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Reprint of "Evolutionary constraints or opportunities?"☆

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ABSTRACT

Natural selection is traditionally viewed as a leading factor of evolution, whereas variation is assumed to be random and non-directional. Any order in variation is attributed to epigenetic or developmental constraints that can hinder the action of natural selection. In contrast I consider the *positive role* of epigenetic mechanisms in evolution because they provide organisms with opportunities for rapid adaptive change. Because the term "constraint" has negative connotations, I use the term "regulated variation" to emphasize the adaptive nature of phenotypic variation, which helps populations and species to survive and evolve in changing environments. The capacity to produce regulated variation is a phenotypic property, which is not described in the genome. Instead, the genome acts as a switchboard, where mostly random mutations switch "on" or "off" preexisting functional capacities of organism components. Thus, there are two channels of heredity: informational (genomic) and structure-functional (phenotypic). Functional capacities of organisms most likely emerged in a chain of modifications and combinations of more simple ancestral functions. The role of DNA has been to keep records of these changes (without describing the result) so that they can be reproduced in the following generations. Evolutionary opportunities include adjustments of individual functions, multitasking, connection between various components of an organism, and interaction between organisms. The adaptive nature of regulated variation can be explained by the differential success of lineages in macro-evolution. Lineages with more advantageous patterns of regulated variation are likely to produce more species and secure more resources (i.e., long-term lineage selection).

1. Introduction

The theory of evolution is one of the most challenging endeavors in science because it attempts to integrate an enormous amount of information about living organisms, including genetics, molecular biology, physiology, ecology, population dynamics, systematics, and phylogeny. Another challenge is the slow rate of evolutionary change and the lack of detailed information on its intermediate steps. The data supporting hypotheses on short-term evolutionary change include a few observations in natural and laboratory populations, whereas evidence of long-term evolutionary change comes almost exclusively from paleontology and comparative morphology. Existing data on macro-evolution usually do not include information on molecular and developmental mechanisms. These challenges result in the resilience of traditional views on evolution, which are difficult to refute based on data or logic. One of such persistent claims is the notion of randomness and non-directionality of heritable variation. This notion is supported by the randomness of nucleotide substitution in the DNA. Known biases in the probability of nucleotide substitution do not cause any adaptive change in the phenotype and do not make evolution faster or more efficient. Another evidence of randomness comes from the variation of phenotypic qualitative traits such as measures of various body parts. Neo-Darwinism portrays variation as random and "blind" in order to defend the primary role of natural selection in evolution and prove the absence of goal-directed agents in nature (Dawkins, 1986; Dennett, 1995). For example, Dennett wrote about Teilhard de Chardin: "He emphatically denied the fundamental idea: that evolution is a mindless, purposeless, algorithmic process" (p. 320).

However, phenotypic variation is not random but regulated by various internal and external factors, and this regulation generally facilitates organism functions and increases survival and reproduction rates. This implies that developing organisms are *active, self-organizing, and goal-directed agents*. Actual variation always represents only a narrow subset of all logically possible forms, which indicates that variation is subject to strong constraints. As Huxley wrote, "A whale does not tend to vary in

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the direction of producing feathers, not a bird in the direction of developing whalebone" (Huxley, 1893, p. 181). These constraints are present before any selection takes place, and thus, they should not be confused with correlations enforced by purifying selection (Schwenk, 1995).

Darwin was well aware of the constraints on variation. In the "Origin of species", he discussed the phenomenon of "correlation of growth": "I mean by this expression that the whole organization is so tied together during its growth and development, that when slight variations in any one part occur, and are accumulated through natural selection, other parts become modified. which are responsible for coordinated change in many traits if one of the traits is subject to selection." (Darwin, 1987, p. 133). However, he apparently assumed that natural selection can always find a way to overcome these constraints if they hinder the emergence of useful combinations of traits. Darwin accepted only one evolutionary consequence of such correlations: the change of some traits may be caused by their correlation with other traits which undergo change under the pressure of natural selection. In contrast, Gould and Lewontin argued that constraints may be so strong that they "become more interesting and more important in delimiting pathways of change than the selective force" (Gould and Lewontin, 1979, p. 581). Thus, the study of constraints may help in predicting possible directions of evolutionary change. But constraints were considered only in relation to their negative role in evolution–the role of barriers that prevent the development of perfect adaptations.

