revolution. The new emphasis on parts and populations anchored Wilson’s barbell and relegated

the organism to a transient vessel, a mere conveyance for selfish genes (Dawkins, 1977). On the one hand, the Modern Synthesis succeeded in reconciling Darwinian evolution with population genetics (Provine, 1971); on the other, the successes of molecular biology convinced many that whole organisms could be reduced to individual traits and crucial biochemicals produced through the actions of single genes (Keller, 2000; Moore, 2001). Although many prominent scientists tried very hard to offer plausible alternatives and amendments to these two dominant perspectives (Alberch, 1982; Gottlieb, 1992; Gould & Lewontin, 1979; Lehrman, 1953; Stent, 1977), they were unable to stem the tide.

Proximate causes are the immediate conditions that give rise to behavior. Such causes include activity in particular neural circuits, the actions of neurotransmitters at specific receptors, the modulating influence of hormone molecules, and the transduction of sensory stimuli into neural responses. In contrast, *ultimate* causes refer to the function or purpose of behavior, which in evolutionary terms is the result of natural selection acting on populations. Although the distinction between proximate and ultimate causation is evident in the early writings of both biologists (Baker, 1938; Huxley, 1916; Lack, 1954) and comparative psychologists (Craig, 1918; Dewsbury, 1999), this dichotomy of causes was promoted most effectively by Ernst Mayr (Beatty, 1994; Mayr, 1961), a central figure in the rise of the Modern Synthesis. Interestingly, Mayr used proximate and ultimate causation as independent explanations to defend evolutionary interpretations from criticisms coming from mechanistic physiologists and molecular biologists (Amundson, 2005; Dewsbury, 1999; Mayr, 1974). In effect, Mayr appealed to the explanatory categories of proximate and ultimate causation to delineate the fields of molecular–cellular and population biology, thereby creating the very barbell that Wilson conveniently “predicted” in 1975.

Of course, what was missing from both the Modern Synthesis and the reductionism of molecular biology was an adequate appreciation for the role of development as a mediating cause of organic change. As long as genes were viewed as root causes of individual characteristics (necessary for a modern synthetic interpretation of evolution), and gene frequencies in populations were viewed as sufficient metrics of evolution, it was possible to skip over the messy details of how a fertilized egg is transformed into an organism that can, in turn, be a target of natural selection. Tinbergen (1963) and Hailman

(1967) at least called attention to the value of developmental analyses of behavior and expanded the traditional dichotomy of causes into four “causes and origins” of behavior: (1) causation or control (immediate physiological mechanisms), (2) development (history of change in the individual), (3) adaptive significance (mechanisms acting on past populations, such as natural selection), and (4) evolution (history of change in the population). But whether viewed as two, four, or even more classes of cause, such classification schemes have reified the notion that biological causes can be treated as distinct and independent entities.

Tinbergen’s four-question scheme has been widely adopted in textbooks and behavioral training programs and has contributed a great deal to the clearer formulation of research questions in ethology and comparative psychology (Dewsbury, 1994; Hailman, 1982; Hogan, 1994; Sherman, 1988). But it also has obscured deep underlying connections between these areas of inquiry. For instance, we are coming to appreciate that—in contrast to the comparative anatomy of behavior espoused by Lorenz (1937, 1981)—behavior is not an entity such as a bone or internal organ that has a continuous existence. Rather, each behavioral performance is unique and ephemeral, although it may be recognizably similar to other performances by the same individual in the past or other individuals of the same species. Behavior is elaborated in time despite the common research practice of treating individual behavioral acts as instantaneous for purposes of analysis. From these perspectives, the causation of behavior, which encompasses the “proximate” physiological mechanisms that generate behavior, also should be seen as a question of historical origins, albeit on a much briefer time scale and therefore within the same continuum of phenomena as development.

Theorists since Darwin also have recognized parallels in patterns of change on developmental and evolutionary time scales. Early attempts to explain the phylogenetic information evident in embryological development were founded on notions such as Haeckel’s biogenetic law, which stated that embryos pass through the same sequence of stages during development as the adult forms of ancestral species during evolution (Haeckel, 1866). Although strong forms of recapitulation have long since been discredited (Gould, 1977), developmental issues have risen in prominence again over the last several decades within both the evolutionary (Kirschner & Gerhart, 2005; West-Eberhard, 2003) and molecular (Carroll,

2005) domains. Moreover, the success of unsupervised processes such as natural selection in explaining evolutionary change has led to similar shifts of emphasis on emergent process and multicausal interactions in changes occurring within the lifetime of an individual. For example, the twin processes of variation and selection have been proposed as general principles leading to greater organization without preexisting instructions in various domains of development, including antibody production in the immune system (Burnet, 1957; Jerne, 1955), operant learning (Hull, Langman, & Glenn, 2001; Skinner, 1981), motor development (Sporns & Edelman, 1993), neural development (Changeaux, 1985; Sporns, 1994), and moment-to-moment functioning of the nervous system (Edelman, 1987).

