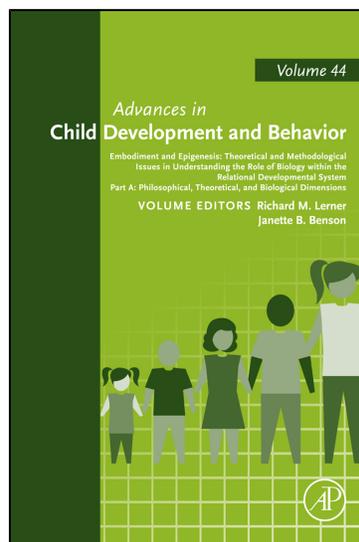


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The Origins of Variation: Evolutionary Insights from Developmental Science

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Abstract

Evidence from contemporary epigenetic research indicates that it is not biologically meaningful to discuss genes without reference to the molecular, cellular, organismal, and environmental context within which they are activated and expressed. Genetic and nongenetic factors, including those beyond the organism, constitute a dynamic relational developmental system. This insight highlights the importance of bringing together genetics, development, and ecology into one explanatory framework for a more complete understanding of the emergence and maintenance of phenotypic stability *and* variability. In this Chapter, I review some examples of this integrative effort and explore its implications for developmental and evolutionary science, with a particular emphasis on the origins of phenotypic novelty. I argue that developmental science is critical to this integrative effort, in that evolutionary explanation cannot be complete without developmental explanation. This is the case because the process of development generates the phenotypic variation on which natural selection can act.

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"At the present time there is hardly any question in biology of more importance than this of the nature and causes of variability"

(Darwin, 1882, p. vi)



1. INTRODUCTION

It has been over 150 years since Charles Darwin and Alfred Russell Wallace's papers outlining their remarkably similar theories of evolution were read to the Linnean Society (1858). Their theories of evolution rested on two basic ideas: (1) the common descent of all living organisms and (2) natural selection as the major agent of evolutionary change. Darwin's more detailed theory of evolution laid out the following year in *The Origin of Species* (1859) was founded on the notion of descent with modification (changes occur over generations producing new species over time). While Darwin's theory of evolution certainly set biology on a new course, offering an explanation for the remarkable biological diversity observed across plants and animals, it did not explain the origins of phenotypic modifications or novelties, a fact pointed out by St. George Mivart in his book, *On the Genesis of Species* (1871).

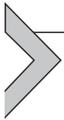
Mivart was one of Darwin's most prominent critics (documented by the fact that Darwin devoted almost an entire Chapter in the final sixth revision of the *Origin* to address Mivart's criticisms of his theory). Mivart was among the first to point out that natural selection can account for the preservation and increase in frequency of phenotypic traits and characters within a population, as Darwin proposed, but could not account for their origin (see also Cope, 1886). Harris (1904, p. 401) captured Mivart's insight succinctly when he wrote that "natural selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest." For Mivart, natural selection was not a creative force in evolution, but rather was the eliminator of the unfit. Mivart (1871, p. 240) noted that "natural selection favors and develops useful variations, though it is impotent to originate them." His insight that natural selection can only change the frequency or range of phenotypic variations already present in a population led Mivart to relegate natural selection to a more minor role in evolution than Darwin had proposed and to argue that other factors that were capable of generating the variations upon which selection can then act must be at play. Mivart thought that these factors must somehow be based on the united action of internal and external forces that modified individual development, but he

was necessarily vague as to how this might work, referring to this process as “obscure and mysterious”. Of course, Mivart and his contemporaries of nineteenth century biology knew relatively little about the details of development or the internal and external forces at play in evolutionary change. Nevertheless, Mivart’s insight that the origins of new forms or traits must come about through changes in the process of development was a shift in thinking about the mechanism of evolution, one that has received serious attention within the biological sciences only relatively recently (e.g., Arthur, 1997; Carroll, 2005; Gerhart & Kirschner, 1997; Hall, 1999; Müller & Wagner, 1991; Raff, 1996; West-Eberhard, 1989, 2003).

The lack of concern with the role of development in evolution over much of the past century was not due to Darwin, who came to increasingly appreciate the importance of development to heredity over the course of his career (see Winther, 2000). Rather, the dismissal of development can be traced to the pervasive influence of the “Modern” evolutionary synthesis of Darwinian and Mendelian principles forged by Theodosius Dobzhansky, Ronald Fisher, Julian Huxley, Ernst Mayr, Sewell Wright, and others in the 1930s and 1940s (Amundson, 2005; Gottlieb, 1992; Lickliter & Honeycutt, 2009; Robert, 2004). This view of evolution held that variation in populations was the result of random genetic mutation and recombination, and as a result, proposed that populations evolve by changes in gene frequencies due to genetic drift, gene flow, and natural selection. The “Modern Synthesis” of the twentieth century thus promoted population genetics as key to understanding evolutionary change and dismissed the importance or relevance of development in understanding evolutionary issues.

Due in large part to the prominence of population genetics in evolutionary theory over much of the twentieth century, it is only within the past several decades that developmental and evolutionary scientists have focused their theoretical and empirical efforts on exploring the nature of the links between development and evolution (see Gottlieb, 1992; Hall, 1999; Sanson & Brandon, 2007; West-Eberhard, 2003 for examples). A concern with how development is involved in evolutionary change is now evident among biologists and psychologists working in formally diverse areas of research, including genomics, cellular and molecular biology, developmental biology, evolutionary theory, ecology, and comparative and developmental psychology, as well as philosophers of biology (e.g., Arthur, 2004; Bateson & Gluckman, 2011; Davidson, 2001; Gilbert & Epel, 2009; Hall, Pearson, & Müller, 2004; Lickliter & Honeycutt, 2003; Moore, 2008; Nijhout, 2003; Richardson, 1998; Robert, 2004).

