



Book Review

The Integrative Biology of Phenotypic Plasticity

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A review of Massimo Pigliucci, *Phenotypic Plasticity: Beyond Nature and Nurture*, Johns Hopkins University Press, Baltimore, 2001, xvi + 328 pp. ISBN 0-8018-6788-6, \$80.00 (Hb).

Gene-environment interactions are of interest not only for the study of human behavior but have also become a focus of research on other species. Recent developments in the field of plasticity studies, which examines such interactions, are given a thorough survey in Pigliucci's new book. The first in a series of monographs on integrative biology edited by Samuel Scheiner, *Phenotypic Plasticity* summarizes the results of research in many disciplines, giving equal time to plants and animals. Following a discussion of the definition and history of plasticity, there are chapters on the genetics of plasticity and the significance of phenotypic plasticity in molecular and developmental biology and ecology, each of which can be read independently and provides an informative review of the field with which it deals. This project is motivated in part by recent debates about the influences of nature and nurture on human behavior. Genetic determinists such as Jensen maintain that the human intelligence quotient depends on genotype whereas Gould, Lewontin, and others have emphasized the importance of environmental factors. Pigliucci presents phenotypic plasticity as a way of moving beyond the gene-environment dichotomy because in many cases plasticity results from non-additive interactions between genotype and environment.

Recent definitions of plasticity

The first two chapters of Pigliucci's book explain the key terms used to describe plasticity. He defines phenotypic plasticity as "the property of

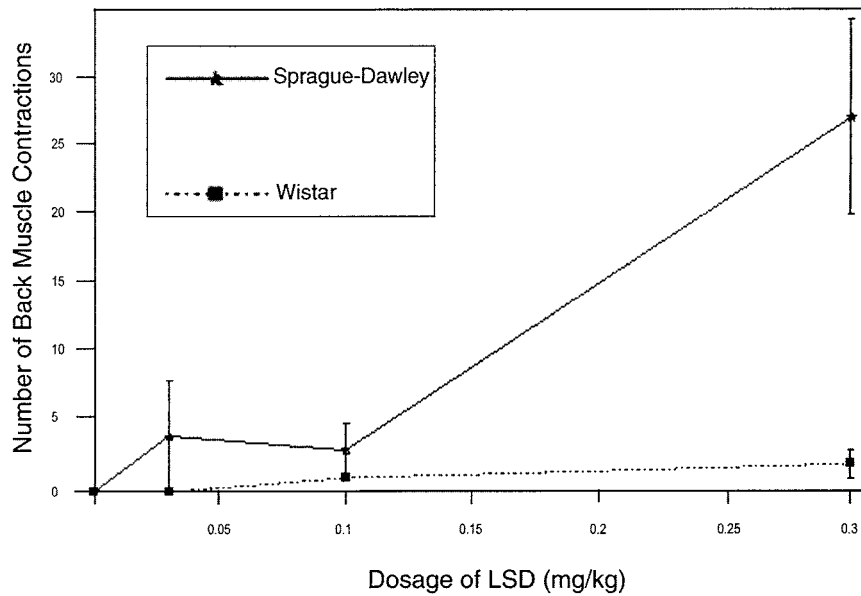


Figure 1. An example of a norm of reaction (**NoR**). The data are from Ouagazzal et al. (2001); *x*-axis – dosage of LSD; *y*-axis: number of back muscle contractions.

a given genotype to produce different phenotypes in response to distinct environmental conditions” (Pigliucci 2000: 1). Random developmental “noise” differs from plasticity in that the latter constitutes a response to an environmental signal whereas the former does not (Bull 1987: 304). Phenotypic plasticity can be visualized using norms of reaction (NoRs). A NoR curve is a function describing the response of a genotype to a quantitative environmental manipulation, which is listed as the *x*-axis of a graph. The *y*-axis of the graph corresponds to the phenotype each genotype exhibits in each environment. Using a NoR, the reactions of several genotypes to the same environmental manipulation, such as varying temperatures or amounts of food, can be compared. A study by Ouagazzal et al. (2001) illustrates the NoR approach (see Figure 1). They investigated the effect of three dosages of LSD on back muscle contractions in genetically-distinct strains of rats. NoRs were assembled from these data by listing the dosage of LSD as the environmental manipulation on the *x*-axis and the number of contractions observed in each isogenic line on the *y*-axis. NoRs like this one quantify the “degree of plasticity” of a given genotype (Pigliucci 2001: 8). A genotype is non-plastic if it shows the same phenotype in all environments. Such a genotype will produce a flat NoR. But if the NoR has an appreciable slope, the genotype is plastic (Pigliucci 2001: 8).

