

Review

The growth of developmental thought: Implications for a new evolutionary psychology

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Abstract

Evolution has come to be increasingly discussed in terms of changes in developmental processes rather than simply in terms of changes in gene frequencies. This shift is based in large part on the recognition that since all phenotypic traits arise during ontogeny as products of individual development, a primary basis for evolutionary change must be variations in the patterns and processes of development. Further, the products of development are epigenetic, not just genetic, and this is the case even when considering the evolutionary process. These insights have led investigators to reconsider the established notion of genes as the primary cause of development, opening the door to research programs focused on identifying how genetic and non-genetic factors coact to guide and constrain the process of development and its outcomes. I explore this growth of developmental thought and its implications for the achievement of a unified theory of heredity, development, and evolution and consider its implications for the realization of a new, developmentally based evolutionary psychology.

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Contents

1. Introduction	354
2. The roles of development in evolution	355
3. Heredity, development, and evolution	355
4. Development and evolutionary psychology	360

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5. Concluding thoughts: towards a new evolutionary psychology	364
Acknowledgments	365
References	365

1. Introduction

The interdependence of development and evolution emerged as a dominant theme in evolutionary biology at the beginning of the 21st century. The reintroduction of development into evolutionary thought has been fueled by a growing recognition that (1) all phenotypic traits arise during ontogeny as products of individual development, and (2) evolutionary change occurs by variation in the patterns of development that give rise to individual development. Contrary to the assumptive base of the neo-Darwinian synthesis of the last century, a number of evolutionary theorists are now proposing that the introduction of phenotypic variation upon which natural selection acts is not strictly limited to random genetic mutation, drift, and recombination, but can result from a wide range of epigenetic processes contributing to individual development (e.g., Jablonka & Lamb, 2005; Neumann-Held & Rehmann-Sutter, 2006; Pigliucci, 2001; West-Eberhard, 2003). This shift in thinking has fostered a growing interest in the dynamics of development within evolutionary biology (e.g., Burian, Gilbert, Mabee, & Swalla, 2000; Gerhart & Kirschner, 1997; Hall, 1999; Hall & Olson, 2003; Raff, 1996) and increasing acknowledgment that evolutionary change reflects changes in development (e.g., Arthur, 2004; Johnston & Gottlieb, 1990; Kirschner & Gerhart, 2005; Robert, 2004). As many readers are no doubt aware, the link between development and evolution has not always been viewed in this way.

For most of the last century the standard account of phenotypic development was deeply reductionistic—genes were thought to directly control the process of development. From this view of development, the instructions for building organisms were thought to be present in their genes and genes were also the exclusive means by which these instructions were transmitted from one generation to the next. Development was thus characterized as the process by which genotypic specification is translated into the traits and qualities of individual organisms. This genocentric view dominated the life sciences during most of the 20th century, prompting the formulation of the “Modern Synthesis” of evolutionary biology (an attempt to integrate Darwin’s theory of evolution with Mendel’s theory of genetics) during the first half of the century and facilitating significant advances in genetics and molecular and cellular biology in the second half of the century. Despite these advances and despite the considerable scientific resources invested in the Human Genome Project over the last decade, in recent years it has become increasingly clear to a growing number of biologists, psychologists, and philosophers that understanding biological or psychological development solely in terms of genes is implausible and will not succeed (see Beurton, Falk, & Rheinberger, 2000).

This insight has led investigators working in biology, psychology, and philosophy to reconsider the established notion of genes as the primary cause of development, opening the door to research programs focused on identifying how genetic and non-genetic factors coact to guide and constrain the process of development and its outcomes. In this paper, I briefly review this growth of developmental thought and its implications for the

achievement of a unified theory of heredity, development, and evolution. I also consider the potential contribution of such an epigenetic theory to the realization of a developmentally based evolutionary psychology (EP).

