



From the *Reaktionsnorm* to the Adaptive Norm: The Norm of Reaction, 1909–1960¹

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1. Introduction

After the recovery of Mendel's work around 1900, the discrete nature of the Mendelian factors led to a temporary popularity of discrete jumps or "saltations" as the primary mechanism of evolutionary change. Hugo de Vries (1901–1903), one of the first to produce Mendelian results, proposed a "mutation theory" of evolution. Wilhelm Johannsen (1909) argued that evolution consisted of discontinuous changes between "pure lines". Among those who resisted these manifestly non-Darwinian moves was Richard Woltereck. At a June 1909 meeting of the German Zoological Society held to commemorate the centenary of Darwin's birth, Woltereck (1909) interpreted years of work on *Daphnia* and *Hyalodaphnia* species to support the Darwinian view that evolution occurred through natural selection acting on small continuous variations.

Woltereck studied morphologically distinct strains of *Daphnia* and *Hyalodaphnia* species from different German lakes. These were pure lines which maintained their form through several generations of parthenogenesis. He focused on continuous traits such as head-height at varying nutrient levels (Figure 1). Only such continuous traits could shed light on the question whether underlying evolutionary processes were continuous or discontinuous. In the case of head-height, the phenotype varied between different pure lines, was affected by some environmental factors such as nutrient levels, was almost independent of others such as the ambient temperature, and showed cyclical variation with factors such as seasonality. However, the response of the phenotype to the same environmental change was not identical in different pure lines. Woltereck drew "phenotype curves" to depict this phenomenon (Figure 2). These curves changed for every new variable

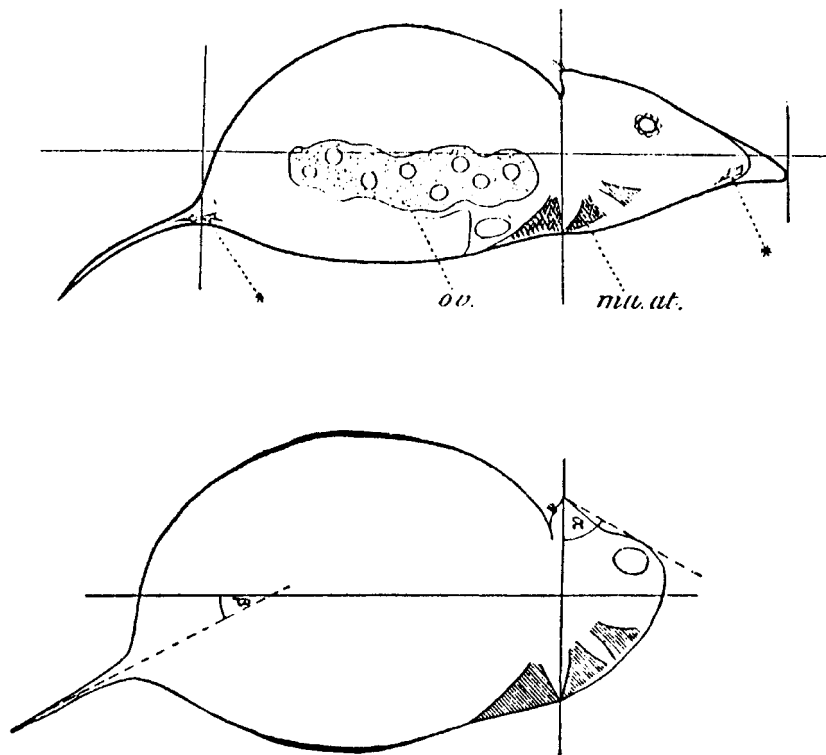


Figure 1. Side views of *Hyalodaphnia cucullata* female (left figure) and *Daphnia longispina* (right figure). These are Figures 1 and 2 from Woltereck (1909: p. 114). In the upper figure, head height is measured along the horizontal axis between the topmost and middle vertical lines. The relative head height (which was the phenotype that Woltereck considered) is the head height divided by the distance between the first and last vertical lines (and multiplied by 100 to be expressed as a percentage). (*mu. at.*: muscles of the antenna; *ov.*: ovary). In the lower figure α and β are examples of quantitative characters.

that was considered. There were thus potentially an almost infinite number of them and Woltereck coined the term “*Reaktionsnorm*” to indicate the totality of the relationships embodied in them (p. 135).²

Woltereck argued that what was inherited was this *Reaktionsnorm* and that hereditary change consisted of a modification of that norm. He identified the *Reaktionsnorm* with the genotype: “*Der ‘Genotypus’ ... eines Quantitativmerkmals ist die vererbte Reaktionsnorm*” (p. 136).³ Thus, since the reaction norm consisted of continuously varying phenotype curves, Darwinism was saved from the saltationist challenge because selection would act on small changes in the genotype (*qua Reaktionsnorm*). Noting that his own conception of the genotype also only referred to the potentialities inherent