Schlichting and Smith (2002) have proposed an alternative definition of phenotypic plasticity according to which plasticity could be examined at the level of individual organisms. They take plasticity to refer to “any change in an organism’s characteristics in response to an environmental signal” (Schlichting and Smith 2002: 190). Pigliucci’s and Schlichting and Smith’s definitions are mutually exclusive because when plasticity is defined in terms of the NoR of a genotype it cannot be measured on an individual (Scheiner and Lyman 1989; de Jong 1995), but must instead be calculated by determining the mean phenotype manifested by groups of individuals of the same genotype at each level of the environmental manipulation.

Early definitions of plasticity

Chapter 3 of Pigliucci’s book deals with the history of plasticity in the biological literature since the German zoologist Richard Woltereck used the term *Reaktionsnorm* in an article on the effects of diet on carapace length in *Daphnia* and seasonal changes in the *Daphnia* reproductive cycle (Woltereck 1909). Woltereck’s definition of the NoR differs from the modern one to the extent that he called functions representing the response of a genotype to an environmental variable “phenotypic curves” and used “Reaktionsnorm” to describe the totality of phenotypic curves that could be plotted for a particular quantitative characteristic (Woltereck 1909: 135; Sarkar 1999). As Pigliucci’s treatment of plasticity between 1909 and Schmalhausen’s *Factors of Evolution* (1949) is much less extensive than his account of developments since 1965, when A.D. Bradshaw’s review of plasticity in plants (Bradshaw 1965) renewed scientific interest in the topic, I will sketch that early history here. One of the figures omitted from Pigliucci’s history of plasticity is the Swedish geneticist and agricultural researcher H. Nilsson-Ehle, whose work Bradshaw quoted as the epigraph of his review (Bradshaw 1965: 115). Nilsson-Ehle was the first scientist to use of the word “plasticity” to describe the effect of the environment on the phenotype of an organism. In a 1914 paper, he referred to the adaptation of alpine plants to lowland environments as “plasticity [*plasticitet*]” (Nilsson-Ehle 1914: 549). He also called the plant *Polygonum amphibium*, which develops land- or water-based forms depending on environmental cues and is still used as a model system in plasticity research (e.g. Mitchell 1976), “especially plastic” (Nilsson-Ehle 1914: 549). This is not to say that Nilsson-Ehle’s definition of plasticity was identical to the contemporary one. He took plasticity to be purely adaptive, classifying it as one of the mechanisms of adaptive “self-regulation” by which an organism responds to environmental change (Nilsson-Ehle 1914: 549). Though other writings from this period (Nilsson-Ehle 1913) indicate

that Nilsson-Ehle understood the distinction between the genotype and the phenotype introduced by the Danish botanist Wilhelm Johannsen (Johannsen 1909), in the 1914 paper, Nilsson-Ehle does not define plasticity as a property of a single genotype.

Pigliucci's discussion of this period would have benefited from a more detailed examination of the work of Richard Woltereck. He argues that Woltereck "completely misunderstood the significance of his findings" and believed that "the idea of an independent, underlying genetic factor should be abandoned" (Pigliucci 2001: 50). Woltereck and Johannsen's theories of inheritance differed in important respects; most notably, Woltereck wished to equate what Johannsen called the genotype with the NoR (Woltereck 1909: 136; Sarkar 1999). But Pigliucci mischaracterizes Woltereck's legacy when he states that certain of Woltereck's errors "still haunt plasticity research today" (Pigliucci 2001: 50). Woltereck's view of the relationship between the genotype and environment was much more in keeping with contemporary investigations of phenotypic plasticity than was that of Johannsen; indeed, the genetic determinism of early twentieth-century biology is partially attributable to Johannsen's view of the environment as an "unavoidable nuisance" (Falk 2001). Johannsen denied that continuously varying traits were heritable and sided with British "Mendelians" who claimed that evolution proceeds by "saltations," abrupt leaps (Provine 2002). Woltereck sided with the opposing camp in this debate, the "Darwinians," who contended that natural selection operates on continuously varying traits in a gradual, non-saltationary manner (Sarkar 1999). Examining the influence of environmental factors on a number of phenotypes in *Daphnia*, Woltereck offered a particularly detailed account of the effect of food, temperature, and the density of conspecifics on the *Daphnia* reproductive cycle, which shifts between biparental reproduction and parthenogenesis.