2. The roles of development in evolution

As pointed out by the morphologist Alberch (1980, 1982) over 25 years ago, development contributes to evolution in two major ways: it both generates the reliable reproduction of phenotypes across generations and introduces phenotypic variations and novelties of potential evolutionary significance. In the first case, the process of development constrains phenotypic variation such that the traits and characters presented to the filter of natural selection are not random or arbitrary. This is the *regulatory* function of development in evolution. It results from the physical properties of biological materials (including genes and chromosomes) and the temporal and spatial limitations on the coactions of the internal, external, and ecological factors involved in the developmental process. These constraints collectively serve to restrict the “range of the possible” in terms of phenotypic form and function. The limited number of body plans observed across animal taxa serves to highlight this regulatory role of development. On the other hand, the availability, coordination, and persistence of formative functional and structural influences involved in the process of development can vary across individuals, and the dynamics of these developmental interactions can result in modified phenotypic outcomes. This production of phenotypic novelties is the *generative* function of development and has significant implications for our understanding of the ways and means of evolutionary change (see Gottlieb, 1998; Johnston & Gottlieb, 1990; Lickliter & Schneider, 2007; Müller & Newman, 2005). In particular, the generative function of development provides the source of phenotypic variation upon which natural selection can act (West-Eberhard, 2003, 2005).

The core of this idea has a long and complex history in both biology and psychology (Baldwin, 1896; Lloyd Morgan, 1896; Osborn, 1896). For example, following the thread of an idea proposed by Etienne Geoffroy Saint-Hilaire more than 100 years earlier, the embryologist deBeer (1940) argued that evolutionary change in the phenotype can only come about by changes in development. However, for deBeer and most other theorists working on the relation between development and evolution during the first half of the last century (e.g., Garstang, 1922; Goldschmidt, 1940) alterations in development that were proposed to initiate evolutionary changes were thought to result from genetic modifications resulting from random mutation, drift, or recombination. Epigenetic processes were not seriously considered in discussions of evolutionary change (even by those focusing on the importance of development) because it was generally supposed that non-genetic factors could not be reliably replicated across generations and therefore could not provide for the heritable variation upon which natural selection could act.

3. Heredity, development, and evolution

Thinking on the scope and nature of inheritance has undergone a considerable shift over the last several decades, due in large part to discoveries in molecular and cellular biology indicating that a variety of developmental resources beyond the genes reliably reoccur across generations. Consistent with the epigenetic emphasis of a developmental systems

framework (e.g., Gottlieb, 2003; Gottlieb, Whalsten, & Lickliter, 1998; Oyama, 2000), we now know that parents can reliably transfer to offspring a variety of non-genetic factors that directly influence phenotypic outcomes, including methylation patterns, chromatin marking systems, cytoplasmic chemical gradients, and a range of sensory stimulation necessary for normal development (reviewed in Harper, 2005; Jablonka & Lamb, 1995, 2005; Lickliter, 2005; Mameli, 2004). In mammals, where the embryo develops within the body of the female, these epigenetic factors can include non-cytoplasmic maternal effects, including uterine effects (vom Saal & Dhar, 1972).

For example, when a female gerbil embryo develops in a uterine environment in which most adjoining embryos are male, its prenatal exposure to the relatively high level of testosterone produced by its male siblings results in later physical maturation and the display of more aggressive and territorial behavior than that displayed by other females (Clark & Galef, 1995). These testosterone-exposed females go on to produce litters in which the proportion of male offspring is greater than the normal 1:1 sex ratio, and as a result their daughters also develop in a testosterone rich uterine environment. This results in maternal lineages differing over generations in the sex ratio and behavioral tendencies of the offspring they produce, without initial changes in gene frequencies between the lineages.

Related work with mice has shown that female embryos that develop in intrauterine proximity to two female siblings mature to be more attractive to males as adults than females that develop prenatally between two male siblings (vom Saal & Bronson, 1978), suggesting that individual differences in male adult sexual behavior and assortative mating can be rooted in epigenetic factors present in the fetal environment. In leopard geckos, male mate choice is shaped by the embryonic temperature experienced by potential female mates during incubation, with adult males choosing females incubated at embryonic temperatures different from themselves. Given a simultaneous choice between females from different incubation temperatures (30.0 and 34.0 °C), males from one incubation temperature (30.0 °C) prefer females incubated at 34.0 °C, whereas males from another incubation temperature (32.5 °C) prefer females incubated at 30.0 °C. (Putz & Crews, 2006). Based on these and similar results documenting how early subtle environmental factors can establish morphological, physiological, neural, perceptual, and behavioral variation between and within sexes, Crews and Groothuis (2005) have argued that patterns of mate choice and sexual and aggressive behavior observed across reptiles, birds, and mammals are best understood in the context of an individual's entire life history, including maternal and other environmental effects at play during the embryonic period.

