Woltereck's Genotype

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Summary

The reaction norm, originally introduced by Richard Woltereck in 1909, describes the range of phenotypes available to a single genotype under different environments. It is a foundational concept in genetics and evolutionary thought. At its inception, it represented a counterpoint to a hereditarian Mendelism championed by Wilhelm Johannsen, though both authors ultimately agreed that the reaction norm was essentially identical to the “genotype” term introduced earlier the same year by Johannsen. Woltereck both literally and figuratively wrote “Genotypus = Reaktionsnorm”. However, some have argued that Woltereck’s interpretation of the reaction norm was incomplete up to the point of Johannsen’s commentary on it. Here, I demonstrate that the reaction norm constituted a direct and intentional challenge to Johannsen’s original notion of fixed differences between types, and present new translations of relevant texts from both Johannsen and Woltereck. I conclude that both authors’ acceptance of the equivalence between genotypes and reaction norms constituted a redefinition of the genotype by Woltereck that was ultimately accepted (with apparent poor grace) by Johannsen.

Introduction

All organisms respond to routine environmental variation with alterations of form, physiology, or behavior. These alterations can occur without altering the underlying heritable material, suggesting a separation between heritable and non-heritable biological variation. This separation appears no later than Goethe’s 1790 essay on metamorphosis (Goethe 1989), and probably earlier. Goethe made a distinction between *typus* (the implicate biological rules of an organism) and outward form (Steiner 1988). This distinction prefigures Weismann’s later categories of germ-plasm (material bearing heritable information) and soma (non-heritable form) (Weismann 1893). It is now familiar to biologists in the terms “genotype” and “phenotype”. Goethe (but not all later authors) understood intuitively that the *typus* encoded not only the fixity of specific forms, but also rules for how those forms might respond to the environment:

“...a plant growing in low-lying, damp spots will even develop smoother and less refined leaves than it will when transplanted to higher areas, where it will produce rough, hairy, more finely detailed leaves...” (§24, *Metamorphosis of Plants*)

Science required over a century to catch up to the poet in this case: Quetelet, De Vries, Johannsen, and Woltereck all referred to “types”, but only the last seems to have fully appreciated their protean nature.

Today, we use the term “phenotypic plasticity” as a name for this observed variability in forms in response to environmental variation (West-Eberhard 1989).

Reaction norms in the present day.

As discussed later in this essay, Richard Woltereck introduced the reaction norm as a concept in 1909, explaining a series of experiments that revealed different responses of different cultured *Daphnia* lines to the same environmental stimuli (Woltereck 1909).

Over the course of the next century, this foundational idea percolated throughout all of genetics. It was famously employed by Theodosius Dobzhansky and his student Richard Lewontin, the first an architect of the Modern Synthesis and the second a pioneer of population genetics and the molecular revolution (Lewontin 1974; Sarkar 1999; Pigliucci 2001). The reaction norm is now known as the genotype-by-environment interaction confounding present-day quantitative geneticists.

An entirely separate branch of work flourished in the Soviet Union, where the reaction norm formed the empirical basis upon which Lysenkoism was ultimately perpetrated (Amasino 2004). Notably, Dobzhansky was educated in the pre-Lysenko Soviet genetics milieu, where the norm of reaction found ideological favor as a counter to “capitalist” hereditarianism (Sarkar 1999; Gordin 2012), before he ultimately emigrated to the USA.

The mutationists and the genotype: De Vries and Johannsen.

In his magisterial *Mutation Theory* (De Vries, Hugo 1909), originally published in German in 1901, De Vries laid out controversial but compelling arguments against the action of continuous selection in Darwinian evolution. He argues instead that selection could not act on most so-called “fluctuating variation” of organisms, because most such variation was not heritable. Instead, he argued that for “evolution by jerks”, occasioned by discrete but heritable “mutations” of large effect. (These could in turn be acted upon by selection.) De Vries placed strong emphasis on this distinction between the discrete mutational variants that discriminated his “elementary species” and the continuous nature of this fluctuating variation which was, he argued, largely due to environmental effects. He and his followers were variously called “mutationists”, “Mendelists”, or “Mendelian-mutationists” (Stoltzfus and Cable 2014), recognizing their inspiration from Mendel (whose work De Vries re-discovered, along with Tschermak and Correns).

