

Richard Woltereck's Concept of Reaktionsnorm

Richard Woltereck first described the concept of Reaktionsnorm (norm of reaction) in his 1909 paper "Weitere experimentelle Untersuchungen über Art-veränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden" (Further investigations of type variation, specifically concerning the nature of quantitative differences between varieties of *Daphnia*). This concept refers to the ways in which the environment can alter the development of an organism, and its adult characteristics. Woltereck conceived of the Reaktionsnorm as the full range of potentialities latent in a single genotype, evocable by the environmental circumstances of a developing organism. Biologists used variants of Woltereck's concept of Reaktionsnorm, often called the reaction norm or norm of reaction, throughout the twentieth century in attempts to explain how developmental responses to the environment can evolve, and even alter the tempo and direction of evolutionary change.

Woltereck's concept of Reaktionsnorm arose from his experiments on the water flea *Daphnia*, conducted at the Biologische Station at Lunz, in Lunz am See, Austria, in the first decade of the twentieth century. Woltereck was a lecturer in zoology at the University of Leipzig, in Leipzig, Germany, where he delivered courses on marine zoology, embryology, and the morphology and physiology of protozoa. He became the director of the Station at Lunz when it was constructed in 1905. The exceptional laboratory equipment and facilities at Lunz allowed Woltereck to experiment on aquatic organisms and to investigate the mechanistic relationships between heredity, variation, and adaptation. Like his mentor August Weismann, who had used *Daphnia* experimentally in the 1870s, Woltereck collected these small aquatic crustaceans from a variety of ecologically distinct lakes and ponds on the Station's campus. Woltereck found *Daphnia* to be an especially favorable organism on which to experiment because of the ease of cultivating them in the laboratory, their rapid rate of reproduction, and the existence of many distinct morphological varieties in the ponds around the Station.

In his work on *Daphnia*, Woltereck set out to challenge the idea of saltationism, the view that evolution proceeds in discontinuous leaps. With the rediscovery of Mendelian heredity around 1900, many zoologists at the time believed that evolution proceeds through large, discontinuous changes in the characters of organisms, and they emphasized the transmission of discrete units of inheritance from parent to offspring. Woltereck thought that natural selection on continuous phenotypic variation—such as fruit size in plants or stature in animals—played an equally important role in evolution. To demonstrate this importance, he appealed to the design of Wilhelm Johannsen's pure line experiments, in which Johannsen cultivated lineages of barley and bean plants from single self-fertilized individuals. He called those lineages pure lines. According to Johannsen, the members of a pure line shared a common genotype, or hereditary disposition. He argued that in natural populations selection could do no more than sort among these fixed hereditary types. Some people interpreted Johannsen's results as evidence of the insufficiency of natural selection to cause lasting evolutionary change.

Woltereck thought that if he could experimentally demonstrate a lasting evolutionary response to selection on continuous traits within a population of genotypically identical individuals, he would undermine the saltationist view. Woltereck generated pure lines of *Daphnia*, which reproduce asexually, from a variety of ecologically distinct ponds, and he subjected them to different environmental conditions, such as varying levels of nutrients, to elicit adaptive evolutionary responses. In the course of these experiments he noticed that certain morphological characteristics, such as head height, developed differently when the *Daphnia* were raised in different environments. Moreover, the response of such traits to the environment differed in each pure line and each genotype. Woltereck organized his data by drawing functional graphs, with trait values on the dependent axes

and values of a manipulated environmental factor on the independent axes. For example, he plotted relative head height against varying nutrient levels. Woltereck called each of these graphs—relating a single trait value to a single environmental variable—a phenotypic curve. Each phenotypic curve described an aspect of the complete Reaktionsnorm. Woltereck argued that Johannsen's genotype concept was not a rigid determinant of the characters of an organism, but represented the full range of potential phenotypes latent in its Reaktionsnorm.

Many of Woltereck's peers endorsed his concept of Reaktionsnorm. Embracing the notion, Johannsen equated the concept of genotype with the concept of Reaktionsnorm. Woltereck's concept gained traction most noticeably in the Soviet Union in the 1920s, where many biologists applied it to the investigation of alternate developmental trajectories in a variety of polymorphic organisms, and they used it to undermine claims about the inheritance of acquired characteristics. In a 1926 paper concerning the inheritance of acquired characteristics, Theodosius Dobzhansky emphasized Johannsen's equation of genotype and Reaktionsnorm, and used the latter to explain mutations in *Drosophila* that were manifested phenotypically in certain environmental conditions. In the 1940s, Ivan Ivanovich Schmalhausen used the concept to develop his theory of stabilizing selection, according to which aspects of the Reaktionsnorm newly exposed to selection by novel environmental conditions could become stable, genetically-determined characters. Schmalhausen reasoned that environmental perturbations during development can serve as a source of evolutionary novelty, a line of argument reinvigorated by Mary Jane West-Eberhard, a biologist at the Smithsonian Tropical Research Institute in Panama in 1989.

The use of the term reaction norm in twenty-first century biology differs from Woltereck's original concept in a variety of ways. For example, biologists commonly use it to refer to developmental changes in a single trait over the range of environments considered for the purposes of a given study, and they invoke it in discussions of genotype-by-environment variance in quantitative genetics. At the University of Chicago, in Chicago, Illinois, in 1985, Sara Via and Russell Lande proposed a mathematical model for the evolution of reaction norms based on quantitative genetics. Their model treated reaction norms not as continuous functions of environmental factors, but as discrete correlated character states expressed in specific environments. In 1986, Stephen Stearns, director of the Zoologisches Institut at the University of Basel, in Basel, Switzerland, applied the notion of a reaction norm to the effect of environmental conditions on the development of fish, specifically with respect to the age and size at which fish reach sexual maturity. The concept of reaction norm is widely used by ecologists, evolutionary biologists, geneticists, and agriculturalists. It is also used by evolutionary developmental biologists as a way to relate developmental genetic mechanisms to phenotypic adaptations involving specific responses to the environment.

Sources

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