

The Evolution of Mind
*Fundamental Questions
and Controversies*

Edited by
STEVEN W. GANGESTAD
JEFFRY A. SIMPSON



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Evolutionary Psychology and Developmental Systems Theory

DEBRA LIEBERMAN

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.

Recently, scientists who adopt a developmental systems perspective have taken aim at evolutionary psychology, suggesting that evolutionary psychologists ignore development and are ignorant about the multiple causal factors guiding the development of an organism's phenotype (e.g., Lickliter & Honeycutt, 2003). Nothing could be further from the truth. Evolutionary psychologists not only consider multiple causal factors in the *evolution* of particular traits (e.g., see Cosmides & Tooby, 1981, for a discussion of how multiple cellular factors produced two different sized gametes) but also the interaction of multiple factors in the *development* of an organism's phenotype (e.g., see Bugental, 2003, for a discussion of the multiple social factors that influence the life experiences of children born with medical and physical disorders). A misunderstanding of the theoretical framework employed by evolutionary psychologists has led to inaccurate portrayals of evolutionary approaches to understanding psychological processes (see Lickliter & Honeycutt, 2003; Oyama, Griffiths, & Gray, 2001). What follows is a brief discussion of developmental systems theory (DST), what it has to offer an evolutionary psychological approach to understanding the mind, misconceptions that some developmental systems theorists hold regarding evolutionary psychology, and an example of how an evolutionary psychological approach does indeed consider development based on my own work on the development of sexual aversions between close genetic relatives.

WHAT IS DST?

DST is an approach to understanding the evolution and development of organisms. The main platform of DST challenges all dichotomous accounts of development and human behavior that attempt to partition the causal factors governing the production of an organism's phenotype into specific contributions made by, for example, the organism's genes and, separately, the organism's environment. Perhaps most objectionable to DST is the notion that development can be viewed as an unfolding of genetic programs against a passive environmental backdrop. Rather, proponents of DST argue that development occurs through the interplay of multiple causal factors, both internal and external to the organism. According to Oyama and colleagues (2001), "DST views both development and evolution as processes of construction and reconstruction in which heterogeneous resources are contingently but more or less reliably reassembled for each life cycle" (p. 1).

Evolutionary psychologists, perhaps along with most scientists today, would agree that all features of an organism are joint products of the organ-

ism's genes and environment. Partitioning the phenotypic effects due to one's genes and those due to the environment is not a goal of evolutionary psychology; behavioral genetics is a field that tries to identify the heritability of particular traits, that is, the proportion of variance *between individuals* that can be attributed to genetic differences. Furthermore, evolutionary psychologists would agree with developmental systems theorists' statement that development results from the interaction of multiple causal factors. But this statement does no work; that is, it does not explain *why* the "heterogeneous resources" are assembled in the particular ways they are versus the infinite number of other possible constructions and reconstructions. Evolutionary psychology offers a framework for answering this question by considering specific causal factors and how they impacted an organism's probability of survival and reproduction.

In contrast, proponents of DST do not privilege any single causal factor (especially a genetic one) in the explanation of the evolution or development of an organism's phenotype. Rather, their goal is to restore the balance by considering multiple causal factors (i.e., the heterogeneous resources) as potentially *equal* contributors to an organism's phenotype: "Not only is most standard interactionism shot through with asymmetries, but the notions of causal *symmetry*, or *parity*, which do have a democratic ring, inform the very concept of a developmental system" (Oyama, 2001, p. 183; original emphasis). In other words, DST starts with the assumption that no single factor or selection pressure (e.g., nuclear DNA, mitochondrial DNA, pathogen, predator) can provide a causal account of an organism's phenotype. As holistic and harmonious as this may sound, equality of causal factors is not something to be assumed; it is something to be demonstrated empirically. It is more rigorous to start with scientific first principles and build a model from which hypotheses may be generated, rather than design a model around an ideology and ignore (or privilege) certain causal accounts.