De Vries attributes the success of artificial selection to a combination of forces. These include isolation of unitary types, accidental hybridization, and parental effects. He argued that the well-known phenomenon of regression was merely a reversion to type within each elementary species, and extensively quotes plant breeders to the effect that this reversion is usually total in the absence of perpetual selection. In other words, the elementary species is responsive to selection only so far as environmental effects allow it to be, while its innate qualities remain

unchanged in the absence of spontaneous mutation. This he contrasts directly to the view of selectionists such as Wallace, who emphasized the perpetual and continuous nature of evolutionary change on all scales of variation. De Vries specifically noted the success of the Swedish plant breeder Nilsson in discovering that apparently uniform batches of cereal seed in fact contained complex mixtures, from which true-breeding constant types could be isolated (pp. 114-117).

Johannsen carried forward de Vries' work by focusing on Nilsson's isolation of elementary species and using it to exhaustively examine selection and heredity in plants. He repeated this isolation of species or "types" and reports a confirmation that isolated self-fertilized "pure lines" of this kind are unresponsive to selection in properly controlled experiments (Johannsen 1903), which I rendered as:

"...attempts to alter the correlation between length and breadth of beans through selection were unsuccessful within the pure lines, while it was easy to isolate different types, e.g. short and broad forms, from the initially quite homogeneous-appearing population." (Press 2020c)

In other words, selection works in populations because you isolate types, but in pure lines there is no *heritable* variation to select on (De Vries and Johannsen do not deny that selection can still effect change in pure lines; it is merely that this selection is on more transient variations arising from environmental or parental effects).

Johannsen was more or less a disciple of De Vries. He writes (p. 64): *"This work, more nearly examined, stands in full agreement with the basic thoughts in the great, more often named works of De Vries..."* (Press 2020c).

As I will discuss later, Johannsen went on to expand this work into a book-length treatment of inheritance along similar lines (Johannsen 1909), but by far his best-known publication (which is also nearly his only publication available in English) was "The Genotype Conception of Heredity" (Johannsen 1911), a 1911 paper read to the American Society of Naturalists. This paper also ends with a recommendation of *The Mutation Theory*. The reception of Johannsen's work was quite positive, especially in the United States (the probable reason for his invitation to give this lecture). However, he made enemies of the biometrical school (especially Pearson), who not only strongly disagreed with his ideas but also pointed out substantive inconsistencies in his data. Specifically, they found through reanalysis that his data *did* in fact support the efficacy of selection (Provine 2001).

In other words, Johannsen wrote this paper from his perspective as a mutationist (Allen 1969). This is however mentioned only in passing in more recent commentary, and De Vries comes up not at all (Falk 2014). His divergence from De Vries was principally in his focus on pure lines, his strong emphasis on empirical experiments, and his adaptation of the genotype concept from Weismann's germ-plasm (among other sources, including De Vries' and Goethe's *typus* mentioned above). When he writes about the genotype, or "genotypical differences", he is

talking about elementary types and the mutations that distinguish them, rather than the present-day concepts of DNA sequences and genetic variation. . His simultaneously introduced idea of “phenotype” has stayed more constant, and appears to have been more or less immediately and universally agreed-upon by others in its usage and meaning (Keilhack 1909; Press 2020a).

By 1909, Johannsen had worked up these observations with others into his *magnum opus*, the long book of lectures *Elemente der exakten Erblchkeitslehre*. This is the first known instance of Johannsen using the terms “gene”, “genotype”, and “phenotype” (from the eighth lecture on, these terms are used continuously) (Roll-Hansen 2009; Press 2020e), though he must have been speaking and writing using the terms for some time previously. Much of his work is in Danish and difficult to access; however, a 1905 Danish version of his textbook does not appear to contain any terms that are cognates of “gene” or “genotype”, and omits the etymological discussion of Darwin’s term “pangene” that is present in the 1909 German edition (Johannsen 1905). He instead seems to liberally use the word “Anlæg”, a cognate of the rather generic German term “Anlage” common at the time.

Johannsen introduces the idea of genes as part of his career-long critique of biometry, by showing that the colloquial usage of the word “type” by breeders and statistical workers (especially Quetelet) is imprecise and can lead to positively wrong conclusions, as they are concerned solely with an apparent type derived from physical measurement. This “apparent type” he named the phenotype, and there were instead hereditary units (which he called by the new name of “genes”) that actually determined the hereditary type. While avoiding using the noun form “genotype”, he wrote that the distinctions between his pure lines were “genotypical”, and that these were the differences that led to phenotypic distinctions (and thus selection).