Though Woltereck suggested that the NoR is inherited to the extent that he equated the NoR with the gene (see above), Dobzhansky's writings in the 1920s state explicitly that it is the NoR of the organism that the progeny inherit (Blacher 1980). In a paper in which he criticized theories of the inheritance of acquired characteristics, Dobzhansky (1926) cited the effect of temperature on flower color in the Chinese primrose, *Primula sinensis* to argue that it is not the phenotype of the parent that the offspring inherit but the NoR. At room temperature, one primrose strain produces white flowers whereas at elevated temperatures, red flowers develop (Blacher 1980: 132). Dobzhansky pointed out that while parent and offspring might differ with respect to the flower color phenotype, the NoRs of the plants in response to the environmental parameter, temperature, would be the same. Had Woltereck and Dobzhansky's approaches been adopted, the importance of the NoR and

phenotypic plasticity would have been acknowledged considerably earlier. Thus, it is unwarranted to blame Woltereck for “opening the way to long-standing confusion” (Pigliucci 2001: 50) about the relationship between the genotype and the phenotype in plasticity research.

Definitions of plasticity in developmental, evolutionary, and molecular biology

Phenotypic Plasticity addresses a number of issues of interest to philosophers of science, such as the relationship between the subdisciplines of biology and the nature of scientific debates. Pigliucci documents theoretical differences between the concepts of plasticity used in developmental, evolutionary, and molecular biology as well as examining debates about the meaning of plasticity within each discipline. In addition to making it difficult to determine which phenomena qualify as instances of phenotypic plasticity, controversies surrounding the meaning of plasticity have impeded communication between workers in different branches of biology and rendered their findings philosophically incommensurable, since there is not an agreed-upon definition of plasticity in comparison to which different experiments can be compared.

Molecular biologists define plasticity in terms of “plasticity genes,” “regulatory loci that directly respond to a specific environmental stimulus by triggering a specific series of morphogenic changes,” examples of which include *hsp 70*, which encodes heat shock proteins in *Drosophila melanogaster*, the *Arabidopsis thaliana* phytochrome genes, which mediate the plant’s shade-avoidance response, and a number of other genes whose rate of transcription has been shown to depend on signals from the environment (Pigliucci 2001: 114). In contrast, evolutionary biologists have defined plasticity in terms of two mathematical models, the character state approach and the polynomial approach (Via et al. 1995). Character state models involve discrete environments and polynomial models continuous environments (Scheiner 1993), though it has been demonstrated that the methods are mathematically equivalent (de Jong 1995). In addition to the two classes of models used to study plasticity, within evolutionary biology, there are two views of the relationship between selection and the NoR. S. Scheiner and collaborators have argued that the NoR is a trait subject to selection (Gavrilets and Scheiner 1993), whereas an opposing view, espoused by S. Via, holds that the NoR over a range of environments is the by-product of stabilizing selection in a each environment such that “the reaction norm is an emergent property rather than a character in its own right” (Via 1994: 54). According to Via, selection acts on the mean phenotype in each environment, not on plasticity itself.