WHAT DOES DST ADD TO THE INVESTIGATION OF PSYCHOLOGICAL ADAPTATIONS?

The main contribution of DST is an assumption already present in current evolutionary approaches to studying human behavior: Genes are but one of a host of heterogeneous causal factors governing the evolution and development of organisms. Indeed, in evolutionary psychology, this is the starting point from which *hypotheses are generated* regarding the kinds of psy-

chological adaptations expected to exist given the recurring features of the different environments our species encountered over many generations: biological (e.g., pathogens, non-nuclear DNA), physical (e.g., gravity, temperature, light), ecological (e.g., food sources, predators), and social (e.g., mates, mate competitors). Unlike DST, however, evolutionary psychology has a coherent and rigorous model guiding the investigation of (1) the causal forces responsible for the evolution of the multiple domains of human psychology, (2) the kinds of cognitive programs expected to have evolved as a result of the repeated interactions with our ancestral environments, and (3) how our species-typical psychological adaptations develop over the course of the life cycle. Additionally, understanding the mind in terms of the functions it evolved to perform also lends insight into the manner in which psychological systems can become impaired and, potentially, repaired.

In contrast to an evolutionary psychological framework, aside from the noncontroversial viewpoint that genetic and nongenetic factors contribute to development and have important consequences for the evolutionary trajectory of a species, DST makes no specific predictions and, consequently, is of little use scientifically. This has even been acknowledged by a few of DST's main proponents: "What we have come to term *developmental systems theory* is not a theory in the sense of a specific model that produces predictions to be tested against rival models. Instead, it is a general theoretical perspective on development, heredity and evolution" (Oyama et al., 2001, pp. 1–2, original emphasis). Unlike other metatheoretical models (e.g., evolutionary psychology), DST makes few, if any, specific predictions regarding the kinds of phenotypes, or design features, expected to exist. A theoretical model that makes no predictions has little value in the scientific arena.

DST'S OBJECTIONS TO EVOLUTIONARY PSYCHOLOGY

Despite the lack of a rigorous theoretical model from which hypotheses may be generated or a clear understanding of the principles of evolutionary psychology, a number of researchers within DST have taken aim at the theoretical framework of evolutionary psychology and, in the process, exposed their misunderstandings of the field (e.g., Lickliter & Honeycutt, 2003). Here I discuss two assumptions that proponents of DST mistakenly attribute to evolutionary psychology: (1) phenotypic traits or characters can be prespecified in advance of individual ontogeny, and (2) genes contain the program or instructions for the prespecification of phenotypic traits, and

the environment (or experience) simply provides the trigger for these programs to be expressed (Lickliter & Honeycutt, 2003). Put simply, these are misattributions that, once clarified, will allow for a renewed co-investigation of how complex psychological adaptations develop.

Traits Can Be Prespecified

According to proponents of DST, evolutionary psychologists believe "that the bodily forms, physiological processes, and behavioral dispositions of organisms can be specified in advance of the individual organism's development" (Lickliter & Honeycutt, 2003, p. 820); that is, evolutionary psychologists believe in preformationism. What is missing, claim DST proponents, is an appreciation of how nongenetic factors, including aspects of the physical world (e.g., temperature, light, pH, the social environment), may influence the development of an organism. Again, nothing could be further from the truth. Evolutionary psychology maintains there is a reliably developing, species-typical body plan (or two body plans, if one considers the sexes separately) that occurs within a range of parameters (e.g., physical, biological, and social). Changing any single parameter may change the trait. But within a certain range of parameters, it is not shocking to specify that a developing human embryo is likely (not guaranteed, due to factors such as genetic mutations) to possess a head, two arms, two legs, a visual system, systems for storing and releasing glucose, a system for detecting faces, and systems for avoiding sexual relations with close genetic relatives. Surely neither DST proponents nor evolutionary psychologists believe that a child placed on Mars would develop as he or she would have on Earth.