Despite a plethora of metaphors about developmental programs encoded in genetic blueprints, and the repeated appeals of nativists to genetically determined modules governing specific aspects of behavior and cognition, the study of behavioral development has never been more vibrant. A clear example is the “new” concept of epigenetics and its role in development. In modern genetics, epigenetics refers to changes in developmental outcomes, including regulation of gene expression, that are based on mechanisms other than DNA itself. At a molecular level, gene expression can be affected by experience and sensory-dependent activation of immediate early genes (e.g., *c-fos*), alternative and contingent editing and translation of mRNA transcripts, methylation and chromatin remodeling in the regulation of gene expression, and chaperoned folding and other posttranslational modifications of newly synthesized proteins. Thus, the discovery that gene function is modulated by epigenetic factors has recapitulated, at a molecular level, what developmental psychobiologists working at a behavioral level have known for decades: that development is multicausal, multilevel, embodied, contextual, conditional, and most importantly, not preformed in a genetic blueprint or program (Kuo, 1967; Lehrman, 1953).

Moreover, a renewed appreciation for the formative role of experience—not just in the sense of explicit learning but in the broader sense that Lehrman (1953) emphasized—in the self-organization of complex nervous systems is dramatically altering the developmental and neurophysiological landscape. What is emerging is a science of developmental systems and epigenesis that places all of the factors that guide development and evolution—from genes to social systems—in proper balance (Blumberg,

2005, 2009; Gottlieb, 1997; Oyama, Griffiths, & Gray, 2001; West, King, & Arberg, 1988). Although Wilson’s barbell may have seemed inevitable 30 years ago, it now appears that researchers working at both molecular and population levels of analysis are returning to the whole organism in general and development in particular. Perhaps we are beginning to see glimpses of a new kind of synthesis—elaborated from conceptual foundations in developmental psychobiology and developmental systems theory—which will unify time scales from the neurophysiological to the developmental to the evolutionary.

The foregoing are just a few of the recent trends in developmental behavioral neuroscience that originally spurred us to assemble the present volume. In seeking contributions for this volume, we have attempted to bring together a diverse group of individuals who have been investigating the development of behavior from a variety of perspectives using a variety of techniques. Our criteria for inclusion were nonstandard: we invited contributions from individuals based less on their academic affiliations and more on their topics of research and conceptual perspectives. We believe that this approach to assembling these contributions will help to reveal common themes that have otherwise been hidden within the subdisciplines that most of us inhabit. As a consequence, we hope that this volume will encourage future cross-disciplinary work and spur new insights and, perhaps, even new collaborations.

References

- Alberch, P. (1982). The generative and regulatory roles of development in evolution. In D. Mossakowski & G. Roth (Eds.), *Environmental adaptation and evolution* (pp. 19–36). Stuttgart, Germany: Gustav Fischer.
- Amundson, R. (2005). *The changing role of the embryo in evolutionary thought*. New York: Cambridge University Press.
- Baker, J. R. (1938). The evolution of breeding seasons. In: G. R. de Beer (Ed.), *Essays on aspects of functional biology* (pp. 161–177). Oxford: Clarendon Press.
- Beatty, J. (1994). The proximate/ultimate distinction in the multiple careers of Ernst Mayr. *Biological Philosophy*, 9, 333–356.
- Blass, E. M. (1986). *Handbook of behavioral neurobiology: Developmental psychobiology and developmental neurobiology* (Vol. 8). New York: Plenum Press.
- Blass, E. M. (1988). *Handbook of behavioral neurobiology: Developmental psychobiology and behavioral ecology* (Vol. 9). New York: Plenum Press.
- Blass, E. M. (2001). *Handbook of behavioral neurobiology: Developmental psychobiology* (Vol. 13). New York: Plenum Press.
- Blumberg, M. S. (2005). *Basic instinct: The genesis of behavior*. New York: Thunder’s Mouth Press.
- Blumberg, M. S. (2009). *Freaks of nature: What anomalies tell us about development and evolution*. New York: Oxford University Press.