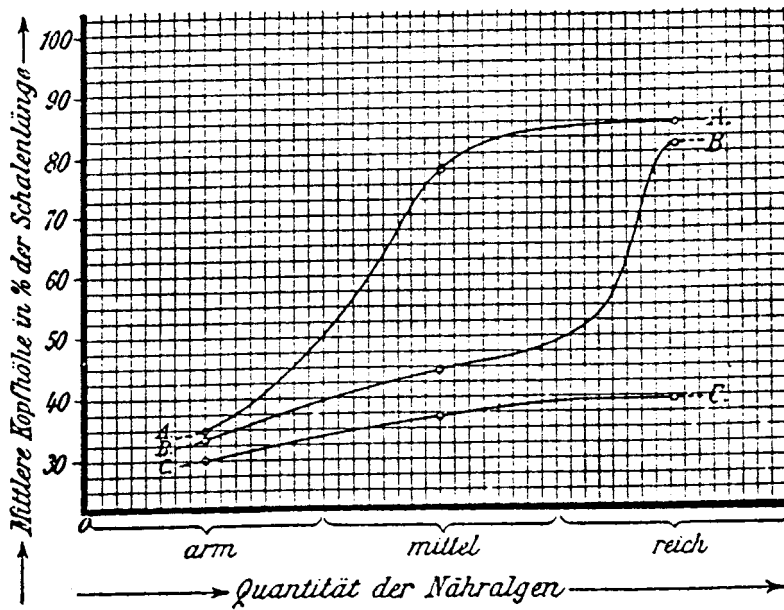


Figure 2. Phenotype curves for females of three pure lines of *Hyalodaphnia cucullata*. This is Figure 12 from Woltereck (1909: p. 139). *Abscissa*: nutrient level; *ordinate*: relative head height. A: strain from Moritzburg; B: from Brosdorf; C: from Kospuden. All strains were grown at a constant intermediate temperature and were from a “middle generation” of parthenogenesis. The curves show non-uniform variation between pure lines.

in a zygote, Johannsen (1911: p. 133) endorsed the concept of the reaction norm, which he thought to be “nearly synonymous” with “genotype”. Nevertheless, he rejected Woltereck’s claim that the continuous variations of phenotype curves could be interpreted as evidence against constant genotypic differences. Instead, he argued that all Woltereck had done was to depict the phenotype curves which arose from the “*reactions of the genotypical constituents*” (p. 145).⁴

Under Johannsen’s interpretation, Woltereck’s contribution may be taken to consist of providing a semi-quantitative picture of what Nilsson-Ehle (1914) a little later dubbed the “plasticity” of the phenotype which he interpreted as having general adaptive significance. In the West (that is, the US and Europe outside what became the Soviet Union), where Johannsen’s sharp distinction between genotype and phenotype became part of the standard picture of genetics, the subsequent decades witnessed a general trend to emphasize the constancy and causal efficacy of the genotype at the expense of the complexity of its interactions. The norm of reaction (NoR) remained a relatively unknown concept during this period (see § 2).

Under Woltereck's interpretation, the genotype was less a deterministic force than an enabling agent in phenogenesis. This view found resonance in the Soviet Union where the NoR emerged as a concept of central importance (see § 3). The two points of view were partly integrated in the 1950s and the evolution of the NoR became a locus of further research starting in the 1960s. In both traditions, contrary to Woltereck's own use, the NoR came to indicate each individual phenotype curve rather than the totality of relationships depicted by such curves. The latter (and customary) the usage will be followed here.

This paper is a brief critical history of the NoR from its initial introduction (discussed earlier in this Section) to about 1960 when it finally becomes part of the standard lexicon of genetics in the West. Section 2 describes how the NoR, despite its invention in Germany, was largely ignored in the West until the 1950s: it had no place in a view of heredity based on the primacy of immutable genes that largely determined phenogenesis. Section 3 describes the different fate of the NoR in the Soviet Union in the 1920s, how it was used to deflate claims of the inheritance of acquired characteristics, and how it was repatriated to the West. The concluding section (§ 4) speculates on the reasons behind the radically different trajectories of the NoR in the two situations and also draws some other philosophical conclusions.

2. The primacy of the gene

Though Woltereck's experiments were widely discussed, at least in Germany (e.g. Baur (1922), Goldschmidt (1920, 1928)), besides some scattered references in the German literature, the NoR was ignored in the genetical literature of the West until 1950. In 1920 Krafka published what are among the first graphical depiction of NoRs. The phenotype was the eye facet number in *Drosophila melanogaster*, Krafka investigated its dependence on temperature for different genotypes (Figure 3). Though he referred to Woltereck's work, he did not explicitly invoke the NoR. In 1930, using data from Krafka and many other sources, Hersch (1930) produced several graphical representations of NoRs for 9 genotypes (and the same phenotype). He tried to provide a mathematical description of the curves (see also Hersch (1934)). Driver (1932) produced similar figures. Neither Hersch nor Driver mentioned Woltereck or referred to the NoR.

Using Krafka's (1920) data, Hogben (1933) drew NoRs for the eye facet number (Figure 4) also without acknowledgement of Woltereck's work. Hogben used the fact that the NoRs were not parallel to argue for the "interdependence" of nature and nurture. This argument, which effectively shows that the phenotypic variation (as measured by the variance) cannot

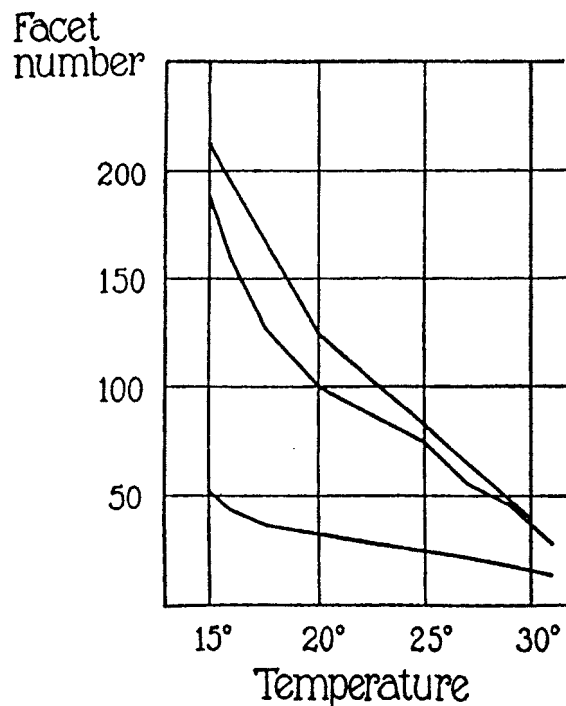


Figure 3. Norms of reaction for eye facet number dependence on temperature of *Drosophila melanogaster* females (from Krafka (1920: p. 419)). *Abscissa*: temperature; *ordinate*: average facet number. the top curve corresponds to the unselected stock; the other lower curves correspond to two mutants (*Low Selected* and *Ultra-bar* respectively). Krafka drew two conclusions from this graph: “(1) The mean facet number at any given temperature is not the same for all stocks. (2) The difference in the mean number of facets between any two temperatures is not a constant for all three stocks. In other words, the number of facets is determined by a specific germinal constitution plus a specific environment” (p. 419).