Johannsen concludes with the criticism of the biometricians that they have only shifted the phenotype by selection, while remaining ignorant of the genotype, which may not have changed.

This interpretation leads inexorably to the conclusion that the genotype is the more important thing for heredity research, though he generally avoided using the noun form “genotype” (not all his followers were so punctilious, (Churchill 1974)). A curious feature of his paper titled “The Genotype Conception of Heredity” is that he states that it is too speculative to speak of “genotypes”.

Woltereck and the reaction norm.

Richard Woltereck, born 1877, was a student of August Weismann, and was strongly influenced by his mentor’s germ theory and selectionism. After a distinguished early career in invertebrate embryology, he eventually became the director of a new laboratory in 1905 in Lunz, Austria (Harwood 1996). While there, he directed a long series of experiments on various *Daphnia*

species, culminating in his 1909 paper delivered to the German Zoological Society introducing the reaction norm idea (Woltereck 1909).

In brief, Woltereck adapted various types of *Daphnia* as Johannsenian pure lines and investigated several obvious phenotypes, including ecologically relevant ones such as cyclomorphosis, under various environments. He did this by culturing parthenogenetic lines; this was an advantage of *Daphnia*, that they could be raised in much greater numbers than plants, had much shorter generation times, and could be induced to parthenogenesis. (Woltereck discusses the advantages of his system over plants in an appendix to his paper). Briefly, Woltereck found that different lines generally had overlapping (“transgressive”) phenotypes across the range of environments, and that this entire range frequently contained a large amount of information about possible phenotypes of a line.

Woltereck repeatedly refers to differences between his lines as *genotypisch*, meaning genotypical (see for example point 1 of his Research Plan in the article (Press 2020b)). He writes: “*The ‘genotype’ (the genotypical foundation) of a quantitative trait is its heritable reaction norm.*”

He relies heavily on Johannsen’s distinction between genotype and phenotype, though he is critical of Johannsen’s presentation of the ideas, and insists that a new term, “reaction norm”, is a better concept for describing the phenotypic potential of an organism than “genotype”. This is specifically because the genotype and the environment do not have cleanly separable influences on phenotype, as Johannsen insisted at some points. (It is notable that Johannsen had previously been criticized for inconsistency and a lack of clarity on his view of the interaction between biotype and environment, regarding specifically the “*Typus*” which later evolved into “*Genotypus*” (Yule 1903).)

In a review of the paper published shortly thereafter, Ludwig Keilhack briefly summarized the Johannsen’s propositions as follows (Keilhack 1909; Press 2020a):

“1. The specific structure that these elementary types (“biotypes”) inherit in their germplasm (“genotypical basis” or “genotype”) are fixed quantities, that over the course of generations do not vary in the least. Change of these structures can only be achieved through spontaneous mutations.

2. The direction of these mutations has no relation to the environmental circumstances. For Johannsen, there is no continuous evolution and no definitive influence of the environment.

[...]

The question now stands whether the controversial propositions of Johannsen also hold for this reaction norm.”

In other words, while the equivalence between genotype and reaction norm is explicit and obvious from Woltereck’s writing, there is a question of whether phenotypic differences between

genotypes are fixed, and whether there is any environmental dependence of their behavior. He further summarizes Woltereck's conclusions on these two points:

"...there also exist partial differences of the reaction norm, which surely indicate the occurrence of partial alterations of the reaction norm (the genotype), whereas for Johannsen only saltational and therefore total modifications of the genotype play any role. Additionally, Woltereck's phenotype curves clearly announce "environmental dependence" of these quantitative racial differences, again in contrast to Johannsen."