- Burnet, F. M. (1957). A modification of Jerne's theory of antibody production using the concept of clonal selection, *The Australian Journal of Science*, 20, 67–69.
- Carroll, S. B. (2005). *Endless forms most beautiful: The new science of Evo Devo*. New York: W. W. Norton.
- Changeaux, J. -P. (1985). *Neuronal man*. Princeton, NJ: Princeton University Press.
- Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biological Bulletin*, 34, 91–107.
- Dawkins, R. (1977). *The selfish gene*. New York: Oxford University Press.
- Dewsbury, D. A. (1994). On the utility of the proximate–ultimate distinction in the study of animal behavior. *Ethology*, 96, 63–68.
- Dewsbury, D. A. (1999). The proximate and the ultimate: past, present, and future. *Behavioural Processes*, 46, 189–199.
- Edelman, G. (1987). *Neural Darwinism: The theory of neuronal group selection*. New York: Basic Books.
- Gottlieb, G. (1992). *Individual development and evolution*. New York: Oxford University Press.
- Gottlieb, G. (1997). *Synthesizing nature–nurture: Prenatal roots of instinctive behavior*. Mahway: Lawrence Erlbaum Associates.
- Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge: The Belknap Press of Harvard University Press.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, B205*, 581–598.
- Haeckel, E. (1866). *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie* (2 vols.), Berlin: Georg Reimer.
- Hailman, J. P. (1967). Ontogeny of an instinct. *Behaviour Supplement*, 15, 1–159.
- Hailman, J. P. (1982). Ontogeny: toward a general theoretical framework for ethology. In: Bateson, P. P. G., & Klopfer, P. H. (Eds.), *Perspectives in ethology* (Vol. 5, pp. 133–189). New York: Plenum Press.
- Hogan, J. A. (1994). The concept of cause in the study of behavior. In: Hogan, J. A., & Bolhuis, J. J. (Eds.), *Causal mechanisms of behavioural development* (pp. 3–15). Cambridge: Cambridge University Press.
- Hull, D. L., Langman, R. E., & Glenn, S. S. (2001). A general account of selection: Biology, immunology, and behavior. *Behavioral and Brain Sciences*, 24, 511–573.
- Huxley, J. (1916). Bird-watching and biological science. *Auk*, 33, 142–161, 256–270.
- Jerne, N. K. (1955). The natural-selection theory of antibody formation, *Proceedings of the National Academy of Sciences*, 41, 849–857.
- Keller, E. F. (2000). *The century of the gene*. Cambridge, MA: Harvard University Press.
- Kirschner, M. W., & Gerhart, J. C. (2005). *The plausibility of life: Resolving Darwin's dilemma*. New Haven, CT: Yale University Press.
- Krasnegor, N. A., Blass, E. M., Hofer, M. A., & Smotherman, W. P. (Eds.) (1987). *Perinatal development: A psychobiological perspective*. Orlando, FL: Academic Press.
- Kuo, Z.-Y. (1967). *The dynamics of behavior development: An epigenetic view*. New York: Random House.
- Lack, D. (1954). *The natural regulation of population numbers*. Oxford: Clarendon Press.
- Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. *The Quarterly Review of Biology*, 4, 337–363.
- Lorenz, K. (1937). The companion in the bird's world. *Auk*, 54, 245–273.
- Lorenz, K. (1981). *The foundations of ethology*. New York: Springer-Verlag.
- Mayr, E. (1961). Cause and effect in biology. *Science*, 134, 1501–1506.
- Mayr, E. (1974). Teleological and teleonomic, a new analysis. *Boston Studies in the Philosophy of Science*, 14, 91–117.
- Moore, D. S. (2001). *The dependent gene: The fallacy of "nature vs. nurture"*. New York: W. H. Freeman & Company.
- Oyama, S., Griffiths, P. E., & Gray, R. D. (Eds.). (2001). *Cycles of contingency: Developmental systems and evolution*. Cambridge, MA: MIT Press.
- Provine, W. B. (1971). *The origins of theoretical population genetics*. Chicago: University of Chicago Press.
- Shair, H. N., Hofer, M. A., & Barr, G. (Eds.) (1991). *Developmental psychobiology: New methods and changing concepts*. New York: Oxford University Press.
- Sherman, P. W. (1988). The levels of analysis. *Animal Behaviour*, 36, 616–619.
- Skinner, B. F. (1981). Selection by consequences. *Science*, 213, 501–504.
- Sporns, O. (1994). *Selectionism and the brain*. New York: Elsevier.
- Sporns, O., & Edelman, G. M. (1993). Solving Bernstein's problem: a proposal for the development of coordinated movement by selection. *Child Development*, 64, 960–981.
- Stent, G. S. (1977). Explicit and implicit semantic content of the genetic information. In Butts, R.E., & Hintikka, J. (Eds.), *Foundational problems in the special sciences* (pp. 131–149). Dordrecht: D. Reidel Publishing Company.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.
- West, M. J., King, A. P., & Arberg, A. A. (1988). The inheritance of niches: The role of ecological legacies in ontogeny. In E. M. Blass (Ed.), *Handbook of Behavioral Neurobiology* (Vol. 9, pp. 41–62). New York: Plenum Press.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford: Oxford University Press.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge: Harvard University Press.