be additively decomposed into genotypic and environmental parts because there is a variable interaction between the genotype and environment, was used by Hogben to argue against a facile genetic reductionism, that is, a brief that phenogenesis can be entirely explained from a genotypic basis (see § 2.2) (Sarkar 1998). It bolstered Hogben’s critique of eugenic proposals to improve allegedly desirable human phenotypes by genetic intervention through selective breeding.

Eventually this argument became a standard use of the NoR in debates over the origin of complex human traits such as IQ (Lewontin 1974). But, in the 1930s and 1940s, the most influential arguments for the significance of genotype-environment interactions were Haldane’s (1936, 1946) algebraic analyses. Meanwhile, genetics and evolutionary biology coalesced around a

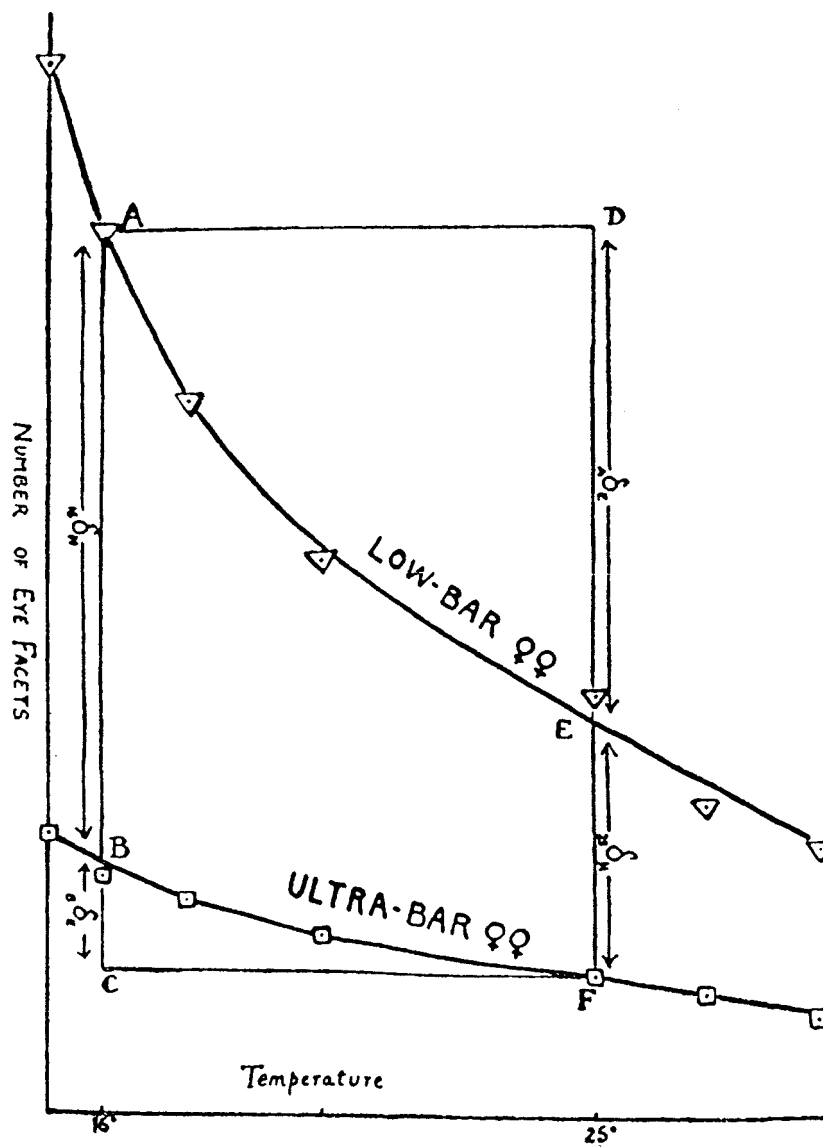


Figure 4. Norms of reaction for eye facet number dependence on temperature of *Drosophila melanogaster* females (from Hogben 1933: p. 384). This graph corresponds to a part of that in Figure 3. (*Low-Bar* is the same as the *Low Selected* genotype.) Hogben's innovation was to point out that the non-parallelism of the NoRs showed the "interdependence" of nature and nurture.

Mendelian core during this period (see, also, Sapp (1987)). This involved attempts to (i) reticulate the structure of Mendelian genetics to encompass the complexity of phenogenesis (§ 2.1); and (ii) delineate exactly the genotypic contribution to phenogenesis and, in the spirit of (i), impute as much causal efficacy to the genotype as possible (§ 2.2).