So if evolutionary psychologists appreciate that nongenetic factors influence the development of an organism, what is the fuss about? One possibility is that DST misinterprets discussions of "reliably developing features" within evolutionary psychology as being synonymous with predetermined explanations. According to Tooby, Cosmides, and Barrett (2003), developmental systems theorists

seem confused by the profound difference between the true claim that normal members of a species embody predictable programs promoting reliable development, and the very distinct and false claims that following such developmental programs to a predetermined outcome is inevitable, unmodifiable, specified solely "in the genes" without regard to environment, or even that such developmental programs are necessarily hard to modify. (pp. 860–861)

Though this misinterpretation has been spelled out clearly, proponents of DST continue to mischaracterize the main tenets of evolutionary psychology.

Genes as Instructions; Environments as Triggers

Another caricature drawn by proponents of DST is that evolutionary psychologists view genes purely as instructions and environments purely as triggers. For example, Lewontin (2001) suggests that scientists adopting an adaptationist framework see ontogeny "as an *unfolding* of a form, already latent in the genes, requiring only an original triggering at fertilization and an environment adequate to allow 'normal' development to continue" (p. 60, original emphasis). The correct view, Lewontin maintains, is that "genes, organisms, and environments are in reciprocal interaction with each other in such a way that each is both cause and effect in a quite complex, although perfectly analyzable, way" (p. 61). Indeed, evolutionary psychology approaches the web of interactions, whereby forms fit functions and multiple factors impinge on the development and survival of an organism, and provides a method for investigating why those forms exist and how they affected survival and reproduction. This method assumes that organisms not only inherit genetic material from past generations but also inherit sensitivities to particular aspects of past environments. Evolutionary psychologists do *not* maintain that the environment is passive; rather, features of the environment influence and are influenced by existing organisms. Furthermore, evolutionary psychologists do not subscribe to preformationism and similarly disagree that forms are "latent in the genes." It would seem, then, that what started as a misattribution has revealed common ground shared by evolutionary psychology and DST.

AN EXAMPLE OF EVOLUTIONARY DEVELOPMENTAL PSYCHOLOGY: DEVELOPMENT OF A SEXUAL AVERSION TOWARD CLOSE GENETIC RELATIVES

Contrary to DST proponents' claims that evolutionary psychology ignores development, much work in the field of evolutionary psychology has centered on the development of cognitive abilities (e.g., see Barrett, 2005; Duchaine, Yovel, Butterworth, & Nakayama, 2006; German & Leslie, 2001). An entire issue of the *Journal of Experimental Child Psychology* (July 2003, Vol. 85) was dedicated to research programs aimed at uncovering the

developmental trajectory of a diverse set of psychological abilities using an evolutionary perspective. Topics included aggression, morality, theory of mind, and kin detection and inbreeding avoidance.

The domain of inbreeding avoidance provides a good illustration of how one can investigate an aspect of human psychology from an evolutionary perspective. Starting with a consideration of the selection pressures that existed in ancestral environments and how they impacted an individual's probability of survival and reproduction, it is possible to generate testable hypotheses regarding the kinds of psychological adaptations (i.e., functionally specialized neural circuitry) that evolved to respond to that particular aspect of the environment in a way that led, on average, to an increase in reproductive success.

There are sound biological reasons why psychological mechanisms designed to avoid mating with a close genetic relative are expected to exist. Throughout our species' evolutionary history, the selection pressures posed by deleterious recessive mutations (e.g., Bittles & Neel, 1994) and short-generation pathogens (e.g., Tooby, 1982) would have severely and negatively impacted the health and viability of offspring of individuals who were close genetic relatives. As a result, individuals who avoided mating with close genetic relatives, and instead, mated with someone who did not share an immediate common ancestor, would have enjoyed greater reproductive success. Indeed, evidence from human and nonhuman populations has illustrated the deleterious consequences of inbreeding (e.g., Hepper, 1991).