As we gain a deeper appreciation of the importance of the process of development to the production of phenotypic variation, new questions are being raised about how and to what extent developmental change contributes to evolutionary change (e.g., Bjorklund, 2006; Blumberg, 2008; Johnston & Gottlieb, 1990; Lickliter & Schneider, 2006; Moore, 2002; Oyama, 1985; Oyama, Griffiths, & Gray, 2001; West-Eberhard, 2003), topics I review in this Chapter. My overarching goal is to explore how an integration of genetic, epigenetic, and environmental levels of analysis can provide a conceptual framework for understanding how developmental systems can generate novel phenotypes. More generally, I argue that evolutionary explanation cannot be complete without developmental explanation. This is because the process of development generates the phenotypic variation on which natural selection can act.



2. SOURCES OF PHENOTYPIC VARIATION

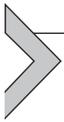
A long-standing problem of both developmental and evolutionary theory has been how to account for the sources of phenotypic variability (as well as phenotypic stability) observed within and across generations. In other words, how is it that some anatomical, physiological, and behavioral traits remain the same across time and some are modified or change across time? As all students of introductory biology know, variation in phenotypic traits and characters evident across individuals of a species was a crucial component of Darwin's theory of evolution by natural selection. He realized that for natural selection to act, individuals must vary in terms of their anatomy, physiology, or behavior. For Darwin (as well as for Alfred Russell Wallace), such variations provided the opportunity for natural selection to filter out those anatomical structures, physiological capabilities, and behavioral forms that are less successful and promote those that offer some reproductive advantage, thereby providing the engine for evolutionary change. Despite the importance of phenotypic variation to Darwin's theory, the sources of phenotypic variation were not well understood in nineteenth or even much of twentieth century biology. Darwin himself admitted "our ignorance of the laws of variation is profound" (1859, p. 167). As it turned out, it was not until the twenty-first century that most biologists finally began to consider phenotypic variation as an important area of study rather than as noise or nuisance to their experimental designs (e.g., Bateson & Gluckman, 2011; DeWitt & Scheiner, 2004; Hallgrímsson & Hall, 2005; Piersma & van Gils, 2010; Pigliucci, 2001;

West-Eberhard, 2003; but see Baldwin, 1902; Bateson, 1894; Brooks, 1883 for notable exceptions).

As a result, a new perspective on the sources of phenotypic variation has taken shape over the past several decades. This perspective is based on a relatively simple but fundamental insight: given that all phenotypes arise during ontogeny as products of development, it follows that the primary basis for phenotypic variation within and across generations must be the patterns and processes of development. *Development is thus critical to evolution because it is the process that provides the phenotypic variation on which natural selection can act.* The thread of this insight can be traced back to several embryologists and developmental biologists working in the first half of the twentieth century, including Walter Garstang (1922), Edward Russell (1930), Gavin de Beer (1930), Richard Goldschmidt (1940), Conrad Waddington (1942), and Ivan Schmalhausen (1949). Although each of these biologists had a distinctive perspective on how to characterize the links between development and evolution, they all promoted the notion that changes in individual development were a potentially important basis for evolutionary change. For example, Waddington (1942) was highly critical of evolutionary models in which genes were portrayed as directly causing development or were directly acted upon by natural selection. Schmalhausen (1949) was likewise critical of genocentric models of development and evolution and, similar to Waddington, emphasized the importance of the environment in inducing changes in development. As I review later, these views were well outside mainstream twentieth century thinking about evolution, but are now being reconsidered across the biological and psychological sciences. This shift has involved moving beyond the notion of genes as the fundamental cause of phenotypic traits, thereby allowing for a reconsideration of a variety of extragenetic factors at play in the emergence, maintenance, and modification of phenotypes within and across generations.

As a result of this conceptual shift, there is growing recognition of the necessity of considering and defining the complex transactions among genetics, development, and ecology in order to understand the range of morphological structures, shifts in behavioral repertoires, and other instances of phenotypic variation observed across plant and animal species (e.g., Bateson & Gluckman, 2011; Gilbert, 2005; Gilbert & Epel, 2009; Nijhout, 2003; Piersma & van Gils, 2010; Schlichting & Pigliucci, 1998; West-Eberhard, 2003). This *relational* approach views the novelty-generating aspects of evolution as being 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, genetic drift, or genetic recombination. This is a paradigmatic shift in emphasis, as genetic factors were argued to be the only evolutionary relevant source of phenotypic variation by the neo-Darwinian or “Modern Synthesis” school of evolutionary biology that dominated twentieth century life sciences (e.g., Dobzhansky, 1937; Huxley, 1942; Mayr, 1963; Williams, 1966).



3. TWENTIETH CENTURY PERSPECTIVES ON DEVELOPMENT AND EVOLUTION

Following the rediscovery of Mendel’s work in 1900 and the growing influence of Mendelian genetics during the next several decades, evolutionary biology came to distance itself from its earlier concerns with embryology and developmental biology and embrace the new science of population genetics (see Amundson, 2005; Gilbert, 1994; Gottlieb, 1992 for useful overviews). Unlike experimental embryology, population genetics was not focused on the development of the individual organism, rather it focused on organisms as members of a breeding population and on how best to calculate the probabilities of changing gene frequencies in this population of breeding organisms under this or that set of circumstances over generations. In particular, population geneticists were interested in understanding the role of genetic mutation, genetic recombination, and selection in the changes in gene frequencies found within a population and how these genetic changes resulted in evolutionary change (Provine, 1971). This approach concentrated on the traits of adults in populations and virtually ignored questions about how these traits were actually realized during the course of individual development. The noted evolutionary biologist Maynard-Smith (1985) argued that attempting explanations of evolution in terms of individual development was an “error of misplaced reductionism”.

The Modern Synthesis (see Mayr & Provine, 1980) was able to effectively sidestep concerns with the role of development in evolution by proposing that there were two relatively independent classes of causal factors responsible for an individual’s phenotypic traits: (1) *ultimate causes*, those that derive from internal or intrinsic factors (e.g., genes), molded over evolutionary time by natural selection and (2) *proximate causes*, everything else that interacts with these internal factors during development to provide the materials or experiences necessary to trigger the expression of form and function thought to be encoded in the genes (e.g., the environment).

