

## INDIVIDUAL DEVELOPMENT AND EVOLUTION: THE GENESIS OF NOVEL BEHAVIOR

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**Individual Development and Evolution: The Genesis of Novel Behavior**, by Gilbert Gottlieb, Oxford University Press, N.Y., 1992, 231 pp.

Comparative psychology is concerned with the development and evolution of behavior. The discipline has received criticism, however, for both a lack of guiding theory in the aforementioned aim, and for misunderstandings of evolutionary theory. Gilbert Gottlieb's book, *Individual Development and Evolution: The Genesis of Novel Behavior*, does much to further comparative psychology's aim and answer its critics. Gottlieb's thesis is that it is ontogenetic novelty that produces evolutionary change. This is in essence an ontological reversal of mainstream evolutionary thought. In developing his argument, Gottlieb provides a conceptual framework that is significant for comparative psychology, adds to the evolutionary dialogue, and damages behavioral explanations derived from an assumption of genetic determinism.

The book is comprised of two sections. It begins with a selective historical analysis of the foundations of population genetics and embryology. Although this section is very informative and written in unusually readable prose for historical treatments, one is not sure where Gottlieb is headed at first. However, by the book's midpoint the reader is suddenly acutely aware of what Gottlieb has done. His historical treatment subtly buttresses his own theoretical argument by pointing out glaring discrepancies between explanations based on the modern-synthesis and empirical observations obtained in the area of embryology.

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Further, Gottlieb cogently demonstrates why and how such divergent paradigms as population genetics and developmental embryology became so divergent. The latter half of the book is a well articulated description of his ideas, attempting to integrate empirical knowledge of contextual effects influencing morphological and behavioral development and modern evolutionary theory. Thus, the "nature-nurture controversy" is resolved by understanding that behavior is the result not of genes, or biology, nor of nurturance, but is, rather, the result of the complex and dynamic interplay of these factors. Psychological organisms are biosocial beings, and nature and nurture are fused in their influence on behavior. One often neglected and misunderstood implication of this fusion is the bidirectionality of epigenetic processes. Genes affect an organism's phenotype, but the organism's behavior (a phenotypic characteristic) is also now shown to impact the genotype itself.

There are two important concepts in Gottlieb's approach that provide ample fuel for empirical work: those of behavioral neophenotypes and of reaction ranges. The former concept is borrowed from Z. Y. Kuo (1967) and refers to the drastic changes in behavioral development that can arise from significant alterations in the contextual conditions of usual organismic development. Gottlieb cites as an example Kuo's experiment in which the previously thought instinctive sexual behavior of male dogs was virtually reversed by controlling the experiential history of the animals. Essential to the creation of neophenotypes are the timing, duration, and quality of contextual alteration.

The second concept discussed is that of the norm of reaction, which is contrasted with the concept of the reaction-range. Largely as the result of mainstream evolutionary thinking, which takes a neo-Haeckelian approach, it has been assumed that an organism's genotype sets narrow limits on the range of phenotypic expression. This line of thinking is referred to as the reaction-range concept. In contrast, the norm of reaction concept assumes that there are no presupposed limits on phenotypic expression. In this conception, genes are limited to a necessary role but of a more limited ontogenetic significance than they have typically been granted.

These two concepts provide propositions from which enormous intraspecies behavioral plasticity can be deduced. Further, these behavioral novelties, Gottlieb contends, can be, and are canalized to produce speciation. While Gottlieb was certainly not the first to recognize or discuss this (e.g., Plotkin, 1988), that his very readable discussion includes evidence for this process should do much to assure

its broad acceptance by biologists and psychologists alike.

Comparative psychologists have been criticized for making comparisons between species that are not phylogenetically related. By coupling the aforementioned concepts with the concept of integrative levels, Gottlieb not only refocuses the discipline of comparative psychology but effectively silences its critics. In short the argument is as follows; differential behavioral phenotypes are primarily the result of supragenetic influences. The impact of these influences is dependent upon temporal factors. Further, the malleability of any given species is dependent upon the complexity and integration of the organism. Thus, comparisons regarding the degree of ontogenetic plasticity, "causes" of that plasticity, and rates of evolution and adaptability can be made not on a clade basis but a grade basis. This orientation provides plenty of work for comparative psychology and addresses the criticism that the levels concept is not a heuristic for us.

The anagenetic model discussed by Gottlieb here and in earlier pieces was developed by Schneirla into an hierarchical or integrative-levels understanding of behavioral evolution. One of the main concepts of the levels notion is that as one moves up the levels, an increase in behavioral plasticity is apparent. The higher levels include more complex and varied behaviors. From a reductionist perspective, and looking only at genes in evolution, it is true that the levels concept is not of much help. However, from the epigenetic perspective taken by Gottlieb, with its shift from genes to a holistic approach, shows the levels concept to be both intuitive and vitally important. Based on the work of Jerrison, Razran and others, Gottlieb points out that increased behavioral plasticity occurs in animals with higher brain to body ratios. The more behaviorally plastic a species is, the more likely it is to develop latent morphological changes when faced with change and the more likely an animal is to be affected by experiences the more likely it is that morphological change will result from those experiences. Species that are more plastic are better equipped to adapt to change. Gottlieb's contention that different adaptive demands on an organism bring out latent morphological changes that then allow a genetically based evolutionary change to follow, is a powerful one. The levels concept, in this light, is central to the concept of evolution - for both its predictive power, and its theoretical base.

As many important works do, this book has implications beyond a single discipline. As such, Gottlieb's ideas have significant contributions to make to the related fields of evolutionary biology and population genetics, although, the contribution is more positive for the former. While at first glance Gottlieb's argument seems to be

antithetical to the modern synthesis, in fact the two, are not incompatible. To incorporate Gottlieb's thesis, modern evolutionary thought need only to rethink the rate of speciation and the mechanism of variation. Rate of speciation is already under considerable discussion within the field of evolutionary biology as the result of the punctuated equilibrium theory promulgated by Eldridge and Gould (1972). Indeed, Gottlieb's thesis, in concert with natural selection, may provide a potential mechanism by which punctuated equilibrium occurs. Additionally, Gottlieb's discussion of the findings of developmental embryology challenges the Mendelian concepts of population genetics.

It is not uncommon in science to find little more than lip service granted to important concepts. In 12 years and six biennial T. C. Schneirla conferences organized around the concept of "integrative levels" (Greenberg & Tobach, 1984) we have found that while most scientists acknowledge the significance of this crucial organizing principle, reductionistic thinking still prevails in the behavioral and the biological sciences. With respect to the book under review here, the same can be said of the concept of development and its significance for understanding evolution and evolutionary theory (on this point see too, Michel & Moore, 1995). Gottlieb's is an important book for all evolutionary scientists, not least because, in his own words: "It is now acknowledged in many different quarters, both within and without the modern synthesis...., that the time has come to include the role of individual development in evolution and I cannot but hope that this small book makes some contribution toward that aim" (p. 194). In accomplishing this goal Gottlieb takes us through more than 200 years of thinking about development, embryology, and evolution to illustrate and underscore the dramatic importance of development in the evolutionary process.

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