Given the existence of this adaptive problem (i.e., the avoidance of sexual relations with close genetic relatives), psychological mechanisms for inbreeding avoidance are expected to exist in those species, such as humans, in which sexually mature individuals regularly encountered one another over the life cycle. But how during development do we learn who counts as a close genetic relative? What systems govern the development of sexual aversions toward those categorized as close kin? Whereas DST would suggest that such systems developed through the equal contribution of multiple factors, genetic and nongenetic alike (which does no work and takes us right back where we started), one of the tools evolutionary psychologists use to answer these kinds of questions is to adopt an engineering perspective; that is, what would a well-designed system whose function was to avoid inbreeding look like?

One model of an inbreeding avoidance system has been proposed by Lieberman, Tooby, and Cosmides (2003). Accordingly, two components are required: (1) systems that estimate the probability of relatedness (i.e., kin detection mechanisms), and (2) systems that use estimates of relatedness to

regulate sexual attraction and avoidance accordingly. The detection of kin is hypothesized to rely on evolutionarily and ecologically valid cues, that is, features of the world that correlated with genetic relatedness in ancestral environments. To the extent that different cues signaled the presence of different kinds of kin (e.g., mother, father, offspring, and sibling), different detection systems are expected to exist. For example, cues signaling that an individual is a mother (e.g., the female who breast-fed me) are likely to differ from the cues signaling that someone is a sibling (e.g., the individual with whom I coresided from early childhood); different kinds of information may have been relevant throughout development for identifying different types of family members. In addition to social cues, information derived from the expression of various underlying gene complexes, such as the major histocompatibility complex, may also aid in the detection of kin (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003).

It is possible to investigate empirically the nature of the cues the mind uses to detect kin by quantitatively matching individual variation in the developmental parameters hypothesized to serve as cues to kinship with individual variation in opposition to incest. The logic underlying this method is that the absence of a cue, or set of cues, will result in lower sexual aversions, whereas the presence of a cue, or cues, will result in heightened sexual aversions. Progress has been made in understanding human kin detection systems due to the generation of models such as the one described previously that consider the kinds of environments that existed ancestrally, and the regularities evolution could have zeroed in on to shape systems that decreased the probability an individual mated with a close genetic relative.

CONCLUSION

In closing, despite some misunderstandings, developmental systems theorists and evolutionary psychologists are aligned in their goal to uncover our species-typical architecture and how it develops over the lifespan. The difference is the framework employed to guide such investigations. Whereas DST starts with the assumption that behavioral dispositions and physical traits are an emerging interaction between everything with equal importance, evolutionary psychologists start with specific selection pressures and hypotheses regarding the probable functional design of organisms confronted with those selection pressures. DST would be strengthened by developing a more rigorous program of research capable of generating spe-

cific, testable models and hypotheses. Ultimately, this will allow for more meaningful scientific debate and foster scientific progress.

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The Importance of Developmental Biology to Evolutionary Biology and Vice Versa

RANDY THORNHILL

I emphasize two topics in this essay. One is some findings of developmental biology that are salient for the study of the evolution of human behavior (and of living organisms in general) but are not applied by researchers as widely as they should be. The second is that ontogenies of organisms are designed by Darwinian selection, a reality that some investigators in two approaches that strive to synthesize developmental biology and evolutionary biology—developmental systems theory (DST) and evolutionary developmental biology (EDB or “evo-devo”)—do not appreciate fully as being necessary for such synthesis.

Lickliter and Honeycutt (2003), West-Eberhard (2003), and others have emphasized that the erroneous belief of alternative genetic versus environmental causes responsible for a phenotype's ontogeny and inheritance is widespread in various forms in the current literature of evolutionary biology. Inheritance is the transmission of a phenotype between generations, which requires the phenotype's ontogeny. A useful discussion of biology's concept of inheritance is provided by Flinn and Alexander (1982) in their critique of dual inheritance models of human cultural behavior. According