This causal dichotomy for explaining phenotypic outcomes was grounded on the assumption that development is primarily internally determined, set on course at conception by genetic programs (*ultimate causes*) that had been designed and selected over evolutionary time. In contrast, *proximate causes* were defined as those factors involved in “decoding the genetic program” (Mayr, 1974). Developmental factors were thus seen as proximate causes, making development essentially irrelevant to the understanding of evolution (Lickliter & Berry, 1990). Widespread acceptance of this proximate–ultimate distinction effectively kept development and evolution as separate scientific concerns during most of the second half of the past century. Since genotypes were thought to be the direct causes of phenotypes, evolutionary biology had no causal or explanatory need for the process of development.

Watson and Crick’s discovery of the structure and function of DNA in 1953 served to reaffirm the genocentric position of the Modern Synthesis: if genes are DNA and copying errors from DNA to RNA to protein is the source of genetic variation, then evolution must indeed be “changes in gene frequencies in populations” (Dobzhansky, 1937). Development was thus increasingly viewed as merely the reading out of genetic programs that were assumed to be the products of natural selection. This gene-centered perspective had at its core an underlying false premise that went unquestioned by many psychologists and biologists over the course of the twentieth century: the bodily forms, physiological processes, and behavioral patterns of organisms could be specified *in advance* of the organism’s development.

However, this assumption of prespecification is a profoundly *nondevelopmental* point of view. Adult traits are seen to be the result of genetic instructions or programs, with little concern for the intervening resources, relations, and causes that transform the adult from the zygote. This view has several serious shortcomings, not the least being that it assumes *as a given* the developmental outcomes that actually require a causal developmental analysis (Gottlieb, 1997; Kuo, 1967; Robert, 2004). Although nativists have continued to apply the notion of prespecification to both developmental and evolutionary issues (e.g., Buss, 2005; Carruthers, Laurence, & Stich, 2007; Pinker, 2002; Spelke & Newport, 1998), it has become increasingly clear that perspectives that favor the notion of prespecified phenotypic traits are not up to the task of making sense of the dynamics of the developmental process and its varied outcomes (Lerner, 1991, 2006; Lewkowicz, 2011; Overton, 2006; Oyama, 1985; Spencer et al., 2009).



4. TAKING A DEVELOPMENTAL POINT OF VIEW

Any successful theory integrating development and evolution must ultimately account for (1) the emergence of complexity of organization by differentiation, (2) the stability of form and function across generations, and (3) the origin and range of variability across individuals of a species (Laubichler & Maienschein, 2007; Lickliter, 2013). Attempts at this intellectual synthesis have engaged (and frustrated) scientists for centuries. Indeed, much of the content of the eighteenth and nineteenth centuries theorizing about development and evolution focused on explaining the possible mechanisms for these three phenomena (see Depew & Weber, 1995; Gould, 1977; Mayr, 1982 for useful overviews). As briefly reviewed above, in the twentieth century, biologists eventually converged on a bottom-up approach to account for the similarities and differences observed across individuals, holding that genes were the key to understanding the fundamental characteristics of development. Genes came to be seen as the cause for an organism's growth and development, as well as the cause for the intergenerational stability and variability of traits and qualities observed within species (see Keller, 2000; Sapp, 2003). Widespread application of this gene-centered framework resulted in significant advances in molecular and cellular biology and fostered the growth and popularity of fields such as sociobiology, behavioral genetics, and evolutionary psychology in the twentieth century. However, recent advances in several fields of biology, including what Conrad Waddington (1957) termed *epigenetics* and what Brian Hall (1992) and others have termed *evolutionary developmental biology*, have made it clear that gene-centered approaches to developmental and evolutionary issues minimize or simply overlook the wide range of factors, transactions, and contingencies at play in both development and evolution.

A key insight contributing to these advances in the biological sciences is that changes in development (brought on by changes in the context of development) are necessary in order to explain the types of variation that can be filtered by natural selection. Recent research with Darwin's finches (genus *Geospiza*), famous for their role in Darwin's formulation of the principle of natural selection, provides a useful example of how the complex interplay of molecular, cellular, and ecological factors contribute to relatively rapid and dramatic phenotypic change (in this case, the variety of beak shapes observed across these 13 species of finches distributed across the Galapagos Islands). Such developmental plasticity provides a potent pathway for organisms to rapidly change structure and function in response to

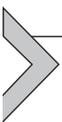
environmental resources and changes (see [West-Eberhard, 2003](#)). In the case of Darwin's finches, in the time frame of just 1–2 million years, a founding group of finches from South America generated more than a dozen different finch species in the remote Galapagos Islands, including some with large pliers-like beaks capable of cracking nuts and seeds and some with forceps-like beaks able to extract insects from fruit. Darwin had noted these birds' remarkable differences in beak size and shape on his visit to the Galapagos Islands during his *Beagle* voyage in 1835, but due to the degree of variation across species, he did not realize at that time that they were all finches. Further reflection on this variation after his return to England contributed to Darwin's formulation of the critical role of natural selection in the direction of evolutionary change.

The standard genocentric explanation of the striking variation in beak size and shape seen across these closely related finch species suggests that genetic mutation, recombination, and reassortment of genes in an island's founder population would occasionally result in variant birds that had somewhat smaller and more forceps-like beaks or somewhat larger and more pliers-like beaks than those of the founder population. These individuals would be more likely to explore and exploit different food niches (insects vs. seeds), potentially leading to increasing geographic and behavioral isolation from one another. Morphological change would be gradual in this scenario, but over many generations, differential reproduction (based in part on relative feeding success) would eventually result in the selection of several variations of the original founders' beak type.

In contrast, recent synthesis of molecular, cellular, and ecological research indicates that the pathway to the remarkable variations observed in beak size and shape is more contingent on the context of development *and* more rapid than traditional views of evolutionary change would suggest (e.g., [Abzhanov et al., 2006](#); [Abzhanov, Protas, Grant, Grant, & Tabin, 2004](#); [Grant, Grant, & Abzhanov, 2006](#)). Current evidence indicates that the size and shape of the finch beak are determined during development by the growth and differentiation of neural crest cells that settle around the mouth of the developing bird embryo. These neural crest cells produce a growth factor protein called bone morphogenetic protein 4 (*Bmp4*), which stimulates the deposition of bone and beak materials during embryogenesis. This protein is produced earlier in embryonic development and at higher levels in the finch species with larger and wider beaks than in the closely related finch species with longer and narrower beaks ([Abzhanov et al., 2004](#)). Further, when *Bmp4* is experimentally introduced into the beak neural crest cells of chicken embryos, they develop broader and larger beaks than control chicks.