A growing body of evidence indicates that a persistent change in any of the networks of coactions involved in the reproduction and maturation of an organism can lead to anatomical, physiological, or behavioral modifications in that individual and in many cases in their offspring and grand-offspring as well (see Harper, 2005 for examples). As a result, any definitions of inheritance that do not include all components of the developmental system that are replicated in each generation and which play a role in the production or maintenance of the life cycle of the organism are bound to be less than complete (Gray, 1992; Lickliter & Ness, 1990; Mameli, 2005; Oyama, Griffiths, & Gray, 2001). Contrary to the tenets of the neo-Darwinian Modern Synthesis of the last century, the scope of what constitutes inheritance involves factors above the level of genes and certainly cannot be complete at the moment of fertilization (see Griffiths & Gray, 1994; Honeycutt, 2007; Moore, 2003; West, King, & Arburg, 1988 for further discussion).

All organisms depend on the transgenerational presence of a large number of highly specific and essential developmental resources, including temperature, photoperiod, particular foods, and parental care. As recently highlighted by West-Eberhard (2005), the skepticism of evolutionary biologists regarding the reliability of environmental factors relative to that of genes is among the oddest blind spots of biological thought.

This expanded view of inheritance does not suggest that genes do not play a necessary and significant role in all phenotypic development, nor does it argue against heritable changes in the phenotype originating in changes in the genotype. It does, however, suggest that the passing on of genes from one generation to the next is not a sufficient explanation for the achievement of any phenotypic outcome (although it is certainly a necessary one). What is passed on—what is made available in reproduction—are genes *and* a host of other developmental resources internal and external to the organism that contribute to the reliable and repeatable emergence of phenotypic forms and functions. At present, the idea that inheritance itself is an epigenetic phenomenon is not widely accepted in many quarters and there is no overarching theory that adequately addresses the breadth of heredity processes at play in individual development and evolution. I believe such a theory is attainable, but has yet to receive the focused conceptual and empirical attention it deserves.

In this light, West, King, and their colleagues have provided a compelling account of how the juvenile and adult social experience of brown-headed cowbirds with other cowbirds is a necessary component of both the development and transmission of male song patterns, female preference for male songs, and courtship and mating preferences (West et al., 1988; White, King, Cole, & West, 2002). The cowbird is a brood-parasite and developing fledglings do not encounter their own species until they are juveniles. As a result, their species-typical behavior was long considered a classic example of “innate” behavior. The elegant and exacting research program of West and King has, however, demonstrated that juvenile and adult male and female cowbirds develop critical vocal and reproductive skills through recurring social interactions with their conspecifics. Further, male song patterns, female preference for songs, and courtship behaviors can be transmitted across generations (Freeberg, 1998). For example, young males that were captured from one geographic area and reared with adult males from another geographic area served as models for their own young, inducing them to behave like the geographically distant males that instructed their fathers (Freeberg, 1996). These types of changes in development that result in novel behaviors that recur across generations can facilitate new organism–environment relationships and these new relationships can bring out latent possibilities for morphological, physiological, or further behavioral change (Gottlieb, 2002a). Changes in behavior driven by the physical or social environment can thus be the first step in generating new phenotypic variants on which natural selection can act. Contrary to the established neo-Darwinian perspective, evolutionary change need not begin with genetic change, and evidence obtained from a range of species suggests it often does not (e.g., Newman & Müller, 2000; Slobodkin & Rapoport, 1974; West-Eberhard, 2003). For example, Gottlieb (2002a) describes a compelling example of how a change in behavior can be the initiator of evolutionary change. Historically, the apple maggot fly laid its eggs on haws (the fruit of hawthorn trees). However, when domestic apple trees were introduced into their home ranges in the 17th century, maggot fly females also began laying their eggs on apples. There are now two variants of the apple maggot fly, one that mates and lays its eggs only on haws and one that mates and lays its eggs only on apples.

