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Development as the Target of Evolution

A Computational Approach to Developmental Systems

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In evolutionary psychology, it is possible to distinguish between laws, things that are true everywhere and at all times, and heuristics, principles that are useful in the generation of hypotheses but are not a priori true. An example of a heuristic is that natural selection tends to cause the spread of mutations that increase the lifetime reproductive success of individuals. This is usually true, but it can be violated, as Hamilton showed. An example of a law is that natural selection occurs if, and only if, Darwin's three postulates are met, and it occurs inevitably in that case.

In the case of individual development, it is a law that only aspects of organisms that are heritable, and that influence the phenotype in ways that impact fitness, can be acted upon by natural selection. Many notions about what the role of genes must be in shaping these aspects of organisms, however, have only the status of heuristics. Rigorous definitions of the prerequisites for natural selection contain no reference to genes; they are formulated entirely in terms of the heritability of phenotypes (Endler, 1992). Genes play an important role in the generation of phenotypes and are an important mechanism of inheritance, but they are not the only one. Metaphorically speaking, natural selection only "sees" phenotypic outcomes. The multitude of causal factors involved in generating these outcomes are all possible candidates for the feedback loop of selection, one step of which can be represented as follows: distribution of phenotypes$_{\text{time1}}$ → differential fitness → distribution of phenotypes$_{\text{time2}}$.

Developmental systems theorists, and others interested in extragenetic factors in development, have emphasized this fact (Griffiths & Gray, 2001; Oyama, 2000; West-Eberhard, 2003). It is true, as they have stressed, that the target of natural selection is entire developmental systems: the entire array of processes and causal factors, including but not restricted to genes, that give rise to phenotypes. This insight has led to progress in areas such as gene–culture coevolution (Boyd & Richerson, 1985), niche construction (Laland, Odling-Smee, & Feldman, 2000), and extragenetic inheritance (Haig, 2002; Jablonka & Lamb, 1995). This insight can also be carried too far, however, as in the assertion that genes cannot "specify" phenotypic outcomes (Lickliter & Honeycutt, 2003). It is trivially true that phenotypic outcomes are contingent on many events and are therefore not causally predetermined in every detail. But if it were the case that genes could not specify phenotypic outcomes—in the limit, that they were random—then genetic evolution by natural selection could not occur at all. Darwin's postulates, which qualify as a bona fide law, guarantee that phenotypic outcomes *must* be specifiable, at least in a statistical sense, if natural selection is to occur. Confusing this statistical sense of "determination" with the rigid Laplacean notion of "determinism," absolute certainty of outcome, has been the cause of much unnecessary debate.

It is illogical to use the insight that natural selection acts on entire developmental systems to downplay the role of selection in shaping the phenotypes of organisms. As evolutionary psychologists, the converse should be our goal: To use this insight to understand better *how* natural selection shapes the phenotypic design of organisms. In this endeavor, it may be useful to begin by considering how we can use evolutionary laws to derive heuristics regarding how we might expect developmental processes to look.

RELIABLE DEVELOPMENT

Because it is the phenotypic endpoints (as well as midpoints) of development that contribute causally to selection, changes in developmental systems that produce fitness-enhancing changes in phenotypic outcomes tend to spread in populations. This means that natural selection shapes developmental systems so as to produce *reliably developing* outcomes given the statistical regularities that the population has experienced over the course of its evolution (weighted by the mass of the population that has been exposed to these regularities, their frequency of occurrence in time, their recency, etc.; Tooby & Cosmides, 1992). Reliably developing aspects of the phenotype often have the appearance of "innateness" in some respects. They are produced whenever the developing individual's environment sufficiently matches the ancestral one along relevant dimensions. For example, developmental schedules of some skills, such as the ability to distinguish between animates and inanimates, are relatively invariant across very different cultures and environments, suggesting that development is not "dose-dependent" along dimensions that vary between these populations (Barrett & Behne, 2005). However, this does not tell us what factors in the environment might contribute causally to development of the competence. Innateness in the folk sense of lack of environmental input is not mandated.

PROPER DEVELOPMENTAL TARGETS

Sperber (1994) distinguished between the proper domain of a computational device or system, which is the set of inputs that the system was designed by natural selection to process, and its actual domain, which is the set of inputs the system actually does process given its input criteria and the nature of the current environment. Whatever is available in the current environment that satisfies these criteria will be processed, whether evolutionarily novel or not. By analogy, one can speak of the proper developmental target of a developmental system: the set of reliably developing phenotypic outcomes that the system was designed, by natural selection, to produce (see Cosmides & Tooby, 2000, for a related discussion on the organizational mode and organizational domain of adaptations). For example, it is likely that natural selection has created a variety of developmental processes designed to produce fear of dangerous animals in the local environment (Barrett, 2005). This system could use environmental cues, such as size, force, and predatory movement cues, to narrow the fear response to appropriate targets. Based on these targets, a child might develop a fear of lions that, although not "innate" (lions per se are not prespecified as a target), is well within the proper range of developmental outcomes for the system. On the other hand, the same system might cause a child to acquire a fear of loud construction equipment. This would be an actual outcome of the developmental process, but not a proper one.