The introduction of other growth factors did not have this effect. Related work has found that a protein that mediates calcium signaling and plays a role in cell and tissue differentiation (calmodulin or CaM) is expressed at higher levels in finch species with longer and narrower beaks than in those with the longer wider beaks (Abzhanov et al., 2006). It appears that a variety of inter-related factors, including the number of neural crest cells, the level of signaling that stimulates or inhibits the production of growth factor protein and calmodulin, and the types of signals that induce cell death of the neural crest cells, are all at play in generating the beak shape variation seen across these finch species. How these various factors and their relations are regulated by the birds' experience and ecology (particularly the type of food sources available) is not fully understood, but given the wide adaptability of neural crest cells, it seems that relatively large modifications in beak size and shape have been accomplished with relatively few changes in the developmental process. This potential for rapid phenotypic adjustment to the contextual features of development has important implications for evolutionary change, in that it would increase the likelihood that members of the population could quickly take advantage of new or changing resources and habitats (Gottlieb, 2002).

The finch beak example illustrates how a focus on the complexities of the dynamics of development and evolution is bringing together genetics; molecular, cellular, and developmental biology; neuroscience; and evolutionary biology to construct a more comprehensive explanation of the ways and means of the stability and variability of phenotypic development (e.g., Lickliter & Harshaw, 2010; Müller & Newman, 2003; Neumann-Held & Rehmann-Sutter, 2006; Overton, 2006). This integrative approach is providing important opportunities for developmental science to contribute to evolutionary theory, a dramatic shift from the state of affairs just several decades ago. As Robert (2008) has pointed out, taking a developmental point of view requires understanding that there is more to development than differential gene expression, that development is not a genes-*plus*-environment phenomenon, and that the causal analysis of development is required to understand evolution.



5. DEVELOPMENTAL SOURCES OF PHENOTYPIC STABILITY AND VARIABILITY

The morphologist Pere Alberch (1982) pointed out over 30 years ago that development contributes to the evolutionary process in at least two key ways, one *regulatory* and the other *generative*. First, the process of

development constrains phenotypic diversity by limiting the “range of the possible” in terms of both form and function. This robustness of development, despite genetic or environmental perturbations, is the *regulatory* function of development (Siegal & Bergman, 2002; Wimsatt, 1986). Some years ago, Maynard Smith and colleagues (1985, p. 266) defined developmental constraint as “a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system”. In the most general sense, developmental constraints result from the physical properties of biological materials and the temporal and spatial limitations on the relations among internal and external factors at play in developmental processes. These constraints effectively bias the course of evolution, limiting the type and range of variation available to natural selection.

The process of development also introduces phenotypic variation and novelties of potential evolutionary significance. This is the *generative* function of development. For example, many phenotypes show graded responses to factors or events that occur along natural environmental gradients (e.g., temperature, pH levels) and dichotomous responses (polyphenisms) to factors or events that occur in a dichotomous manner (e.g., the presence or absence of predators or particular food items, see Nijhout, 2003). This flexibility of phenotypic outcomes in response to variations in or modifications of genetic and environmental factors is referred to as *phenotypic plasticity*. West-Eberhard (2003, p. 33) defined phenotypic plasticity as “the ability of an organism to react to an internal or external environmental input with a change in form, state, movement, or rate of activity”. She argues that such plasticity in response to changed environmental conditions is an important basis of evolutionary novelties (see also Frankino & Raff, 2004; Johnston & Gottlieb, 1990; van der Weele, 1999).

For example, new or novel behaviors brought on by alterations in normal prenatal and/or postnatal rearing environments can lead to new organism–environment relationships, including changes in diet, habitat use, and/or social and reproductive behavior. These behavioral shifts can be maintained across generations if such changes or alterations in the developmental rearing environment persist over time, promoting a cascade of possible changes in morphology and physiology over time (Gottlieb, 2002; Johnston & Gottlieb, 1990; Kuo, 1967).

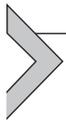
The phenomenon of domestication, the process by which organisms change in terms of morphology, physiology, or behavior as a result of the human control of their breeding, feeding, and care (Hale, 1969), provides

an informative and often overlooked illustration of the complex dynamics involved in this transgenerational shift in phenotypes (Belyaev, 1979; Lickliter & Ness, 1990; Price, 1999). The variance of phenotypes among wild and domestic strains of a single species has long been appreciated. Darwin (1859, 1868), for example, documented the wide array of alterations in size, shape, coloration, productivity, and behavior evident in domesticated animals and speculated on their possible sources. Following the neo-Darwinian synthesis of the first half of the twentieth century and its emphasis on population genetics, most students of domestication assumed that the morphological, physiological, and behavioral differences observed between wild and domestic strains of animals could be explained by random and nonrandom genetic mechanisms associated with captive rearing. These genetic mechanisms include natural and artificial selection, inbreeding, genetic drift, and genetic mutation (Price & King, 1968).

Although the importance of genes as sources of phenotypic variation in both wild and domestic animals is indisputable, domestication is certainly not simply a matter of changing gene frequencies. The transition from free living to captivity is accompanied by many and varied changes in an animal's physical, biological, and social environments and we know that these changes can bring about significant modifications in phenotypic development. For example, Clark and Galef (1981) have shown that specific differences in the morphology, physiology, and behavior of wild and domestic strains of gerbils (*Meriones unguiculatus*) can be traced to relatively minor changes in the developmental resources available in their early rearing experiences. Gerbils reared in standard laboratory cages without access to shelter show accelerated eye opening following birth, earlier sexual maturity, increased docility, and reduced reactivity to humans when compared to gerbils reared in laboratory conditions that allow free access to shelter, as would normally occur in the wild. Of course, the change from free living to captivity for most species is typically accompanied by changes in the availability of not only shelter but also space, food and water, predation, and possibilities for social interaction (Price, 1999). The influence of such changes on the nature and range of phenotypic change under domestication remains relatively unexplored (Lickliter & Ness, 1990).