In other words, Johannsen's genotype concept is flawed or incomplete in his view. One could reasonably argue with this portrayal of Johannsen's position (as Johannsen did, in fact), but reaction norms at the least require a substantive reconsideration of the genotype concept. Keilhack concludes his review rather caustically with a quotation from Johannsen's book:

" 'Overall, when a really exact analysis can be carried through, a genotypical invariance is evident, which is not comfortable with Weismannian speculations regarding determinants.' "

Johannsen's pivot

In a footnote of a 1911 paper (Woltereck 1911), Woltereck wrote:

*"This term of mine from 1909 for the inheritance of variability in a character (see page 148 of the original) was discussed by Johannsen (loc. cit.) and set up as parallel to his famous conception of the heritable ``genotype"...I considered it important that **Johannsen accepted this parallel** [my emphasis]." (Press 2020d)*

Johannsen neatly folded the reaction norm into his notion of genotype following Woltereck's work; as suggested by Yule (Yule 1903), he may really have been somewhat ambivalent on the question of fixity or invariance of the type and then the genotype (his strong statements otherwise notwithstanding). Certainly, by the time of his famous 1911 publication he writes:

"The very appropriate German term "Reaktionsnorm" used by Woltereck is, as may be seen, nearly synonymous with "genotype," in so far as the "Reaktionsnorm" is the sum total of the potentialities of the zygotes in question... The "Reaktionsnorm" emphasizes the diversity and still the unity in the behavior of the individual organism; certainly, the particular organism is a whole, and its multiple varying reactions are determined by its "genotype" interfering with the totality of all incident factors, may it be external or internal. Thence the notion "Reaktionsnorm" is fully compatible with the genotype-conception."

Responding specifically to Woltereck:

"Woltereck is within his right when asserting that we consider different genotypes as having constant differences...but Woltereck, admitting no constancy in the differences, tries to

demonstrate that our view must be fallacious...But when Woltereck thinks that these facts are inconsistent with the existence of constant differences between the genotypes, he shows himself to have totally misunderstood the question!"

He goes on to declare that such heritably encoded reaction norms are well known phenomenologically to e.g. plant breeders, and that what he (Johannsen) means by "constancy" is instead consistent differences between genotypes within environments. Whatever his original meaning, the number of workers who appear to have interpreted Johannsen just as Woltereck did argues for, at best, the incoherence of the original presentation. These other workers included Yule, who settled upon this interpretation deliberately after rejecting others as incoherent in context (Yule 1903):

*"...the germ-plasm structure (or whatever we choose to term the character of the germ cell that determines the character of the soma) is unalterable that **in a pure line all the variations are consequently purely somatic and therefore non-heritable**...I have assumed that the writer means an unalterable germinal structure, as **it is only on such an assumption that the conclusions seem to follow**."* [my emphasis]

It was apparently in response to criticisms such as Yule's that he devotes much of the eighth chapter in his 1909 *Erblichkeitslehre* to a discussion of the "Typus"/"type", resulting in his adoption of the "Genotypus"/"genotype", referring specifically to the unobservable entities he names "genes" in the same chapter ((Johannsen 1909), Lecture 8, translation in (Press 2020e)).

However, the new terminology is not considered to have clarified matters much (Roll-Hansen 2014). One commentator wrote: "It is not altogether clear at this juncture what Johannsen had in mind..." (Churchill 1974). For example, Johannsen writes quite vaguely (1909):

"Differences between these phenotypes are determined by (or contingent upon) the presence of different genes, because the particular phenotypes are not only superficially distinct [in their phenotype], but also distinct on more fundamental levels [die Unterschiede tiefer gehen]." (Press 2020e)

Johannsen's appropriation of the reaction norm was so complete that several recent commentators have written that Woltereck failed to interpret his own data until Johannsen put the pieces together for him in 1911 (Fox *et al.* 2001; Pigliucci 2001; Piersma and Gils 2011; Sommer 2020), or have simply omitted mention of Woltereck when discussing Johannsen's treatment of reaction norms or environmental effects (Roll-Hansen 1979; Roll-Hansen 2009). (To be clear, there is no clear evidence of Woltereck's misunderstanding beyond Johannsen's own assertion.)

A more complete textual analysis reveals that this is only the beginning of the modifications that Johannsen made to his terminology in later editions of his work (Churchill 1974). The updates to Johannsen's *Erblichkeitslehre* book are in large part associated with the reaction norm and

interactions with the environment (Wanscher 1975). They do not seem to directly mention Woltereck.

Woltereck appears to have immediately observed that Johannsen changed the narrative; he asserts his own (more mechanistic) view of the reaction norm or genotype. (This is in contrast to Johannsen, who preferred that the genotype remain as abstract as possible (Churchill 1974).). In a footnote to his 1911 paper (Woltereck 1911), Woltereck writes of one of his theories:

"This entire section is a deliberate "confusion of phenotypes with genotypes" (Johannsen), which is to say an attempt to reunite the various differences that we observe for a variable trait ("genotypic" = autogenous, "phenotype" = ectogenous) with the action of (or collaboration with) the determining substances (genes).