Because apples mature earlier in the summer season than haws, the life cycles of the two variants are desynchronized. In particular, the two fly variants have different mating and egg-laying times (late summer vs. early fall) and thus no longer mate with one another. Evidence indicates that this change in life history characteristics has resulted in differences in gene frequencies between the two populations (Feder, Roethele, Walzk, & Berlocher, 1997).

The novelty-generating aspects of development involved in such evolutionary change are the result of the developmental dynamics of living organisms, situated and competing in specific ecological contexts, and not simply the result of random genetic mutations (see Lickliter & Honeycutt, 2003a; Oyama, Griffiths, & Gray, 2001 for further discussion). Variations in morphologies, physiologies, and behaviors resulting from modification of the timing, rate, or spatial distribution of developmental processes can place their possessors in different ecological relationships with their environments and if these phenotypic variations provide even slight advantages in survival and reproduction, competitors without the novel phenotype will eventually decrease in frequency in a population. As a case in point, a European passerine bird, the blackcap, has recently shown changes in its migratory behavior which appear to result in changes in mating behavior, size of egg clutches, and success at fledging young (Bearhop et al., 2005). Many passerine birds are seasonal migrants and the timing of spring migration constrains when breeding starts each year. Until recently, all European blackcaps migrated back and forth together, spending summers in northern Europe and the British Isles and winters in Portugal, Spain, and North Africa before gathering in mating grounds in southern Germany and Austria to breed. Blackcaps were typically seen in the British Isles only during the summer months, but the number of them wintering in Britain and Ireland has increased dramatically over the last 40 years. This change is thought to be due to the increased availability of winter provisioning provided by bird feeders, landscapers, and other related human activities. The resulting shift in migratory patterns has allowed northern-wintering blackcaps to be exposed some 10 days earlier than their southern-wintering counterparts to the critical photoperiods that contribute to the initiation of migration and the onset of gonadal development. Even though all blackcaps continue to gather each year at the same mating sites in Germany and Austria, isotopic data indicate that northern blackcaps arrive earlier at the breeding grounds and establish territories and mate with other earlier arriving birds; southern-wintering blackcaps arrive at the same mating sites some two weeks later and are more likely to mate with each other, serving to reproductively isolate northern-wintering birds from the later-arriving southern-wintering population. This shift in migratory patterns appears to confer an advantage to the northern blackcaps, who lay about one more egg per season than do their later arriving cohorts from the south (Bearhop et al., 2005).

These results from the European blackcap illustrate one scenario in which a change in behavior (in this case, a change in migratory patterns brought on by changes in winter food availability) can lead to changes in the timing of breeding, which in turn can lead to the effective reproductive isolation of populations and ultimately, divergence and even sympatric speciation. Shifts in behavior brought about by both changes in the environment and the resulting changes in the activity of the organism can lead to new relationships between elements of the developmental system within and across generations, which can lead to further variations in gene activity, morphology, physiology, or behavior (for additional examples see Balakrishnan & Sorenson, 2006; Malausa et al., 2005). Eventually,

a change in gene frequencies may also occur as a result of breeding populations becoming geographically or behaviorally isolated. As recently argued by Jablonka (2006), mounting evidence suggests that evolution is best viewed as a change in the frequency of transmissible (heritable) phenotypes within a population and not simply as a change in the frequency of genes.

Whereas most accounts of development and evolution have traditionally focused on partitioning the organism's phenotypic traits among those that are genetically determined and those that are produced by the environment (see Maynard-Smith, 2000 for a recent example), a developmental systems approach asserts that no such partitioning is possible, even in principle. In fact, the developmental systems approach originated in opposition to accounts of development that assumed a dichotomous relationship between genetic and environmental influences on development (Lehrman, 1953). In contrast, the goal of the developmental systems approach is to identify the specific ways in which the levels of the developmental system coact over the course of ontogeny to generate its phenotypic traits (Gottlieb, 2003; Johnston & Edwards, 2002; Oyama, 2000). As outlined by Gottlieb (1991, 1997), this involves a temporal description of activity at four levels of analysis (genetic, neural, behavioral, environmental) and the bidirectional effects of such activity among these four levels.