TYPE OUTCOMES AND TOKEN OUTCOMES

Fear of lions is an example of a developmental outcome that is a token of a more general type, fear of dangerous animals. In virtually all cases, the proper developmental target of a developmental system is a type of outcome that is more abstract than the actual, observed tokens, which contain a level of phenotypic detail that is not "specified" by the type. Consider, for example, the development of animal concepts. It is likely that humans, and many other animals, have been selected to develop individual concepts of classes or taxa of animals in the local environment, including dangerous predators and edible prey (e.g., Cheney & Seyfarth, 1990, on predator concepts in vervet monkeys). The developmental system dedicated to this in humans might cause an Inuit child in the Arctic to develop the concept POLAR BEAR given the relevant conditions. This is a token outcome of a more general type. A Shuar child in the Amazon basin, on the other hand, might develop the concept JAGUAR but never develop the concept POLAR BEAR. In each case, the conceptual structure contains details that are not specified by the system in any way (POLAR BEAR: white fur, able to swim; JAGUAR: ring-like spots, climbs trees). The type is always more abstract and underspecified than the tokens. Indeed, the system can produce token concepts that are entirely evolutionarily novel for humans (e.g., TYRANNOSAURUS REX; presumably, there was never selection on humans by dinosaurs).

The fact that the system is capable of producing an evolutionarily novel token of a *type* that is nevertheless the product of natural selection may in fact be more the norm than the exception in evolved developmental systems. This could help explain apparently evolutionarily novel skills such as playing chess or driving. We do not yet know what evolved competencies underlie these skills, so we cannot rule out that driving and chess may have components that are tokens of more general types of problem for which there are evolved solutions (e.g., object tracking, collision avoidance, strategic reasoning). In a sense, *every* problem that humans face is novel in its details. Every predator encounter, for example, is novel in an infinite number of ways. The question is whether it has features that can be mapped onto past situation types for which there are adaptations.

A COMPUTATIONAL APPROACH TO EVOLVED DEVELOPMENTAL SYSTEMS

Cognitive scientists have identified three questions that one may ask about the design of an information-processing system:

What inputs does the system accept?
What are the operations that this system performs on the inputs?
What is the computational relation, or mapping function, between inputs and outputs (Tooby & Cosmides, 1992)?

Although such analyses have traditionally been applied to brain systems that are the end products of development, such as the visual system, it is possible to regard developmental systems as computational systems when they have been selected to produce outcomes of a particular type, even if the type is quite abstract (i.e., it has many open parameters). An early attempt at such an approach was Waddington's (1956) notion of an "epigenetic landscape," which points to how a formal computational approach to developmental systems might look. It would describe mapping functions between developmental circumstances and phenotypic outcomes. Proposing explicit hypotheses about such mapping functions could help to resolve long-standing controversies in the field over the roles of culture, environment, and individual experience in development by making testable predictions even without detailed knowledge of the underlying genetic system.

IMPLICATIONS FOR CURRENT DEBATES

Viewing developmental systems as the targets of selection is consistent with the evolutionary-psychological view that natural selection shapes the phenotypic design of organisms. It simply adds that selection does this by shaping the mechanisms that generate this design anew each generation during development, what Tooby, Cosmides, and Barrett (2003) call "design reincarnation" (see also Barrett, in press). This perspective casts doubt on certain traditional dichotomies and oppositions that are often used to call into question evolutionary-psychological interpretations of phenotypes. For example, although phenotypic variation between individuals across cultures or environments is often taken as de facto evidence against evolution playing a role in shaping that aspect of the phenotype, such variation does not by itself count as evidence for or against an evolutionary hypothesis. Instead, both the evolutionary and alternative hypotheses must specify the nature of variation that is expected, if any. We are in a position in which traditional notions of parsimony are questionable, and null hypothesis testing on the basis of these parsimony assumptions is weak (e.g., assume "learned" unless present in infancy; assume "not evolved" if culturally variable). A computational or design stance approach to developmental systems, one

that asks what developmental outcomes the system is designed to produce and how, may help us move beyond the facile view of evolved structures as hardwired and inflexible, and more importantly, help us to understand better how human psychology actually works.

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Evolutionary Psychology and Developmental Systems Theory

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One of the aims of evolutionary psychology and related fields is to map the developmental trajectory of our species-typical cognitive adaptations. Tools that evolutionary psychologists use to generate testable hypotheses and models of cognitive adaptations include consideration of the enduring selection pressures that played a causal role in shaping our cognitive circuitry. Selection pressures are statistically recurring features of the social, ecological, biological, or physical world that affect the probability of survival and reproduction, however distally (Tooby & Cosmides, 1992). Some selection pressures may be external to the organism (e.g., predators, pathogens, and members of the opposite sex), whereas other selection pressures may derive from the changes the organism itself makes in its environment (e.g., for a specialist, depletion of a particular food source creates the adaptive problem of discovering new sources of energy). Regardless of the selection pressure's origin, consideration of ancestral conditions and the factors that significantly and repeatedly affected the probability of survival and reproduction can often greatly aid investigations of (1) the design of our evolved psychological adaptations, and (2) the manner in which these adaptations develop.