

Metaptation: Metaphors for genome evolution

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Living organisms may be only ephemeral collections of atoms assembled according to fundamental physical laws. But what ephemera, when those laws operate over deep evolutionary time! Understanding biology requires metaphors as well as molecules and thermodynamics. Metaphors from engineering are commonly used at the organismal level, while genome studies invite linguistic metaphors (e.g., the adaptive "design" of organisms is "encoded" in the "language" of DNA). But since genomes preserve a record of multiple evolutionary processes besides familiar Darwinian natural selection, comprehending the full richness of the genome calls for a richer set of metaphors than those currently employed.

"Metaptation" (from "meta" to change + "aptation" fitness) provides a descriptive label for genomic patterns which promote evolvability. By analogy with "adaptation" (the result of natural selection directly favoring "fitness"), metaptation results from selection indirectly favoring mechanisms which facilitate and constrain mutation within domains that remain plausibly consistent with fitness. Contrary to a long-standing theoretical argument that selection can never favor mutability over replication fidelity, under changing conditions the advantages of genetic variation can indeed foster certain site-specific mechanisms of mutation. (This concept is well-established in microbiology, where the evolution of prokaryotic and other single-celled organisms can be studied directly.) Several years ago, Ed Trifonov and I independently proposed a "tuning knob" metaphor for the functionality provided by simple tandem repeats. Transposable elements also appear to play important evolutionary roles by creatively "remodelling" the genome. By expanding our repertoire of genetic metaphors to embrace evolutionary change as well as immediate fitness, we may better appreciate how these and other genomic patterns contribute metaptive "protocols" for "natural genetic engineering."

The related abstract below was published in 1985, *Evolutionary Theory* 7:222.

METAPTATION: A descriptive category for evolutionarily versatile patterns of genetic and ontogenetic organization

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Traits which create potential for efficient adaptive evolution are shaped by selection acting at the "second tier," at the level of differential speciation and extinction among lineages. Evolutionary versatility is not merely a fortuitous byproduct of certain adaptations. A lineage whose genomic organization has permitted effective evolutionary change in the past can pass this capacity, with additional modifications, along to descendent branches. One result of such selection has been a gradual refinement of mechanisms which influence the occurrence of viable hereditary variation, and hence the evolutionary acquisition by genomic information systems of an ability to facilitate their own evolutionary transformation.

"Metaptation" (from meta to change + aptation fitness) is offered as a name for evolved patterns of biological organization which promote evolutionary versatility by causing and constraining mutation and by ontogenetically accommodating to the consequences of mutation. Many mechanisms for actively encouraging genetic variation are already known to exist. Recognizing that such mechanisms have evolved for this role, selected on the basis of past contribution to evolutionary survival, offers a paradigm for investigating the nature of genetic and developmental function. Evolutionarily useful transformations may be explicitly coded by variable genes or genetic regulatory sequences. Organizational patterns which confer long term evolutionary versatility may be as sophisticated and as fundamental as the patterns which provide for immediate adaptive morphogenesis.