One research program that has attempted to address these changes is that of Dmitri Belyaev (1979) (see also Trut, Plyusnina, & Oskina, 2004) on the domestication of silver foxes (*Vulpes vulpes*). Selection for tame behavior in silver foxes began in the 1950s and continues to the present. Selection was based solely on behavioral criteria. It is important to note that

such selective breeding (common in cases of domestication) is selecting for “developmental outcomes” (in this case, tameness), not genes. In addition to becoming more doglike in their behavior over the course of more than 40 generations, the silver foxes quickly showed a number of other phenotypic modifications, including changes in the skeleton (shortened legs, tail, and snout and a widened skull), hormonal changes, altered tail and ear posture, and decreased sexual dimorphism. Belyaev (1979) proposed that the experiential conditions of domestication led to neural and hormonal changes that in turn activated dormant genes, thereby revealing hidden genetic potentials previously undetected in wild silver foxes. This idea remains speculative, but Belyaev’s interpretation that certain genes were able to switch from dormant to active states in response to changes in environmental conditions is certainly plausible in the light of recent advances in epigenetics (Hallgrímsson & Hall, 2011) and would help explain the rapid rate of phenotypic changes observed across only a few generations. The more we learn about the mechanisms by which the environment (both internal and external, see Stotz, 2006) can influence the activation and expression of genes (see Bateson & Gluckman, 2011; Gilbert, 2010; Hallgrímsson & Hall, 2011), the more it becomes clear that gene/environment coaction has to be a cornerstone of explanations of phenotypic variation.



6. THE ECOLOGY OF DEVELOPMENT AND EVOLUTION

The growing acknowledgment of the dynamics of development by biologists and psychologists over the past several decades has fueled a renewed interest in how the developmental process contributes to evolutionary change (e.g., Arthur, 2004; Bjorklund, 2006; Gilbert, Opitz, & Raff, 1996; Gottlieb, 1992, 2002; Lickliter & Honeycutt, 2009; Pigliucci, 2007; Robert, 2004; West-Eberhard, 2003). Of particular importance in this concern is the recognition that variations in morphology, physiology, and/or behavior arising from modifications to the developmental process can place organisms in different ecological or functional relationships with their environments. If these phenotypic variations provide even slight advantages in survival and reproduction, then competitors without the novel phenotype will eventually decrease in frequency in the population, thereby contributing to evolutionary change.

For example, a European passerine bird, the blackcap (*Sylvia atricapilla*) has shown changes in its migratory behavior over the past several decades that have resulted in changes in wing shape, beak size, mating behavior,

size of egg clutches, and success at fledging young (Bearhop, Fiedler, Furness, Newton, Votier, & Waldron 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 past 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, as well as an increase in winter temperatures. 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 that winter in the United Kingdom 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 2 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, which lay more eggs per season than do their later-arriving cohorts from the south (Bearhop et al., 2005).

The blackcap provides a compelling example of how a change in behavior (in this case, a change in migratory patterns brought on by changes in 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. Contrary to the assumptive base of the neo-Darwinian synthesis of the past century, the introduction of phenotypic variation on which natural selection acts is not simply the result of random genetic mutations. Rather, variations in phenotypes and the resulting opportunities for evolutionary change are the result of a wide range of epigenetic processes occurring at different timescales and involving factors internal *and* external to the developing individual.

The blackcap example thus suggests that that understanding the limits and the possibilities of developmental systems is crucial for furthering

our understanding of evolution (Lickliter & Harshaw, 2010; Lickliter & Honeycutt, 2009; Oyama, 1985; Oyama, Griffiths, & Gray, 2001). This task will require both description and experimentation, with the goal of explaining how each generation sets up the necessary developmental conditions and resources for the next and how specific changes in developmental conditions lead to specific changes in behavior, anatomy, physiology, and gene expression. For example, differences in physical (body weight, endocrine responses) and behavioral (fearfulness) measures have long been observed between groups of rats whose mothers (Dennenberg & Whimbey, 1963; Whimbey & Dennenberg, 1967) or grandmothers (Dennenberg & Rosenberg, 1967) were handled or not handled as infants. Despite its obvious importance to both developmental and evolutionary concerns, these types of transgenerational effects on both physiological responsiveness (for example, 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 influence 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 hypothalamic pituitary adrenal axis (HPA) stress response and spatial learning (reviewed by Meaney, 2001, 2010). For example, rat pups that receive relatively high levels of maternal 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 (Champagne, Francis, Mar, & Meaney, 2003).

Drawing on decades of work by developmental psychobiologists (see Michel & Moore, 1995), we know that the conditions that best favor the expression of modified or novel phenotypes are species-atypical alterations in environmental conditions and contingencies that occur early in ontogeny (e.g., Blumberg, 2008; Denenberg, 1969; Gottlieb, 1971; Kuo, 1967; Levine, 1956; Renner & Rosenzweig, 1987). Of course, shifts in behavior brought about by alterations to the developmental system can arise at any stage of the life cycle, but are generally more likely to occur earlier in individual development. This point was highlighted by several evolutionary theorists over the past century (e.g., de Beer, 1930; Garstang, 1922; Goldschmidt, 1940; Waddington, 1975), who despite their different backgrounds and perspectives realized the significance of embryonic and neonatal periods

of development for the generation of phenotypic novelties. These early periods of development are a time of rapid morphological, physiological, and behavioral change, and modifications to an individual's developmental system during this time can initiate a host of physical and behavioral changes, and in some cases (given the availability of appropriate developmental conditions) persist across subsequent generations. Developmental science has much to contribute in this area, particularly to explore how previous developmental outcomes and current experiences in specific contexts combine to influence these processes.