For example, the causal interconnections that underlie the expression of reproductive behavior in ring doves illustrate the rich network of internal and external factors involved in their courtship, nest-building, egg-laying, incubation, and parental care. The ring dove example, based on elegant studies by Lehrman (1964, 1965) and Michel (1986), highlights the historical, contingent, and dynamic nature of phenotypic outcomes by demonstrating that (1) hypothalamic, pituitary, and gonadal functions, essential for the range of reproductive behaviors seen in ring doves, are largely determined by the social and physical stimuli associated with the reproductive cycle (e.g., the long days of spring, the presence and activities of the mate, etc.), (2) changes in levels of circulating hormones influence the dove's sensitivity to specific social and physical stimuli (i.e., the presence of a nest, the activities of the newly hatched young), and (3) the dove's prior reproductive experience alters the pattern and regulation of behavior by its influence on the sensitivity of the dove's nervous system to specific hormones and to social and physical stimuli (see Michel & Moore, 1995 for further discussion). To my knowledge, the psychobiology of the dove's reproductive behavior has yet to be studied at the genetic level of analysis.

Taken together, the coactional traffic between neural function, hormones, behavior, and environmental stimuli involved in the reproductive behavior of the ring dove emphasizes the difficult but critically important task of developmental analysis—filling in the bidirectional details among the specific internal and external factors contributing to the generation of any phenotypic trait. An understanding of the ring dove's reproductive behavior was not achieved by studies conducted at only neurological, endocrine, or physiological levels of analysis; it also required detailed information about the organism's physical and social milieu (see Stern, 1989 for similar examples from mammals). In keeping with a basic tenet of the developmental systems approach, the causes of reproductive behavior in ring doves can be said to be distributed across several levels of organization. In any given aspect of the reproductive process, some factors might be more central and predominate more than others, but the various factors at play always operate in a context in which their effects are dependent upon their relation with other factors. Understanding development thus requires a relational concept of causality.

Griffiths and Gray (1994) have referred to the various factors that contribute to the realization of phenotypic outcomes as *developmental resources*. As we have seen, developmental resources include factors that exert their influence within the organism (e.g., genes, products of gene expression, hormones, neural activity) as well as factors external to the organism (e.g., light-cycles, diet, social stimulation). Use of the terminology of developmental resources emphasizes that none of the internal or external factors involved in development are necessarily primary and rejects the implication that the genes are capable of programming or specifying aspects of the phenotype directly (Johnston & Edwards, 2002; Oyama, 2000).

4. Development and evolutionary psychology

The notion of a centralized program for development that resides in the genes and is directly responsible for an organism's traits and characteristics was a general premise of the neo-Darwinian or "Modern Synthesis" of the last century. This view of life was widespread across the life sciences and characterized development as primarily internally determined, set on course at conception and specified by genetic programs designed and selected over evolutionary time. Versions of this perspective on development were prominent in the writings of the architects of the Modern Synthesis (Dobzhansky, 1951; Mayr, 1961; Simpson, 1944), as well as classical ethologists (Eibl-Eibesfeldt, 1989; Lorenz, 1965) and sociobiologists (Dawkins, 1976; Williams, 1966; Wilson, 1975). This perspective assumed that phenotypic outcomes (including behavior) could be prespecified as part of the innate constitution of the organism and in many cases, be realized relatively independently of the individual's specific physical, biological, and social interactions during development. Although this assumption has been called into serious question over the last decade as we have learned more about the dynamics of phenotypic development (see Lewontin, 2000; Lickliter & Honeycutt, 2003a; Moore, 2002; Morange, 2001; Moss, 2003; Oyama et al., 2001; Robert, 2004 for examples), it remains prominent in some quarters of the behavioral sciences, particularly in contemporary efforts to apply evolutionary theory to psychological issues (e.g., Barkow, Cosmides, & Tooby, 1992; Buss, 1995; Cartwright, 2000; Crawford & Krebs, 1998; Gaulin & McBruney, 2002; Pinker, 1997).

