How to Explain the Evolution of Evolvability? Mechanistic Congruence and other Models

Günter P. Wagner
Department of Ecology and Evolutionary Biology
Yale University

There is now a broad agreement that evolution by random variation and selection is not universally possible. Some systems can be improved by random variations and selection others not. From this insight a new problem arises, namely the question how evolvability arises in evolution, and how evolvability can be achieved in evolutionary engineering. I will discuss this problem from the biological point of view, i.e. asking what natural processes can be responsible for the evolutionary enhancement of evolvability of organisms.

One of the main factors influencing evolvability is the probability and the magnitude of deleterious pleiotropic effects. Hence one mode of the evolution of evolvability is the suppression of deleterious pleiotropic effects. Three models have been proposed to account for the origin of mechanisms that suppress deleterious pleiotropic effects: group selection, constructional selection, and a combination of directional and stabilizing selection. To my knowledge there are no published results indicating that group selection can account for the evolution of evolvability directly. The role of group or species selection may be to influence the frequency of species with higher evolvability in the fauna and flora, but it is hard to see how it can be responsible for the establishment of a more evolvable genotype in the first place. Constructional selection is an ingenious mechanism which can lead to less pleiotropy in the genome and thereby increase the over all evolvability (Altenberg 1994). But it is to be noted that in this case the mechanism that increases evolvability is not selection for evolvability directly. Similarly, evolvability can increase by directional and stabilizing selection. Simulation results, however, show that the main selective advantage of suppressing pleiotropic effects does not result from the increased evolvability. Hence there are at least two mechanisms that in principle can increase evolvability, but in neither case is the selective advantage directly related to the effect on evolvability. This leads to the intellectually dissatisfactory implication that evolvability might be a coincidental byproduct of other adaptive processes. There is, however, the possibility that the connection between adaptation and the evolution of evolvability is deeper than that. I propose the notion of mechanistic congruence to account for the connection between adaptation and the evolution of evolvability.

The concept of **mechanistic congruence** is proposed for any situation where two phenomena are manifestations of the same microscopic mechanism. In physics this is the case for pressure and temperature, which both are manifestations of the average kinetic energy of molecules (Laubichler, pers. comm.). Because of that, either can influence the other, increasing the temperature increases the pressure if the volume remains the same and increasing pressure increases temperature. Similarly, the phenotypic plasticity of a macromolecule and its mutational robustness are manifestations of the thermodynamic stability of the molecule. As a consequence, selection against the plasticity also increases mutational robustness. This phenomenon has been called plasto-genetic congruence (Ancel and Fontana 2000). I will argue that evolvability and increase in mean fitness are also a case of mechanistic congruence. Both are manifestations of the same microscopic mechanism, i.e. the presence or absence of deleterious pleiotropic effects. Selection for increased adaptation directly acts against deleterious pleiotropic effects, which is also directly related to evolvability. Evolvability is thus not a coincidental byproduct of adaptation but one that results from a generic mechanistic connection between adaptation and evolvability.

Altenberg, L., 1994 The evolution of evolvability in genetic programming, pp. 47-74 in *Advances in Genetic Programming.*, edited by J. K. E. Kinnear. MIT Press, Cambridge.

Ancel, L., and W. Fontana, 2000 Plasticity, evolvability and modularity in RNA. J. Exp. Zool. (Mol. Dev. Evol.) **288:** in press.