For example, during the later stages of prenatal development the precocial avian embryo is oriented in the egg such that its left eye is occluded by the body and yolk sac, whereas the right eye is exposed to diffuse light passing through the egg shell when the brooding hen is intermittently off the nest during the incubation period. This differential prenatal visual stimulation resulting from the embryo's invariant postural orientation in the egg has been shown to facilitate the development of the left hemisphere of the brain in advance of the right hemisphere. Further, this light-induced developmental advantage for the left hemisphere has been shown to influence the direction of hemispheric specialization for a variety of postnatal behaviors, including visual discrimination, spatial orientation, feeding behavior, and various visual and motor asymmetries (reviewed in [Rogers, 1995](#)). Altering the normal pattern of light stimulation available during prenatal development can modify this typical pattern of brain and behavioral development ([Deng & Rogers, 2002](#)). For example, a left spatial turning bias is seen in the large majority of quail chicks following hatching (>85%, [Casey & Lickliter, 1998](#)). Research has shown that this species-typical turning bias can be reversed by occluding the right eye and stimulating the left eye with light prior to hatching. Further, the induction of such lateralization can be prevented by incubating eggs in darkness or by providing the same level of light stimulation to both eyes in the period prior to hatching ([Casey & Lickliter, 1998](#)). These findings suggest an equipotentiality for hemispheric specialization and indicate that late prenatal experience can have a powerful influence on the stability and the variability of functional lateralization.

Similar findings from birds and mammals have demonstrated that the features of available prenatal and early postnatal sensory stimulation (such as amount, intensity, or the timing of presentation and the sources of stimulation) coact with specific organismic characteristics (such as the stage of organization of the sensory systems, previous history with the given properties

of stimulation, and the current state of arousal of the young organism) to contribute to the developmental course of species-typical perceptual biases and preferences, learning, and memory (Harshaw & Lickliter, 2011; Lickliter, 2005; Spear, 1984; Spear & McKenzie, 1994). Changes in these basic processes can set up a trajectory of experiential events that can result in modifications to typical patterns of species identification, habitat selection, diet preference, and other key aspects of the organism–environment system. Such phenotypic variations provide the opportunity for natural selection to filter out those novelties that are less successful and promote those that provide some reproductive advantage.

Environmental conditions, including social factors, can influence development by a rich interplay of both external and internal signals. Work with desert locusts, a well-known agricultural pest, illustrates the intricate links between internal and external factors contributing to the effects of experience on phenotypic plasticity. The desert locust (*Schistocerca gregaria*) is usually cryptic in color (green), has short wings and a large abdomen, and is solitary. It typically actively avoids other locusts and flies alone at nighttime. However, under certain climatic conditions and the resulting increase in desert vegetation, their numbers can explode, triggering a rapid increase in population density that results in a dramatic transformation of their color (now black and bright yellow) and social behavior (now gregarious). Normally, solitary locusts now molt into adults with longer wings and more slender abdomens and form bands and eventually swarms consisting of billions of locusts, causing catastrophic damage to agricultural crops.

This dramatic transformation includes many morphological, physiological, and behavioral changes involving numerous chemical messengers and changes in the expression of more than 500 genes (Kang, Chen, Zhou, Liu, Zheng, & Li et al., 2004). Anstey, Rogers, Ott, Burrows, and Simpson (2009) have shown that the key agent in this dramatic phenotypic plasticity is the neurotransmitter serotonin, which is synthesized in the locust's thoracic nervous system in response to multiple sensory cues (touch, smell or sight) provided by social contact with other locusts when the population density increases. Within as little as 2 h of proximity to other locusts, elevated serotonin levels (up to three times the levels seen in solitary locusts) can switch behavior from mutual aversion to mutual attraction, recruiting additional chemical messengers and allowing the formation of the enormous locust swarms that wreak havoc on human populations.

Further, the gregarious migratory phenotype can be retained for several generations after the crowding experience that initiated the original

transformation of the solitary phenotype. This transgenerational effect is mediated, at least in part, by the neurotransmitter L-dopa, which is introduced by gregarious females into the foam surrounding their eggs during egg laying. If this foam is experimentally transferred from eggs laid by gregarious female locusts onto eggs laid by solitary females, the solitary eggs hatch into gregarious locusts (McCaffery & Simpson, 1998).

Of particular importance to our concern with the links between development and evolution is the fact that such phenotypic variability across individuals (the grist for the mill of natural selection) can be generated by genetic *and* nongenetic means. These means are varied, including random mutation, drift and other well-recognized genetic processes; they also include less well-studied extragenetic components, such as maternal cytoplasmic constituents, mRNA, and chromatin-modifying enzymes (chromatin is the protein–DNA complex involved in fitting the genome into the cell nucleus), all known to influence changes by which the fertilized egg cell transforms into a complex organism during embryonic development and in later life allows cells to respond to hormones, growth factors, and other regulatory molecules (Crews, 2011; Jablonka & Lamb, 1998).



7. EPIGENETICS: BRIDGING THE GAP BETWEEN GENOTYPE AND PHENOTYPE

Recent advances in genetics and molecular and developmental biology have converged to demonstrate that the expression of genes is affected or modified not only by other genes but also by the local cellular as well as the extracellular environment of the developing organism, including cell cytoplasmic factors, hormones, and sensory, motor, and social stimulation provided by the external environment (reviewed in Davidson, 2001; Jablonka & Raz, 2009; Johnston & Edwards, 2002; Gottlieb, 1998). This advance in our understanding of genomics and its links to ecology has fueled the growth of *epigenetics*, the study of emergent properties in the origin of the phenotype in development and in the modification of phenotypes in evolution (Hallgrímsson & Hall, 2011).