2.1. *The reticulation of Mendelian genetics*

Meanwhile, the first experimental program that explicitly addressed the complexity of phenogenesis and phenotypic variability emerged in the Soviet Union. In Moscow, in the 1920s, an active genetics research group formed around the pioneering population geneticist, S. Chetverikov (Adams 1980). In 1922, Romashoff discovered the “Abdomen abnormalis” mutation in *Drosophila funebris* which resulted in the degeneration of abdominal stripes. There was individual variability in the mutant phenotype which Romashoff (1925) interpreted as a difference in the strength of the mutation’s effect. The manifestation of the mutation depended on environmental factors, in particular on the dryness and liquid content of food, but Romashoff could not rule out the possible influence of other genes. N. W. Timoféeff-Ressowksy studied the recessive “Radius incompletus” mutation of *D. funebris*. In mutant flies, the second longitudinal vein did not reach the end of the wing. Timoféeff (1925) created different pure lines, each homozygous for this mutation. Descendants included phenotypically normal flies. The proportion of normals was fixed for each pure line but varied between lines. External factors had little influence; the differences between the lines were apparently under the control of genotypic factors. Some lines gave a large proportion of mutants but manifested the mutation weakly; in others, the converse was also realized.

Vogt (1926) introduced two new concepts to describe these results: a mutation’s “expressivity” was the extent of its manifestation; its “penetrance” was the proportion of individuals carrying it which manifested any effect at all. In Vogt’s definitions the differences between different lines was ignored. Expressivity and penetrance became properties of the mutation (and, eventually, the allele) rather than a property of a mutation relative to a constant genetic background. Timoféeff enthusiastically endorsed the new concepts (Timoféeff-Ressovsky and Timoféeff-Ressovsky 1926). The terms were introduced into the English literature by Waddington (1938) who incorrectly attributed them to Timoféeff. Waddington’s book, along with Timoféeff’s growing prominence within Western genetics, made the terms common currency by the 1950s.

What the original results of Romaschoff and Timoféeff had shown was a *predictable complexity* in the genotype-environment interaction. Both data sets permitted the construction of NoRs though Vogt’s reinterpretation made

such a move moot. Two related aspects of that reinterpretation deserve emphasis: (i) Vogt, and especially those who used “penetrance” subsequently, ignored the *systematic* differences between pure lines; and (ii) Vogt explicitly introduced expressivity and penetrance as properties of genes (alleles) on par with, though different from, dominance. Given (i) it was now possible, as textbooks do to this day, to define penetrance as the conditional probability that a phenotype will be manifested, given a particular gene. What this ignores is that since data from different genotype backgrounds were being compounded without analysis, there was no reason to expect measured empirical frequencies to converge to a well-defined probability.

The introduction of expressivity and penetrance constituted a convoluted reticulation of the structure of Mendelian genetics by *ad hoc* extension of the concept of the gene. Besides having their standard transmission properties, genes were no longer only recessive or dominant (or displayed varying degrees of dominance); they also had degrees of expressivity and penetrance. There was no clear distinction between expressivity and dominance: expressivity is indistinguishable from the degree of dominance. The purpose that the new concepts served was to maintain a genetic etiology in the face of phenotypic plasticity induced by genotype-environment interactions. Variability in the phenotypic manifestation of a trait became a result of a gene’s expressivity and (indirectly) its penetrance.

2.2. Heritability analysis

A second development, initiated in the US, also contributed to the neglect of the complexity of genotype-environment interactions during this period. In 1918 Fisher (1918) introduced the analysis of variance which permitted the decomposition of phenotypic variability within a population into genotypic and environmental components and their interaction. Independently, Wright (1920) introduced almost equivalent methods. Wright (1921) distinguished between three genotypic components of variability of a continuous trait: (i) additive effects of alleles at all loci; (ii) effects of dominance at each locus; and (iii) the result of interaction between loci (epistasis). Though Wright had implicitly been using a concept of heritability since the 1920s in analyzing breeding options in various animals (especially guinea pigs), Lush (1943) finally explicitly defined and distinguished between “narrow” and “broad” heritability (for a history, see Bell (1977)). The former was the ratio of the component of phenotypic variance (in a population exposed to a specific range of environments) due to additive effects of alleles to the total phenotypic variance of the trait. The latter was that ratio for the total genotypic variance.

Though Fisher (1951) criticized heritability for being too simplistic a statistic for the effective analysis of breeding problems, its use spread (see Lerner (1950)). The problem lies in the interpretation of the statistic. Conventionally, following Lush (1943), broad heritability is interpreted as the fraction of the phenotypic variance that is due to genotypic variation and the rest is attributed to environmental variation.⁵ However, this interpretation is valid only if the genotype-environment interaction is the same for all genotypes and all environments. This is where the NoR enters the story. The conventional interpretation requires that all NoRs be parallel to each other, as Hogben (1933) had implicitly realized, but was only made explicit by Layzer (1974) and Lewontin (1974).⁶ Experimental data on a wide variety of species almost never gave rise to parallel reaction norms though, for human populations, it has often been claimed that genotype-environment interactions are minimal (Plomin 1994). However, these interactions are notoriously hard to detect (Wahlsten 1990).

3. The Soviet espousal

In sharp contrast to the West, the NoR emerged as a potent conceptual tool in Soviet genetics in the 1920s. There it was deployed primarily to deflate claims of the inheritance of acquired characteristics (see Blacher 1982). In 1926, Dobzhansky argued that what was inherited was not a trait but an NOR. For the “Abdomen abnormalis” mutation of *Drosophila funebris* Dobzhansky pointed out that the mutant phenotype was not manifested for generations if the food was dry. However, it reappeared if the offspring were supplied with moist food. He argued that this and other such examples showed that, even when environmental factors induced a trait, an unchanged NoR was inherited. Dobzhansky’s interpretation made the NoR a *Mendelian* unit of inheritance.

3.1. *Stabilizing selection*

Soviet geneticists sharply distinguished between adaptive and non-adaptive NoRs. The former were incorporated into models of “organic selection”, originally proposed by Baldwin (1896), Osborn (1897) and Lloyd Morgan (1900) but ignored subsequently (Huxley 1942: p. 524), and then independently formulated in the Soviet Union by E. J. Lukin and others around 1936 (Gause 1947). In Gause’s (1947) exposition, organic selection was based on four principles:

- (1) Organisms frequently respond to environmental changes by adaptive phenotypic modifications.
- (2) Similar adaptive characters may be genotypically fixed in races normally living in a corresponding environments.