In this paper I argue that factors regulating phenotypic variation play a *positive role* in evolution by providing opportunities for rapid adaptive changes, which would not exist otherwise. Because the term "constraint" has negative connotations, I use another term "regulated variation" to emphasize the adaptive nature of phenotypic variation, which has evolved to provide the functionality of organisms not only in current conditions, but also in possible alternative conditions. Regulated variation helps populations and species to survive in variable environments, although occasionally it may appear non-adaptive and becoming a constraint. Metaphorically speaking, regulated variation can be compared to handrails on a narrow hanging bridge that provide an opportunity for a person to cross the river. Although this idea is old and was discussed by Cuénot, Goldschmidt, Schmalhausen, Lewontin, Gould (Section 2), now we have not only more evidence of this phenomenon, but also more insights into its molecular and genetic mechanisms (Section 3). This interpretation of evolution does not diminish the importance of natural selection. But in contrast to Neo-Darwinism, it emphasizes the active role of organisms in evolution. In particular, it is based on the notion that organisms build up their evolutionary potential (i.e., adaptability) by developing resources for future heritable variations. The effects of adaptability, phenotypic plasticity, and developmental correlations in evolution fit into the category of "extended evolutionary synthesis" (EES) (Pigliucci and Müller, 2010), which goes beyond the "modern synthesis" (MS) presented in writings of Huxley, Fisher, Dobzhansky, Haldane, Wright, and Mayr. The notion of regulated variation provides a generalized approach to these phenomena and may help to develop a unified theory. Moreover, it prompts to reconsider some basic ideas about heredity and evolution. For example, the "blueprint" metaphor of the genome has to be replaced with a "switchboard" metaphor, and organisms have to be recognized as active agents capable of controlling their phenotypes and increasing their adaptability. In Section 4, I discuss types of evolutionary opportunities that differ in the degree of their novelty and level of organization at which they appear. Finally, in Section 5, I argue that selection of lineages can explain why evolutionary opportunities tend to accumulate in macro-evolution.

2. Overview of theories that accounted for evolutionary opportunities

Studies of evolutionary opportunities have a long history. Lucien Cuénot proposed a hypothesis that large heritable changes are more important in adaptive evolution than small changes, and these changes often appear as adjustments of already existing organs and capacities to new functions (Cuénot, 1914). He called this phenomenon "preadaptation", which seems to capture better the expanded evolutionary potential of current adaptations than the term "exaptation" suggested much later by (Gould and Vrba, 1982). Cuénot criticized Darwin's idea of the primary role of environment in evolution. He argued that the structure of organisms often plays the leading role in evolution by narrowing down the set of new functions that can be acquired with the use of already existing structures. Environment does not *determine* structures of organisms because there are various ways of life and function in each environment. Cuénot considered his theory fully compatible with Darwin's idea of natural selection; he thought that natural selection adjusts existing organs for specific functions of organisms. The theory of nomogenesis developed by Berg (1922) included many examples of preadaptations. However, Berg did not understand the explanatory power of the theory of natural selection, and hence, failed to differentiate between strong and weak aspects of Darwin's heritage.

Richard Goldschmidt argued that macro-mutations in insects (e.g., aristopedia, tetraptera) generate highly-organized novel structures which may appear functional, and hence, may provide opportunities for adaptive evolution (Goldschmidt, 1940). He also noticed that organisms possess a capacity to produce mutant phenotypes under stress conditions without any mutation (he called them "phenocopies"), which implies that the norm of reaction exists independently from mutations (Goldschmidt, 1935). The term "norm of reaction" means morphological responses to environmental factors (Woltereck, 1909).

Ivan Schmalhausen pioneered in the analysis of the role of phenotypic plasticity and robustness in evolution (Schmalhausen, 1949). He introduced the notion of "stabilizing selection" which means selection for phenotypic plasticity and robustness to cope with heterogeneous environment in space and time. In contrast to the negative "purifying selection" that eliminates deleterious alleles, "stabilizing selection has a positive and constructive role, for it leads to the establishment of new morphogenetic correlations" (p. 93). Phenotypic plasticity facilitates changes of heredity via natural selection that adjust the norm of reaction. This mechanism was later re-discovered and named "genetic assimilation" (Waddington, 1961). Schmalhausen proposed that plasticity of variation is an evidence of species' capacity for evolution, and this capacity can be first reserved and then mobilized in stressful and changing conditions. Accumulation of variability is achieved via genetic dominance, neutralization of harmful mutations, and balance of harmful and advantageous effects of mutations. Mobilization of variability includes the increase of homozygosity due to the fragmentation of populations as well as release of phenotypic variability through elimination of regulatory correlations and direct induction of new phenotypes by stress conditions. Finally, Schmalhausen was among the first to analyze the phenomenon of adaptability at both individual and species levels. The theory of Schmalhausen was far ahead of his time. He complemented the Darwin's theory of selection with deep understanding of the self-regulatory capacity of living organisms and their active participation in the phenotype-building and evolutionary process. Unfortunately, his theory was mostly ignored because it contradicted to the "passive sieve" metaphor of evolution promoted by MS. Very few western biologists were familiar with the theory

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