The study of plasticity has long been important in developmental biology, though the term “phenotypic plasticity” is used less in developmental studies than in evolutionary research. Pigliucci distinguishes “development” from “behavior”, identifying the latter with short-term changes in an organism and the former with irreversible, long-term alterations of morphology. He then describes cases of “developmental plasticity” in many species, instances in which hormonal or environmental cues alter the course of development in characteristic ways. Heterophylly in plants, the capacity to form leaves suited to an aquatic or terrestrial habitat, illustrates this sort of plasticity. More space should have been devoted to the relationship developmental biology and evolutionary theory and recent efforts to unify the two under the headings of “evolutionary developmental biology” (Hall 2000). Scientists working in the developmental evolutionary context may be able to remedy one of the shortcomings Pigliucci identifies in plasticity research, the dearth of studies “investigating differences in plastic responses among closely related species” (Pigliucci 2001: 76). Investigations of homologies and dissimilarities in development within genera and at higher taxonomic levels can offer insights about how plasticity in development is linked to the capacity for evolutionary change. For instance, phenotypes such as leaf size and flower number that show the most plasticity within angiosperm species also show the most interspecific variation within lineages (Givnish 2002: 224).

Plasticity research aims to integrate the developmental, evolutionary, and molecular approaches so as to elucidate phenomena pertinent to all three fields. What Pigliucci calls the “window for plasticity,” a phase during which development is particularly sensitive to environmental disturbances, is one such process. In the 1930s, Goldschmidt determined that if certain periods of ontogeny were disrupted by environmental insults such as heat shock, abnormal phenotypes were produced that were identical to genetic mutants (“phenocopies”); he concluded that the genes modified by mutation and the genes effected by the environmental shock acted on the same developmental pathways (Hamburger 1980). Light sensitivity in *A. thaliana* represents a more recently discovered “window for plasticity” (Pigliucci 2001: 153). Between days 4 and 45 of the lifecycle, the plant is highly sensitive to light signals such that short days trigger vegetative growth and long days early flowering. Yet after day 45, the flowering ceases to depend on photoperiod and the window for plasticity closes. Such windows are of interest from an evolutionary point of view because they may offer insight into how selection shapes development and provide a way of integrating developmental and evolutionary biology. While micro-evolutionary processes have been modeled extensively since the work of Haldane, Fisher, and Wright in the 1920s, macroevolution is understood much less well. As a consequence, no

“general theory of development, and the diversity of developmental patterns” is available at present (Raff 2000: 78). The principal impediment to synthesizing evolution and development may be the difficulty of connecting the empirical findings of morphologists with the mathematical formalisms of evolutionary theorists. Pigliucci notes that “[t]he existence of *windows for plasticity* is of course very important because it has consequences for the timing of genetic variation for plasticity and thus on the responses of traits to selection” (Pigliucci 2001: 153). Unfortunately, data on developmental plasticity and the timing of gene-expression at the molecular level are not easily parameterized into variables of quantitative genetic models. Though gene expression can be said to have “timing” to the extent that a gene may be transcribed during one interval of time but not another, genetic variance in Fisher’s sense cannot be said to have a “timing,” as it refers not to change in a single parameter over time but to the covariance between two properties of an allele, the average effect and the average excess (Crow 2002).¹

Conclusion

The problem of translating between the idioms used in developmental, evolutionary, and molecular biology constitutes a serious obstacle to integrating the concepts of plasticity used in various branches of biology. Substantive differences in researchers’ uses of the term “plasticity” complicate this project. Pigliucci initially defines “plasticity” as the property of a genotype and the NoR as a function representing a single genotype (Ch. 1). However, many of the studies he cites as examples of plasticity such as Rhen and Lang’s (1995) investigation of sex-determination in turtles and Windig’s (1994) paper on the effect of temperature on butterfly wing patterns measure plasticity not on genotypes but families. Pigliucci should have made it clear when he was describing the plasticity of families, populations, and higher taxonomic groups as opposed to the plasticity of single genotypes. Despite this terminological difficulty, Pigliucci makes a valuable contribution by promoting inter-disciplinarity within biology. *Phenotypic Plasticity* also demonstrates that the extensive research on plasticity in the last fifteen years has not exhausted this fascinating topic. Pigliucci’s efforts to integrate various definitions plasticity should be taken up by additional scientists and a history of the origins of the plasticity concept in Russian and Swedish genetics still needs to be written.

Acknowledgments

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Note

¹ The average effect of an allele refers to the mean effect of an allele on a phenotype within a population and the average excess of an allele refers to the difference between the phenotype of the carrier of the allele and the average phenotype within a population (Fisher 1999[1930]).

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