The metatheoretical basis of what has come to be known as EP centers around the notion that innate rules of perception, cognition, and behavior can be prespecified in the genes and transmitted across generations in reproduction. In its strongest form, the established EP viewpoint assumes that many human perceptual and cognitive processes, as well as some overall executive functions, are preformed and triggered by species-typical experience (MacDonald & Herschberger, 2005; Pinker, 2002). Development is thus seen as the unfolding of a program or specification that is already in place, imported into the life cycle by means of the genome. Despite such views on the prespecification of development, most proponents of EP claim that they are "interactionists" and that they have moved beyond outdated notions of strict genetic determinism (e.g., Gaulin & McBruney, 2002; Krebs, 2003). However, the EP version of interactionism represents a deep-seated conceptual separation between causal components that represent nature (genes) and those that represent nurture (see Lickliter & Honeycutt, 2003b for discussion). Tooby and Cosmides (1990, p. 388) have provided a succinct description of this dichotomous form of interactionism:

the individual organism, fixed at conception with a given genetic endowment regulating its developmental programs, encounters its specific ontogenetic

environment, which it processes as a set of inputs to these developmental programs. In other words, the organism blindly executes the programs it inherits, and the ontogenetic conditions it encounters serve as parametric inputs to these programs.

From this view, gene-based developmental programs are the underlying cause of phenotypic traits and non-genetic factors simply activate or trigger these developmental programs specified in the individual's genome. Researchers who appeal to this type of predetermined epigenesis to account for human development and behavior thus attribute the cause of development to either: (a) phylogenic factors, which are assumed to have operated on the ancestors of the individual and which deliver (via the genes) specifications for phenotypic traits, or (b) ontogenetic factors, which occur during the life of the individual and facilitate (or interfere) with the unfolding of these gene-based specifications. This dichotomization of phylogeny and ontogeny as alternative causes for phenotypic development was endorsed by a number of prominent evolutionary theorists in the last century (e.g., Dobzhansky, 1951; Jacob, 1982; Mayr, 1961). The essential logic of this dichotomy is captured in a quote from Ernst Mayr, who over many decades vigorously championed the distinction between evolutionary and developmental causation (1982, p. 68):

Organisms, in contrast to inanimate objects, have two different sets of causes because organisms have a genetic program. Proximate causes have to do with decoding of the program of a given individual; evolutionary causes have to do with the changes of genetic programs through time, and with the reasons for these changes.

The conceptual framework of EP continues this long-standing tradition, arguing for the heuristic value of decoupling proximate (ontogenetic) and evolutionary (phylogenetic) levels of explanation (Buss, 1999; Crawford & Krebs, 1998; Gaulin & McBruney, 2002). As a result, most evolutionary psychologists have sidestepped the role of development in evolution, claiming that they are concerned with phylogenetic rather than ontogenetic causality. Proponents of EP argue that they focus on the “ultimate” causation of human behavior and its function or adaptive value, with the aim of understanding how human behavior was designed or shaped by natural selection over the course of evolution. This emphasis has resulted in minimal interest in development in most of the EP literature (but see Bjorklund & Pellegrini, 2002; Blasi & Bjorklund, 2003; Geary & Bjorklund, 2000).

Thus, we have evolutionary psychologists continuing to speak of “recipes from genes” (Krebs, 2003, p. 845) or “evolved decision rules” (Buss & Reeve, 2003, p. 851), both examples of what I have previously termed the *phylogeny fallacy* (Lickliter & Berry, 1990). The phylogeny fallacy incorporates two related non-developmental assumptions, both of which are suspect in light of current knowledge in the life sciences: (1) specification for an organism's particular phenotypic outcomes can exist independently and in advance of real-time developmental processes, and (2) phylogeny and ontogeny can provide alternative causal explanations for the realization of the phenotypic traits. In contrast to these assumptions, converging evidence from genetics, developmental biology, and developmental psychology points to the fact that the phenotype of any individual is the consequence of a unique web of interactions between the genes it carries, the complex, multidetermined molecular interactions within and across individual cells, and the nature

and sequence of the physical, biological, and social environments through which it passes during development (see Coen, 1999; Gottlieb, 1997; Lewontin, 2000; Müller & Newman, 2003; Neumann-Held & Rehmann-Sutter, 2006; Oyama et al., 2001). Simply put, evidence drawn from across the life sciences tells us that phenotypes are *generated*, not expressed, in individual development.