(3) It is proved that conversion of modifications into mutations is not possible. (4) Hence modifications can only be *substituted* by coincident mutations, if the latter are associated with some advantages in the process of natural selection (1947: p. 22).

The most influential version of this theory was due to Schmalhausen (1986 [1949]) who referred to organic selection as “stabilizing selection.”⁷ Stabilization consisted of the replacement of an adaptive phenotypic response by a phenotypically identical genotype response, ensuring the phenotype’s transmission to future generations.

Assuming that the NoR was “hereditary”, Schmalhausen distinguished “adaptive norms” from “morphoses”:

every genotype is characterized by its own specific ‘norm of reaction’, which includes adaptive modifications of the organism to different environments. When expression of the adaptive modifications is so complete that it transforms the entire organization, the genotype is said to possess adaptive norms, which are particular expressions of the general norm of reaction ... Nonadaptive modifications are of an entirely different character. They arise as new reactions which have not yet attained a historical basis. Either the organism encounters new environmental factors with which it never had to deal before or its norm of reaction is changed (disturbed) as a result of mutation (pp. 7–8).

A mutation was a “change in ... reaction norm” (p. 10). Expressivity and penetrance were properties of mutations. Schmalhausen explicitly restricted the scope of the latter concept to “a group of mutants of similar origin” (p. 16) unlike Vogt.

Once distinguished, adaptive norms moved to center stage. They were buffered against environmental changes. Using the capacity for growth in the shrimp, *Artemia salina*, and the fish, *Periophthalmus variabilis*, as examples, Schmalhausen argued: “in the process of evolution there have arisen definite optimum norms of growth which are determined by the ecologic [sic] position of the organism, especially by its relationships with other organisms. Modifications are possible thus only within the relative narrow limits of this norm. Therefore, it is not the *modification itself* but its confinement within definite limits that should be regarded as an *adaptation*” (pp. 184–185). Even an adaptive

change of a particular part or a trait of an organism corresponding to a change in the external environment disturbs the harmony of the parts. The selective value of any beneficial variation in the mode of reaction is thus reduced. Accordingly, the capacity for adaptive response is supplemented by other reactions. These are certain mutual interrelationships which

introduce some harmony in the changes experienced by the organism as a whole (p. 193).

Since adaptive norms were *ipso facto* selected for, their persistence (unlike that of morphoses) would be ensured both by having a genotype basis and by selective spread in future generations.

Moreover, “[p]rocesses of autoregulation restrict the adaptive normal reactivity within definite limits” (p. 194). The violation of these limits resulted in morphoses or in new pre-adapted norms. Schmalhausen concluded:

it is possible to shift the threshold levels of reactivity both by individual variations or mutations and their combinations, and by natural selection which produces different hereditary types.

Such reactions are canalized into the narrow channel of a more specific norm which is adapted to definite conditions of the external environment.⁸ . . . Moreover, characteristic and equally adaptive norms may develop for different environmental conditions” (p. 195).

Gause (e.g., 1941, 1942, 1947) developed similar ideas but emphasized that “the possibilities of genotypic response to changed environment are much wider than phenotypic ones. Hence with extreme alteration of conditions direct selection of genoadaptations takes place, but when the environment changes less directly the work of organic selection can be observed with certainty” (1947: pp. 32–33). Primarily using several *Paramecium* species, Gause established an experimental program to study the effects of organic selection.

Meanwhile, apparently in ignorance of the Soviet work, Waddington (1940a, b, 1942) developed similar ideas through in a more rudimentary form. Waddington’s (1940a) proposal that development was “canalized” was identical to Schmalhausen’s claim of “autoregulation” of NoRs. However, Waddington (1942), unlike Schmalhausen, placed his ideas centrally within ongoing discussions in Western genetics by pointing out that the evolution of canalization of traits seemed similar to the possible evolution of dominance. If dominance was an evolved phenomenon, as Fisher held against Wright (who argued that it arose from ordinary enzyme kinetics) then the evolution of dominance provided a model for the evolution of a buffered phenotype. Waddington thought that this argument could be used to subsume other forms of buffering including canalization. In an attempted synthesis of Schmalhausen’s theory of stabilizing selection and Waddington’s ideas on canalization with conventional population genetics, Lerner (1954) developed a more general model of “genetic homeostasis”.

3.2. *Adaptive norms*

If Schmalhausen had already brought adaptive norms to center stage, it remained for Dobzhansky to direct attention almost exclusively to them. Dobzhansky moved from the Soviet Union to the US in 1927 (Coe 1994). One consequence of this move was the repatriation of the NoR to the West. In 1937, in *Genetics and the Origin of Species*, which was Dobzhansky's version of what came to be called the "evolutionary synthesis", he introduced the NoR to the Anglophone world. That account reflected the consensus view from the Soviet Union: "one must constantly keep in mind the elementary consideration which is all too frequently lost sight of in the writings of some biologists; what is inherited in a living being is not this or that morphological character, but a definite norm of reaction to environmental stimuli ... [A] mutation changes the norm of reaction" (1937: p. 169).

On occasion, Dobzhansky used the NoR in this general sense that included both adaptive norms and morphoses. In 1950, with him as Sinnott and Dunn's co-author of the fourth edition of *Principles of Genetics*, "reaction range" was used to refer to NoRs (Sinnott, Dunn and Dobzhansky 1950: p. 22). Phenotypic variability in the reaction range showed how phenogenesis depended on heredity-environment interactions. "Environmental plasticity" was emphasized; it could vary between traits in the same organism (p. 22) and between different environmental ranges (p. 23). The reaction range could only be incompletely known since no genotype could be experimentally exposed to all possible environments. Hence, any trait could be modified beyond known values by appropriate environmental intervention (p. 23).