The modifying environmental influence could interfere in the reaction between substrate and gene through an alteration of the activation energy of the latter. Such an effort, which will be so aggressively condemned by the prevailing direction of Mendelism, appears to me to be inevitable in my heretical conception of the genes (as substances of constitutionally variable energy), and particularly from the reaction norm concept."

Thus, Woltereck viewed his work as an attempt to reunite an overextended abstraction of the "gene" with real physiology, by viewing the genes (in this particular case) as chemical entities that participate in reactions. The reaction norm is then a very physical and mechanistic phenomenon reflected in chemistry; hardly what Johannsen meant when he writes:

"As to the nature of the "genes" it is as yet of no value to propose any hypothesis; but that the notion "gene" covers a reality is evident from Mendelism. The Mendelian workers have the great merit of being prudent in their speculations. In full accordance with this restraint—a quite natural reaction against the morphologico-phantastical speculations of the Weismann school—it may be emphatically recommended to use the adjectival term "genotypical" instead of the noun "genotype." We do not know a 'genotype,' but we are able to demonstrate "genotypical" differences or accordance."

Johannsen appears to have altered his opinion later, and was receptive to later arguments that the genes could be enzymatic in substance (Churchill 1974).

Language and cultural shifts.

Reactions to this terminological quibbling varied. The increasingly Anglophone scientists of capitalist West tended to take Johannsen's paper as the final word on the subject. After the founding of the USSR, Soviet scientists continued reading Woltereck and dismissing Johannsen's "hereditarian" approach (Sarkar 1999). It is likely in no small part due to this that the reaction norm and related ideas were reintroduced to the West through Dobzhansky and, through him, Schmalhausen (Nicoglou 2015a).

Historical comparisons of German and US genetics communities from 1900-1933 found little evidence (at that time at least) for a linguistic barrier, but substantial differences in research interest that may explain a lack of interest in the US (Harwood 1993).

It is unclear to what extent the divide was linguistic later on, but it is certain that after the First World War, German dramatically declined as a scientific language. The research output of continental European universities generally cratered, and German research was to some extent ostracized, both during and after the war (Cardwell 1975; Stanley 2019). From a United States perspective, German language course enrollment in US secondary schools declined by approximately 95% relative to the beginning to the end of the war; teaching German was criminalized in some US states (Sterniak 2008). It went from the most popular language among students to a distant third; a similar decline occurred a generation later following the horrors of the Second World War.

In short, English became the dominant imperialistic language over the course of the 20th century, replacing German as the language of the natural sciences (Phillipson 2008).

It is difficult to mourn an imperialistic language, even when it is replaced by another like it. Nonetheless, collateral damage from this transition leaves a substantial body of scientific work in limbo, where a current generation thinks nothing of reading it and cites accordingly, but the later generations continue to cite without necessarily being able to read. This appears to have been the case with Woltereck.

As Russian genetics self-destructed under Lysenko (Sarkar 1999; Gordin 2012), the now US-centric research program of the Modern Synthesis expanded and ultimately gave rise to newer fields such as molecular biology, eventually bringing the reaction norm and the idea of plasticity along with it (Nicoglou 2015b). However, an appreciation of its importance took time and evangelization. For example, Sturtevant's 1965 history of genetics has no mention of reaction norms, and essentially no mention of environment at all (Sturtevant 2001). Research programs in this English-based tradition came to dominate biology. Hence, we now know this debate largely through the single early article written in English. This article was by no means the last word. Woltereck published two more related articles directly following from his 1909 paper in 1911, in which he further responded to Johannsen, as well as a comprehensive book in 1919 (an eclectic but high-volume publishing career continued until his death).

Conclusion

Woltereck's statement that Genotypus = Reaktionsnorm is essentially the formulation in currency today: most geneticists accept that the genotype (now seen as DNA sequences) defines a series of processes that allow organisms to express different developmental and physiological programs according to environmental conditions. This conception was absent from Johannsen's early writing about types and genotypes, until Woltereck introduced the reaction

norm. After that point, Johannsen was obliged to adjust his idea of the genotype to better reflect the physiological phenomena highlighted by the reaction norm.

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