Conrad Waddington first described epigenetics early in the 1940s as the branch of biology that studies the causal interactions of genes with their environment that bring the phenotype into being (Waddington, 1942). Of course, the genetic, molecular and cellular details of phenotypic development were poorly understood at that point in time. Indeed, in the

first half of the twentieth century, the gene was largely a theoretical concept without a physical identity (Crews & McLachlan, 2006). Nevertheless, based in part on his experimental work with fruit flies, Waddington came to question the canonical view that there was a simple correspondence between genes and phenotypic traits and proposed that only an understanding of the interaction of genes with each other and with the internal and external environment of the organism could successfully account for phenotypic development. Waddington was advocating a new conceptual framework for the study of development and evolution, one that emphasized changes in what he termed “developmental systems”. From this view, the contribution of the genome always depends on the influence of the features of its surrounding contexts, beginning with the cytoplasmic environment provided by the mother’s egg at conception. Waddington’s efforts to integrate genetics, development, and evolution was well ahead of the prevailing consensus of his time and was motivated by what he viewed as the inability of population genetics to provide a workable model of the operation of genes in development and evolution (Hall, 2001).

The epigenetic framework of development and evolution outlined by Waddington, as well as a handful of other biologists and psychologists working in mid-twentieth century (e.g., Gottlieb, 1971; 1987; Ho & Saunders, 1979; Kuo, 1967; Løvtrup, 1974; Matsuda, 1987), went relatively ignored for the next several decades. This was due in large part to the widespread acceptance of the gene-centered framework of the Modern Synthesis across the life sciences during this time. However, a growing body of evidence drawn from genetics, cellular and developmental biology; neuroscience; and developmental psychology has converged in recent years to provide substantial support for the validity of the epigenetic framework (e.g., Bjorklund, 2006; Hallgrímsson & Hall, 2011; Gottlieb, Wahlsten, & Lickliter, 2006; Ho, 1998; Jablonka & Lamb, 1995, 2005; Meaney, 2010; Michel & Moore, 1995; Szyf, Weaver, & Meaney, 2007). Epigenetics-oriented approaches to development and evolution have the phenotype rather than the genotype as their primary focus of interest and in the general sense, are concerned with aspects of the process of development that lead to flexibility or plasticity when the environment or genome changes (West-Eberhard, 2003). Epigenetic research is now documenting the intricate relational regulatory networks involved in the developmental process, as well as pointing to the need to revise several enduring ideas regarding development and heredity over the past century. These include the notions that (1) genes contain

specific programs or instructions for building organisms, (2) genes are the exclusive means by which these instructions are reliably transmitted from one generation to the next, and (3) there can be no meaningful feedback from the environment to the genes (see Lickliter & Honeycutt, 2009 for discussion).

A wide range of recent findings in epigenetics (e.g., Crews, 2011; Meaney, 2010; Zhang & Ho, 2011) have made clear that gene activity or expression is determined by the developmental system as a whole, with positive and negative feedback loops between genes, cells, organs, body, and environment. For example, in rats, higher levels of nurturing maternal behavior leads to postnatal remodeling of the hippocampal glucocorticoid receptor gene (*GR*, known to be involved in glucocorticoid feedback sensitivity and response to stress). These changes in *GR* emerge over the first week of life, are reversed with cross-fostering to less-nurturing females, and persist into adulthood (Weaver et al., 2004). The epigenetic framework emerging in contemporary biology highlights the developmental contingency of gene expression and thus focuses research attention on dynamic developmental processes at many levels of organization, and in its best forms, without an implicit bias as to what factors or levels are driving the process. Further, in keeping with a relational developmental systems perspective, epigenetics emphasizes that all developmental processes take place in context. Larsen and Attalah (2011) provide a poignant example of this idea, pointing out that a fertilized egg, once cracked open and stirred, can no longer produce an embryo, even though its entire genome remains intact.

As the philosopher Richard Burian (2005, p. 177) has described it, “the context-dependence of the effects of nucleotide sequences entails that what a sequence-defined gene does cannot be understood except by placing it in the context of the higher-order organizations of the particular organisms in which it is located and in the particular environments in which those organisms live.” A growing number of developmental biologists and psychologists are thus expanding the focus of their research attention to not only the internal features of the developing organism (genes, cells, and hormones) but also the contributions of the physical, biological, and social resources available to the individual in its developmental context (e.g., diet, temperature, social interaction, see Gilbert, 2005). These internal and external resources generate a range of phenotypic outcomes of interest to psychologists, including behavioral profiles or “personalities” (see Groothuis & Trillmich, 2011) observed within and across species.



8. THE IMPORTANCE OF BEHAVIOR TO EVOLUTIONARY CHANGE

In neo-Darwinian views of evolution, changes in phenotype are seen as the outcome of genetic change in a population (presumably produced by natural selection). However, as discussed earlier, phenotypic change must come before natural selection is possible. In other words, variation must exist in a population before selection among the variants can occur. In this light, a number of biologists and psychobiologists have proposed that behavior can potentially play a leading role in evolutionary change (e.g., Bateson, 1988; Ho, 1998; Johnston & Gottlieb, 1990; Oyama, Griffiths, & Gray, 2001; Plotkin, 1988; Stamps, 2003; Wcislo, 1989). While the importance of behavior as an agent of evolutionary change is not a new idea (Baldwin, 1896; Hardy, 1965; Lloyd Morgan, 1896; Wyles, Kunkel, & Wilson, 1983), it has yet to be fully incorporated into evolutionary theory. The work of Gilbert Gottlieb (1987, 1991, 1992) provided an innovative framework for making sense of how changes in behavior could contribute to the evolutionary process. In Gottlieb's view of evolution, enduring transgenerational phenotypic change can occur at the behavioral, anatomical, and physiological levels before it occurs at the genetic level. His theory proposes that changes in development that result in a novel behavioral shift that recurs across generations can facilitate new organism–environment relationships. These new relationships, which can include “invasion” of novel environments, can bring out latent possibilities for morphological or physiological change. Eventually, a change in gene frequencies may also occur as a result of geographically or behaviorally isolated breeding populations. Thus, changes in behavior can be the first step in creating new phenotypic variants on which natural selection can act (Gottlieb, 1992, 2002).

In this view of evolutionary change, genetic change is often a secondary or tertiary consequence of enduring transgenerational behavioral changes brought about by alterations of normal or species-typical development. These developmental modifications often put individuals in new relations with their local environments, subjecting them to new selection pressures and increasing the likelihood of eventual change in the genetic composition of the population. This perspective introduces a plurality of possible pathways to evolutionary change, complementing genetic factors such as mutation, recombination, and drift.