Dobzhansky developed these themes in his 1955 book, *Evolution, Genetics, and Man*: "the norm of reaction of a genotype is at best only incompletely known ... The existing variety of environments is immense and new environments are constantly produced. Invention of a new drug, a new diet, a new type of housing, a new educational system, a new political regime introduces new environments (1955a: p. 75). There was no sharp distinction between hereditary and non-hereditary diseases (p. 76).⁹ Schmalhausen's sharp distinction between adaptive norms and morphoses had begun to fade: except in rare cases, a radical change of environment could well make a morphosis adaptive. The rare cases were those in which a morphosis was a result of internal disharmony during phenogenesis. But Dobzhansky, unlike Schmalhausen, and like a true geneticist from that period, generally ignored embryology.

For Dobzhansky, by 1955, the origin of the adaptive norm, but now that of an *entire population*, had become a basic problem of population genetics. He redefined "adaptive norm" and, therefore, the NoR as a population-level entity (Dobzhansky 1955b). Gathering data on adaptive norms was already an

important part of Dobzhansky's program to elucidate the genetics of natural populations of *Drosophila*. Dobzhansky and Spassky (1963) gave another new twist to the definition of an adaptive norm:

Natural populations of *Drosophila*, man, and presumably of all sexual, diploid, and outbreeding organisms contain a multitude of genotypes. A majority of these genotypes make their carriers tolerably well adapted to survive and to reproduce in environments which the population frequently encounters in its natural habitats. The array of such genotypes constitutes the adaptive norm of the species or population. Some genotypes yield, however, low fitness in the habitual environments; these compose the genetic load of a population. And finally, some genotypes confer a fitness distinctly above the mean of the adaptive norm; these are the genetic elite of the population (p. 1467).

These definitions incorporate three innovations: (i) the adaptive norm now consisted of the set of genotypes itself rather than phenotypic manifestations of those genotypes. Dobzhansky thus accommodated the Soviet articulation of the NoR to the genocentrism of the West; (ii) the genetic elite did not constitute the adaptive norm in spite of having the highest fitness. The reason for this was that Dobzhansky and Spassky found that "an intensive study . . . revealed that they behave as 'environmental narrow specialists'; they produce superior homozygotes only in a certain environment, and when the environment is altered turn out to act as subvitals which reduce the viability more or less strongly" (p. 1482). Adaptive norms consist of generalists; and (iii) the definition of the genetic load was radically different from the standard one due to Crow (1958): the proportion by which the population fitness is decreased from that of an optimum genotype. Completely misunderstanding Crow's point, Dobzhansky and Spassky argued that no such optimum exists in nature except, possibly, as "a single individual in a single environment" (p. 1482). They proposed a categorization of all genotypes of a population (p. 1483):

1. Adaptive Norm – within two standard deviations of the mean;
2. Genetic Load (or Genetic Burden) – more than two standard deviations below the mean;
3. Genetic Elite – more than two standard deviations above the mean.¹⁰

4. Concluding remarks

Dobzhansky's advocacy ensured the NoR a permanent place in Western genetics. In the Soviet Union, with Lysenko's complete takeover of studies

of heredity in 1948, genetics was suppressed and the vibrant tradition of the 1920s came to an end. Schmalhausen, for example, was removed from his professorship and forced to return to purely embryological work. Dobzhansky used the NoR to emphasize phenotypic plasticity, a result of the complexity of the gene-environment interactions leading to phenogenesis. During the politically charged debates over race and IQ in the early 1970s, Dobzhansky's student, Lewontin (e.g.: 1974) drew the same lesson from the NoR and very effectively deployed the variability of the NoRs to deflate hereditarian fantasies of the genetic etiology of intelligence and other complex phenotypes.

However, Hogben's priority in the use of this argument should not be forgotten. It should also be acknowledged that the NoR is but one conceptual tool that can be used to underscore the complexity of phenogenesis. Haldane's algebraic arguments provide another. The incorporation of the NoR inside the tradition of genetics reflects historical contingency as much as the phenogenic complexity it exemplifies, the contingent factor being the dual career of Dobzhansky bridging the gulf between the golden era of Soviet genetics and, after 1930, the genocentric biology of the West. Moreover, the NoR – or Haldane's algebraic arguments – do not capture a critical aspect of phenogenesis, that it is itself historically contingent, depending not only on interactions between genotype and environment, but on a temporally precise sequence of those interactions subject to the whims of environmental stochasticity.

Finally, though claims of this sort are notoriously difficult to establish fully, the consonance between social ideology and the dominant views of genetics in the Soviet Union and the West should not pass completely unnoticed. The Soviet interpretation of the NoR, which was close to Woltereck's original one, made the NoR a heritable factor. It is not accidental that it found popularity in a communist state with an official scientific and socio-economic ideology, dialectical materialism, that emphasized environmental influences on individuals.¹¹ Dialectical materialism also promoted an ontology of processes over entities that was in cognitive dissonance with the Western ideology of genes as almost infinitely stable entities which determined traits. Most Soviet geneticists, until their suppression during the Lysenko era, attempted to find an interpretation of genetics that was less static and mechanistic than in the West. The NoR, by emphasizing the inheritance only of a capacity subject to environmental modulation helped provide such an interpretation of Mendelism.

