THE STUDY OF PLASTICITY COMES OF AGE

Author: SAHOTRA SARKAR
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Contrary to the common conception of genes, significant phenotypic differences between organisms are some-
times independent of genotypic differences and depend predictably on the developmental environment of the organism. This phenomenon was first systematically studied in 1909 by German zoologist Richard Woltereck, who introduced “norms of reaction” to depict them. Each norm of reaction is a graph that represents the phenotypic value of a genotype across a range of environments. In 1913, Swedish botanist Herman Nilsson-Ehle introduced the term plasticity to describe the varying response of the same genotype to different environments. By definition, there is phenotypic plasticity for a trait if its norm of reaction is not constant across the entire range of environments in which the organism is viable. While the norm of reaction became a part of genetical practice in the Soviet Union and, to a lesser extent, in Germany in the 1920s, it was largely ignored in the West. The only notable exception was its use by Lancelot Hogben in 1932 to demonstrate that there is a nonlinear interaction between the genotype and the environment in the phenogenesis of many traits. In a similar spirit, the gene was identified with a norm of reaction in the Soviet Union; thus, a gene was said to confer an inheritable potential to display a trait rather than to determine the presence of the trait. (For a detailed history, see “From the Reaktionsnorm to the Adaptive Norm: The Norm of Reaction, 1909–1960,” which I wrote in 1999 for Biology and Philosophy, vol. 14.) Plasticity was similarly largely ignored as a field of research until a very influential review by Bradshaw in 1965 which argued that plasticity was an adaptive feature of organisms. That paper sparked an expansion of both experimental and theoretical studies of plasticity and the norm of reaction, which has continued to this day. Experimental studies have largely been confined to plants and animals capable of asexual reproduction, because they require the creation of multiple copies of the same genotype, though norms of reaction have been constructed even for some highly inbred vertebrate lines and Drosophila strains. Theoretical modeling of the evolution of plasticity started with the construction of optimization models in the 1970s and continued with attempts to model it as a quantitative trait in the 1980s, and the hypothesis that there are specific plasticity genes emerged in the 1990s. Such plasticity genes were supposed to be regulatory in their action, and the early 1990s saw an occasionally bitter dispute between those who believed in the existence of such genes, which were favored by selection, and those who argued that the plasticity of a trait arose because of selection for particular values of the trait itself in different environments. In retrospect, this dispute was probably avoidable since the two positions seem to be compatible. Quantitative genetics is silent about the specificity of the action of the genes subject to selection; claims of the existence of specific “plasticity genes” are claims at a different level of detail, compatible with plasticity being a quantitative trait.

All this recent work on plasticity is synthesized in Phenotypic Plasticity. Pigliucci has been an active researcher on plasticity, one of those who have helped bring plasticity studies to the mol-

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FOREWORD
Biology in the 21st Century
ERNST MAYR

PREFACE
A New Century of Biology
W. JOHN KRESS AND GARY W. BARRETT, VOLUME EDITORS

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GARY W. BARRETT, ROBERT S. HOFFMANN, AND W. JOHN KRESS

CONTRIBUTORS
Chapter 1 Introduction—The New Revolution in Biology
GARY W. BARRETT AND W. JOHN KRESS
Chapter 2 Bacteria in the Origins of Species: Denise of the Neo-Darwinian Paradigm
LYNN MARQUIS
Chapter 3 Bodies and Body Plans, and How They Came to Be
MARVALEE H. WAKE

Chapter 4 Ecosystems: Energetics and Biogeochemistry
GENE E. LIKENS
Chapter 5 Behavior, Ecology, and Evolution
GORDON H. ORIANS
Chapter 6 Conserving Biodiversity into the New Century
GHILLEAN T. PRANCE
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EDWARD O. WILSON
ecular level (see chapters 4–6 of his book). He has also been a participant in the controversy over the evolution of plasticity—he is a partisan for specific plasticity genes. This perspective pervades the book, which makes no pretense of being a neutral review. The fact that Pigliucci is willing to express strong opinions, for instance, by predicting a bright future for molecular studies or by arguing that plasticity is a central concept for evolutionary theory in the future, makes this book much more interesting than most syntheses. Nevertheless, the reader should be aware that many of the positions espoused in the book are still under discussion in the field.

The book has 11 chapters. The first defines plasticity as the angle that the norm of reaction makes with the x-axis. The second introduces the basic techniques for studying plasticity, and the third gives a brief history of the concept of plasticity. The third chapter is somewhat weak insofar as the history is sketchy—Nilsson-Ehle and Hogben are not even mentioned.

The fourth, fifth, and sixth chapters take up the genetics, molecular biology, and developmental biology of plasticity. These are perhaps the most interesting in the book, as they make a strong case for studying plasticity at the molecular level. By elucidating the developmental mechanisms of plasticity, these molecular studies may finally resolve the ongoing disputes about the evolution of plasticity: whether there are specific plasticity genes, and what aspect of plasticity or the norm of reaction may have been the target of selection. These questions have resisted solution by classical techniques because of their lower resolution. Although the author’s belief in plasticity genes comes out most explicitly in these chapters, Pigliucci does not overtly rebut opponents of that belief.

The seventh and eighth chapters take up behavior and the ecology of plasticity and give a fairly representative review of what is known. The final three chapters describe the evolution of plasticity and the role of plasticity in evolution (including evolutionary theory).

Overall, the chapters are self-contained and well written. An epilogue reaffirms the wisdom of Hogben’s insight in the early 1930s—namely, for most traits nature is inextricably linked to nurture, and there can be no solution to the nature–nurture debate in which either side emerges triumphant. It is a particularly important point to keep in mind in the wake of the human genome project and the tendency to interpret it as having shown the primacy of the genome in the origin of most traits. In this sense, the book is quite timely, though not directly related to the genome project. The study of plasticity is finally coming of age, and this book provides a useful introduction to the field.

SAHOTRA SARKAR
Program in the History and Philosophy of Science
Department of Philosophy
University of Texas at Austin
Austin, TX 78712-1180