In their commitment to adaptationism, most evolutionary psychologists reason that natural selection, operating on random genetic mutations, recombination, and drift, is the creative force behind both the design and the realization of a wide range of human behavioral and cognitive traits (Buss, Haselton, Schackelford, Bleske, Wakefield, 1998; Crawford & Krebs, 1998; MacDonald & Herschberger, 2005). In contrast to this line of thinking, recent advances in developmental and evolutionary science support the notion that it is changes in development that are responsible for generating novel phenotypes, which must then pass through the filter of natural selection (Hall, Pearson, & Müller, 2004; Gottlieb, 2002b; West-Eberhard, 2003). Natural selection cannot serve as a creative generator of phenotypic form or phenotypic change. *Natural selection is simply the filter that preserves reproductively successful phenotypes, which are themselves products of individual development.* It follows that by itself, natural selection can only be invoked to explain the frequencies of traits in a population, and not why individual organisms have the particular traits they do (Endler, 1986; Sober, 1995; Walsh, 2003).

In my view, theory building in EP would benefit from an empirical concern with how human behavioral and cognitive traits are generated and maintained in developmental processes (see Caporael, 2003; Quartz, 2003 for similar arguments). All phenotypes have a specific developmental history that explains their emergence, and a developmental mode of analysis is thus the only method that has the potential to fully explicate the structures and functions of maturing and mature organisms. In this vein, Atchley and Newman (1989) have highlighted several types of factors—genetic, maternal, environmental—that affect the stability and variability of developmental outcomes. Their model for integrating genetics with developmental analysis recognizes that multiple factors, including contingencies in mating (which create the developing organism's genome) and contingencies of the maternal environment in which the individual develops (including cytoplasmic and uterine factors in the case of mammals) mediate variability and stability in developmental outcome. As a result, understanding the developmental pathways of morphological, physiological, and behavioral phenotypes requires knowing the dynamic and contingent coactions of internal and external factors operating over the course of individual ontogeny. This approach has a long tradition in developmental psychobiology (e.g., Gottlieb, 1971; Kuo, 1967; Lehrman, 1953) and was well described by Moltz (1965, p. 44) over 40 years ago:

An epigenetic approach holds that all response systems are synthesized during ontogeny and that this synthesis involves the integrative influence of both intraorganic processes and extrinsic stimulative conditions. It considers gene effects to be contingent on environmental conditions and regards the genotype as capable of entering into different classes of relationships depending on the prevailing environment context. In the epigeneticist's view, the environment is not benignly supportive, but actively implicated in determining the very structure and organization of each response system.

This synthesis of internal and external factors and their temporal and spatial relations cannot be specified or predetermined in a genetic program. Development is an historical

process, not a programmed one. This key insight has several important implications, including that the specific physical, biological, and social environments of developing organisms cannot be reduced to “supportive conditions” or an abstract “poser of problems” that must be solved, perspectives still commonplace within the established EP framework.

EP’s characterization of the environment as being essentially supportive or disruptive to the realization of developmental outcomes naturally follows from the central assumptions that phylogenetic factors (often referred to as “distal” causes) can somehow be separated from *and* are more causally significant in directing human development and behavior than ontogenetic (proximate) factors. This bias can be traced in large part to the non-controversial tenet that to be subject to natural selection, *phenotypes must be inheritable*. I take no issue with this claim. However, like the majority of evolutionary biologists of the last century, most evolutionary psychologists continue to presume that such inheritance is strictly genetic (Bjorklund, 2003). As discussed above, this restricted definition of inheritance promotes a decidedly one-sided view of gene–environment interactions and sidesteps converging evidence from genomics, molecular and cellular biology, developmental biology, and developmental psychology indicating the importance of inheritance above the level of the genes (Harper, 2005; Jablonka & Lamb, 2005; Sapp, 2003).