The analogous argument for Western genetics is slightly harder to make only because an official metaphysical ideology is, characteristically, not explicitly propounded in capitalist democracies. However, it is hard not to recognize a concordance between social patterns of the inheritance of prop-

erty on the one hand and assumptions about the immutability of genes the causal efficacy of genes on the other. This is not to suggest a definite causal relationship from social ideology to intellectual programs. It is merely to assert that the same societies that endorsed eugenics as a social measure were also receptive to other forms of genocentrism.

Notes

¹ For discussions of these issues over many years, thanks are due to Raphael Falk and Richard C. Lewontin. For comments on an earlier versions of this analysis, thanks are due to Thom DeWitt, Rees Kassen and Sam Scheiner. For hospitality and support during the period when this paper was written, thanks are due to the Max-Planck-Institut für Wissenschaftsgeschichte in Berlin. It is a pleasure to dedicate this paper to Dick Lewontin.

² For a more detailed analysis of Woltereck's paper, see Falk (1999).

³ "The genotype of a quantitative trait . . . is the inherited reaction norm".

⁴ Throughout this paper italics within quotations are faithful to the original.

⁵ In contrast to broad heritability, which is the relevant statistic in this context, narrow heritability – which can be accurately estimated for experimental populations – has an important instrumental value. It shows the extent to which selection for a trait can change its frequency in that population within the range of experimental environmental treatments. This is important for breeders. (See Sarkar (1998) for a detailed critique of heritability analysis.)

⁶ See also Moran (1973), Feldman and Lewontin (1975), and Jacquard (1983).

⁷ Schmalhausen also used "stabilizing selection" to mean (i) centripetal selection and, especially, (ii) selection for internal regulatory mechanisms as Simpson (1949) pointed out in his review of the book. The latter use of "stabilization" will be implicit in some of the quotations from the book that follow in the text.

⁸ The term "canalized" is due to the translator (Isadore Dordick) and was not used by Schmalhausen who was, at this point, unaware of Waddington's (1942) work (see below in the text). Schmalhausen would presumably have used "stabilized" (Gilbert 1994).

⁹ As Falk (1999) has perceptively noted, from "such a view, hereditary defects and diseases become at most socially meaningful terms, not biologically determined ones".

¹⁰ "Genetic burden" was necessary only if "genetic load" came to be established in use as defined by Crow.

¹¹ Engels's *Dialectics of Nature* was published for the first time, simultaneously in German and Russian, in 1925 beginning the process of codification of this ideology in the conventional version of "dialectical materialism".

References

- Adams, M. B.: 1980, 'Sergei Chetverikov, the Kol'tsov Institute, and the Evolutionary Synthesis', in E. Mayr and W. B. Provine (eds.), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Harvard University Press, Cambridge, MA, pp. 242–278.
- Baldwin, J. M.: 1896, 'A New Factor in Evolution', *American Naturalist* **30**, 441–451.
- Baur, E.: 1922, *Einführung in die experimentelle Vererbungslehre*, Gebrüder Borntraeger, Berlin.

- Bell, A. E.: 1977, 'Heritability in Retrospect', *Journal of Heredity* **68**, 297–300.
- Blacher, L. I.: 1982, *The Problem of the Inheritance of Acquired Characteristics*, Amerind Publishing Co., New Delhi.
- Coe, S. D.: 1994, 'Theodosius Dobzhansky: A Family Story', in M. B. Adams (ed.), *The Evolution of Theodosius Dobzhansky: Essays on His Life and Thought in Russia and America*, Princeton University Press, Princeton, pp. 13–28.
- Crow, J. F.: 1958, 'Some Possibilities for Measuring Selection Intensities in Man', *Human Biology* **30**, 1–13.
- de Vries, H.: 1901–1903, *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung der Arten in Pflanzenreich*, 2 Vols, Veit u. Co., Leipzig.
- Dobzhansky, T.: 1955a, *Evolution, Genetics, and Man*, John Wiley and Sons, New York.
- Dobzhansky, T.: 1955b, 'A Review of Some Fundamental Concepts and Problems of Population Genetics', *Cold Spring Harbor Symposia on Quantitative Biology* **20**, 1–15.
- Dobzhansky, T. and Spassky, B.: 1963, 'Genetics of Natural Populations. XXXIV. Adaptive Norm, Genetic Load and Genetic Elite in *Drosophila pseudoobscura*', *Genetics* **48**, 1467–1485.
- Driver, E. C.: 1931, 'Temperature and Gene Expression in *Drosophila*', *Journal of Experimental Zoology* **59**, 1–28.
- Falk, R.: 1999, 'Can the Norm of Reaction Save the Gene Concept?', in R. Singh, C. Krimbas, D. B. Paul and J. Beatty (eds.), *Thinking About Evolution: Historical, Philosophical and Political Perspectives*, Cambridge University Press, New York, pp.
- Feldman, M. W. and Lewontin, R. C.: 1975, 'The Heritability Hang-up', *Science* **190**, 1163–1168.
- Fisher, R. A.: 1918, 'The Correlation between Relatives on the Supposition of Mendelian Inheritance', *Transactions of the Royal Society of Edinburgh* **52**, 399–433.
- Gause, G. F.: 1941, 'The Effect of Natural Selection in the Acclimatization of *Euplotes* to Different Salinities of the Medium', *Journal of Experimental Zoology* **87**, 85–100.
- Gause, G. F.: 1942, 'The Relation of Adaptability to Adaptation', *Quarterly Review of Biology* **17**, 99–114.
- Gause, G. F.: 1947, 'Problems of Evolution', *Transaction of the Connecticut Academy of Sciences* **37**, 17–68.
- Gilbert, S.: 1994, 'Dobzhansky, Waddington, and Schmalhausen: Embryology and the Modern Synthesis', in M. B. Adams (ed.), *The Evolution of Theodosius Dobzhansky*, Princeton University Press, Princeton, pp. 143–154.
- Goldschmidt, R.: 1920, *Mechanismus und Physiologie der Geschlechtsbestimmung*, Gebrüder Borntraeger, Berlin.
- Goldschmidt, R.: 1928, *Einführung in Die Vererbungswissenschaft*, 5th ed., Julius Springer, Berlin.
- Haldane, J. B. S.: 1936, 'Some Principles of Causal Analysis in Genetics', *Erkenntnis* **6**, 346–357.
- Haldane, J. B. S.: 1946, 'The Interaction of Nature and Nurture', *Annals of Eugenics* **13**, 197–205.
- Hersh, A. H.: 1930, 'The Facet-Temperature Relation in the Bar Series of *Drosophila*', *Journal of Experimental Zoology* **57**, 283–306.
- Hersh, A. H.: 1934, 'On Mendelian Dominance and the Serial Order of Phenotypic Effects in the Bar Series of *Drosophila Melanogaster*', *American Naturalist* **68**, 186–189.
- Hogben, L.: 1933, *Nature and Nurture*, W. W. Norton, New York.
- Huxley, J. S.: 1942, *Evolution: The Modern Synthesis*, George Allen & Unwin, London.
- Jacquard, A.: 1983, 'Heritability: One Word, Three Concepts', *Biometrics* **39**, 465–477.