In a seminal paper exploring the nature of the links between development and evolution, Johnston and Gottlieb (1990) provided an example of how new phenotypes may arise due to an enduring change in behavior before changes in gene frequencies. They describe a scenario in which a population of rodents whose normal diet consists of soft vegetation encounters a new food source of relatively hard but highly nutritious seeds. As the animals learn to sample and eventually increase the representation of seeds in their diet, a number of developmental effects of their new diet become evident, including possible changes in body size and composition, fecundity, age of sexual maturation, and indirect changes in morphology. For example, as the diet changes from soft vegetation to harder seed items, the mechanical stresses exerted on growing jaw tissues during development will change. Given that patterns of bone growth are known to be determined, in part, by forces exerted on the growing bone (Frost, 1973), the skeletal anatomy of the jaw will likely be different in the animals that experience hard vs. soft diets early in life. Such changes in diet have, in fact, been shown to affect the jaw and skull of rats (Bouvier & Hylander, 1984). In this example, behavioral change in members of a population (a preference for a new diet of hard seeds) leads to specific anatomical changes (modification of the jaw and teeth). Such changes can endure across generations, and as long as the new diet remains available, may eventually lead to changes in gene frequency as a result of long-term behavioral or geographic isolation among variants within the population. Following this line of thinking, West-Eberhard (2005, p. 6547) has argued that “genes are probably more often followers than leaders in evolutionary change”.

Developmental scientists are well suited to provide systematic investigation of the developmental and ecological dynamics contributing to such behavioral plasticity or malleability. Starting with the pioneering work of Hymovitch (1952), Levine (1956), and Cooper and Zubek (1958), a large body of research has explored the influence of early experiential alterations on later exploratory behavior and problem-solving abilities (see Renner & Rosenzweig, 1987 for a review). Expanding on this research tradition is critical to a more complete understanding of the mechanisms responsible for shifts in behavior and psychological functioning due to changes in species-typical environments, resulting in changes in the activity of the organism and leading to potential variations within and across generations in anatomy, morphology, or physiology (see Garipey, Rodriguiz, & Jones, 2002). The example of Darwin's finches discussed earlier highlights how, in a relatively short time, birds arriving from the mainland were able to occupy many

different habitats. Finches' observed behavioral flexibility and adaptability likely played an important role in their successful colonization of new environmental settings (Tebbich, Sterelny, & Teschke, 2010).

The observed behavioral changes reported in enriched rearing and early handling experiments (i.e., enhanced exploratory behavior, increased problem-solving abilities, and resistance to stress) are the types of behaviors that could promote the seeking out and utilization of new habitats, leading to a host of other potential phenotypic novelties and setting the stage for possible evolutionary change. In this light, Gottlieb (1997) pointed out that animals that have had considerable variation in social and physical experiences early in life are more likely to seek out variation later in life, showing greater levels of exploratory behavior and novelty seeking than animals having more limited early experience. This sort of behavioral plasticity, the willingness to approach and explore novel objects, places, or situations (termed "neophilia" by Thorpe, 1956), can increase the likelihood of particular individuals utilizing or migrating to new habitats, where they could encounter different types of functional demands. Although many changes in functional demands would be transient, others, including diet, day length, and climate, could be long lasting and persist across generations, revealing latent morphological or physiological variability not expressed in the original environment. How these processes work and the underlying biology involved remains poorly understood (but see Duckworth, 2009) and psychology can provide a developmental and ecological perspective to the ways and means of transgenerational processes and their effects.

A related task for developmental science is to provide more detailed empirical evidence for the role of behavior as a leading edge in the evolutionary process. Changes in behavior brought about by changes in prenatal and postnatal rearing environments have been well documented in comparative psychology (e.g., Kuo, 1967; Lickliter, 2005; Michel & Moore, 1995; Renner & Rosenzweig, 1987) but how such changes are significant to evolutionary issues has received little empirical or conceptual attention. Experimental demonstrations of how novel behavioral phenotypes lead to genetic, morphological, or physiological alterations can help further explicate the specific biological and psychological mechanisms involved in the behavioral initiation of evolutionary change. This approach can investigate behavior as the *product* of development and also as a component of the *process* by which development takes place (Stotz, 2008). This type of approach will require a multidimensional process-oriented methodology that includes a variety of levels of analysis beyond the behavioral

level, including the environmental regulation of gene expression and cellular function, the effects of sensory stimulation on neural and hormonal responsiveness, and the direct and indirect effects of a developing organism's biological, ecological, and social organization (see [Meaney, 2010](#); [West-Eberhard, 2005](#)).



9. PATHS INTO THE FUTURE

We have not yet arrived at a comprehensive synthesis of development and evolution, but it seems to be underway. Whether the relational developmental approach to evolution outlined in this Chapter is up to this task remains to be seen, but it does provide a perspective that has moved many biologists and psychologists beyond outdated notions of genetically *or* environmentally determined phenotypic development. This shift, long overdue, is raising new questions for developmental and evolutionary scientists about the importance of activity and experience, the nature and extent of heredity, and the sources of phenotypic stability and variability (see [Charney, 2012](#); [Harper, 2005](#); [Dworkin, Foster, Ledon-Rettig, Moczek, Nijhout, & Sultan et al., 2011](#); [Overton & Müller, 2012](#); [Reid, 2007](#); [West-Eberhard, 2003](#)). In addition, conceptual reformulations and empirical evidence emerging from new disciplines and topics of research (genomics, epigenetics, evolutionary developmental biology, ecological developmental biology, and systems biology) are providing developmental science increasing opportunities to contribute to a fuller understanding of the evolutionary process. This scholarship should ultimately provide a real synthesis of development, evolution, and heredity. My focus in this Chapter has been to explore how a developmental point of view is helping forge a more complete explanation for the origin of novel phenotypic traits, one of the most enduring challenges of evolutionary biology. Much work remains to be done on this project, but we can now say with confidence that understanding evolutionary change will require an understanding of development.

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