A compelling illustration of this insight comes from numerous demonstrations that modified early experience in one generation can predictably influence phenotypic outcomes in subsequent generations, even in the absence of the original experiential modification. For example, differences in physical (body weight, endocrine responses) and behavioral (fearfulness) measures have been observed between groups of rats whose mothers (Denenberg & Whimbey, 1963; Francis, Diorio, Liu, & Meaney, 1999) or grandmothers (Denenberg & Rosenberg, 1967) were handled or not handled as infants. Despite their obvious importance to both developmental and evolutionary concerns, the coactions across levels of the developmental system that contribute to these types of transgenerational effects on both physiological responsiveness (in particular, the development of the hypothalamic adrenocortical system) and behavioral responsiveness (including curiosity, novelty seeking, and emotional regulation) remain poorly understood. We do know, however, that aspects of maternal behavior such as licking and grooming can modify gene expression in rat pups, as measured by increases in mRNA coding for proteins involved in behaviors known to be affected by differences in maternal care, such as the HPA stress response and spatial learning (reviewed by Meaney, 2001). For example, rat pups which receive relatively high levels of licking and grooming following birth have more hippocampal glucocorticoid receptors. These receptors serve as a brake on the HPA stress response and as a result these pups show less physiological and behavioral response to stress throughout the life span than do those which received lower levels of maternal grooming as pups (Champagne, Francis, Mar, & Meaney, 2003). Further, as adults, females born to mothers that provided more licking and grooming tend to lick and groom their own pups more than females which received less maternal nurturance (Liu, Diorio, Tannenbaum, & Caldji, 1997), another example of how maternal lineages can differ over generations in their offspring’s behavioral tendencies without initial changes in gene frequencies between the lineages.

Such demonstrations of the bidirectional traffic between behavior and gene expression illustrate a key tenet of the developmental systems framework—the emergent products of development are epigenetic, not just genetic. In addition to their genes, organisms reliably

inherit a wealth of developmental resources and as the rodent maternal behavior example makes clear, this typically includes a stimulative environment containing parents and peers, as well as the varied provisions of their ecological and social niche (Freeberg & White, 2007; Lickliter, 2005; West & King, 1987). Features of an organism's developmental system can thus extend across generations and provide for both the stability *and* the variations in phenotypic outcomes that researchers in biology and psychology seek to understand.

5. Concluding thoughts: towards a new evolutionary psychology

The relationship between genotype and phenotype was thought to be relatively simple and straightforward for most of the last century; the genotype was thought to code the “instructions” for the phenotype. Advances across developmental science over the last several decades have demonstrated that this is not the case. The recent shift in thinking about development to include a deeper appreciation of its probabilistic and contingent nature has been fostered by a growing body of evidence demonstrating the importance of activity and experience to the developmental process. Development always occurs “in the middle of things” and as a result developmental outcomes are shaped by the specific experiences, conditions, and contexts individual organisms encounter as they live their lives. Understanding how this works in terms of the interdependence of development and evolution will require both description and experimentation, with the goal of explaining how one generation sets up or provides the necessary developmental conditions and resources for the next. In other words, understanding the persistence and change of phenotypic forms over time will require an empirical focus on the activities and resources that generate them.

Recognizing development as a process that is situated, contingent, and activity-dependent represents a major shift in thinking from the prespecified view of development that was widespread in the life sciences for most of the last century (and that continues to be promoted in much of contemporary evolutionary psychology). Given the importance of context and contingency to all phenotypic outcomes, it seems obvious that simplistic genetic determinism cannot be true (see Burian, 2005 for additional arguments). This recognition represents a significant first-step toward the goal of a unified theory of heredity, development, and evolution. As the historian and philosopher Keller noted in *The Century of the Gene* (2000, p. 9), “it seems evident that the primacy of the gene as the core explanatory concept of biological structure and function is more a feature of the 20th century than it will be of the 21st”. In my view, the consequences of a broader-based approach to understanding the ways and means of development and evolution will be far-reaching. At the very least, this shift in scope will raise new questions about the importance of activity and experience, the nature and extent of heredity, and the sources of phenotypic stability and variability (see Harper, 2005; Robert, 2004; Oyama, 2000 for additional discussion).

The pursuit of these questions can forge new links between biology and psychology and can contribute to the realization of a long overdue *developmentally based* evolutionary psychology. By explicitly not making a distinction between genetic and environmental systems of inheritance (e.g., Tooby, Cosmides, & Barrett, 2003), a developmental systems approach can provide an evolutionary perspective on human behavior and cognition that moves beyond notions of genetically *or* environmentally determined development.

This “new and improved evolutionary psychology” (see Buller, 2005) can complement and extend current work in evolutionary developmental biology and contribute to the larger project of reintegrating developmental and evolutionary theory in the 21st century. It is becoming increasingly clear that how well we understand evolution will depend in large part on how well we understand development.

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