- Johannsen, W.: 1909, *Elemente der exacten Erblchkeitslehre*, Gustav Fischer, Jena.
- Johannsen, W.: 1911, 'The Genotype Conception of Heredity', *American Naturalist* **45**, 129–159.
- Krafka, J.: 1920, 'The Effect of Temperature Upon Facet Number in the Bar-eyed Mutant of *Drosophila*', *Journal of General Physiology* **2**, 409–464.
- Layzer, D.: 1974, 'Heritability Analyses of IQ Scores: Science or Numerology?' *Science* **183**, 1259–1266.
- Lerner, I. M.: 1950, *Population Genetics and Animal Improvement*, Cambridge University Press, Cambridge.
- Lerner, I. M.: 1954, *Genetic Homeostasis*, Oliver and Boyd, Edinburgh.
- Lewontin, R. C.: 1974, 'The Analysis of Variance and the Analysis of Causes', *American Journal of Human Genetics* **26**, 400–411.
- Lloyd, Morgan, C.: 1900, *Animal Behavior*, E. Arnold, London.
- Lush, J. L.: 1943, *Animal Breeding Plans*, 2nd ed., Collegiate Press, Ames.
- Moran, P. A. P.: 1973, 'A Note on Heritability and the Correlation between Relatives', *Annals of Human Genetics* **37**, 217.
- Nilsson-Ehle, H.: 1914, 'Vilka erfarenheter hava hittills vunnits rörande möjligheten av växters acklimatisering', *Kgl. Landbruks-Akad. Handl. Tidskr* **53**, 537–572.
- Osborn, H. F.: 1897, 'The Limits of Organic Selection', *American Naturalist* **31**, 944–951.
- Plomin, R.: 1994, *Genetics and Experience: The Interplay Between Nature and Nurture*, Sage Publications, Thousand Oaks.
- Provine, W. B.: 1971, *The Origins of Theoretical Population Genetics*, University of Chicago Press, Chicago.
- Romaschoff, D. D.: 1925, 'Über die Variabilität in der Manifestierung eines erblichen Merkmales (Abdomen abnormalis) bei *Drosophila funebris* F', *Journal für Psychologie und Neurologie* **31**, 323–325.
- Sapp, J.: 1987, *Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics*, Oxford University Press, New York.
- Sarkar, S.: 1998, *Genetics and Reductionism*, Cambridge University Press, New York.
- Schmalhausen, I. I.: 1986 [1949], *Factors of Evolution: The Theory of Stabilizing Selection*, University of Chicago Press, Chicago.
- Simpson, G. G.: 1949, 'Factors of Evolution: A Review', *Journal of Heredity* **40**, 322–324.
- Timoféeff-Ressovsky, H. A. and Timoféeff-Ressovsky, N. W.: 1926, 'Über das phänotypische Manifestation des Genotypes. II. Über idio-somatische Variationsgruppen bei *Drosophila funebris*', *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen* **108**, 146–170.
- Timoféeff-Ressowsky, N. W.: 1925, 'Über den Einfluss des Genotypus auf das phänotypen Auftreten eines einzelnes Gens', *Journal für Psychologie und Neurologie* **31**, 305–310.
- Vogt, O.: 1926, 'Psychiatrisch wichtige Tatsachen der zoologisch-botanischen Systematik', *Journal für Psychologie und Neurologie* **101**, 805–832.
- Waddington, C. H.: 1938, *An Introduction to Modern Genetics*, George Allen & Unwin Ltd., London.
- Waddington, C. H.: 1940a, 'The Genetic Control of Wing Development in *Drosophila*', *Journal of Genetics* **41**, 75–139.
- Waddington, C. H.: 1940b, *Organisers and Genes*, Cambridge University Press, Cambridge, UK.
- Waddington, C. H.: 1942, 'Canalization of Development and the Inheritance of Acquired Characters', *Nature* **150**, 563–565.

- Wahlsten, D.: 1990, 'Insensitivity of the Analysis of Variance to Heredity-Environment Interaction', *Behavioral and Brain Sciences* **13**, 109–120.
- Woltereck, R.: 1909, 'Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphnien', *Verhandlungen der deutschen zoologischen Gesellschaft* **19**, 110–173.
- Wright, S.: 1920, 'The Relative Importance of Heredity and Environment in Determining the Piebald Pattern of Guinea Pigs', *Proceedings of the National Academy of Sciences (USA)* **6**, 320–332.
- Wright, S.: 1921, 'Systems of Mating', *Genetics* **6**, 111–178.