Primer

Developmental evolution

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Biologists and psychologists are re-thinking the long-standing premise of genes as the primary cause of development, a view widely embraced in 20th-century biology. This shift in thinking is based in large part on: (1) the growing appreciation of the complex, distributed regulatory dynamics of gene expression; and (2) the growing appreciation of the probabilistic, contingent, and situated nature of development. We now appreciate that what actually unfolds during individual development represents only one of many possibilities. This expanded focus on the developmental process, often referred to as a *developmental systems* approach, has far-reaching implications for developmental and evolutionary theory, including new ways of thinking about the consequences of activity and experience, the emergence of novel properties or traits, the nature and extent of heredity, and the origins of phenotypic variability.

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INTRODUCTION

Does development influence evolution? Over the last 150 years, the answer to this question has taken many forms. It might seem obvious that knowledge of development would be necessary to understand evolution. Indeed, many biologists held this view during much of the 19th century. In fact, Darwin viewed characters or traits as resulting from changes in the process of individual growth and reproduction,[1] insisting that all inheritance must be a product of both the transmission and the development of traits. However, little was known about the process of development during Darwin's time and for many years thereafter. Ultimately, the dominant school of evolutionary thought in the 20th century—known today as the Modern or Neo-Darwinian Synthesis—abandoned any interest in development as a contributor to evolution.[2]

Although the many mysteries and complexities involved in the processes of development are far from solved, we now know that these processes involve widely distributed interactions across many levels of the individual and its environment. Scientists working with species as divergent as fruit flies, angler fish, macaques, and humans[3–5] have provided compelling evidence over the last several decades that the development of any physical or behavioral trait is the result of a complex web of co-actions among the organism's genes, molecular interactions within and across cells, and the nature and sequence of the physical, biological, and social environments in which the individual develops.

This growing appreciation of the interactive, distributed, and contingent nature of development has inspired many biologists and psychologists to reconsider the long-standing premise of genes as the primary cause of development, a core tenet of 20th-century biology. This realization has, in turn, fostered the growth of research programs focused on identifying how the relations among genetic and nongenetic factors both guide and constrain the course of development.[6,7] The implications of this broader-based approach to our understanding of development—referred to as a *developmental systems* approach—are considerable and far-reaching, including novel ways of thinking about the roles of activity and experience in development, the emergence of novel properties and traits, the nature and extent of heredity, and the origins of phenotypic variability. Given the breadth of these implications, I focus in this essay on one particular dimension—the links between developmental and evolutionary change.

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THE ROLES OF DEVELOPMENT IN EVOLUTION

Darwin's theory of evolution, described in the *Origin of Species*, was one of descent with modification. He did not, however, explain the origins of such modifications, a fact pointed out by St. George Mivart in 1871[8] (Figure 1). Mivart recognized that natural selection can account for the preservation and increase of phenotypic traits within a population, as Darwin proposed, *but not for their origin*. This is where development enters the picture. Although Mivart did not identify development as a source of novel traits or characters, growing evidence from molecular, developmental, and evolutionary biology have indicated that this can be the case.

Broadly speaking, development contributes to evolution in two important ways: (1) It generates the reliable reproduction of phenotypes across generations and (2) it introduces phenotypic variations and novelties of potential evolutionary significance.[9] In the first case, the process of development constrains phenotypic variation such that the traits and characters sifted through the filter of natural selection are not random or arbitrary. This is the *regulatory* function of development in evolution. It involves the physical properties of biological materials (including genes and chromosomes), and the temporal and spatial limitations on the coactions of internal, external, and ecological factors. These constraints collectively serve to restrict the 'range of the possible' in phenotypic form and function. For example, the limited number of body plans observed across animal species highlights the regulatory or constraining role of development. Most animals have a body form that is bilaterally symmetrical, meaning that it can be divided into matching halves along a central axis. This bilateral arrangement, with one of each sensory channel (eye, ear, nostril) and limb pair on either side, is seen in nearly all animals, including humans.

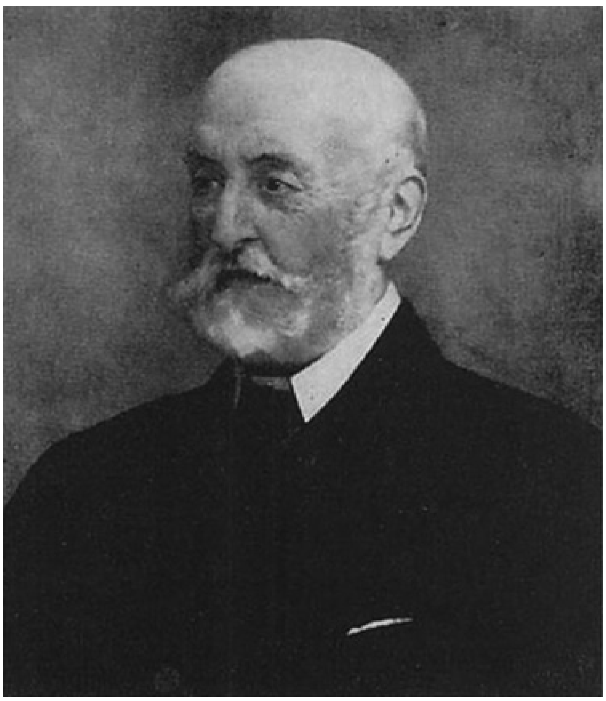

FIGURE 1 | St. George Jackson Mivart (1827–1900). Mivart was among the first to recognize the limited role of natural selection in explaining evolutionary change.

Importantly, developmental influences can also vary across individuals, and the complex interactions of these influences across all levels, from biochemical to cultural, can result in modified phenotypic outcomes. For example, the developmental environment (e.g., temperature) can determine the sexual phenotype in some species of reptiles and fish, induce morphological changes that allow individuals to better escape predation in several amphibian species, and determine caste affiliation in some social insect species (see Gilbert[10] for discussion and additional examples). This production of phenotypic change, called the *generative* function of development, has significant implications for understanding the mechanisms of evolutionary change.[11] In particular, the generative function of development provides a source of phenotypic variation upon which natural selection can act.[12] Simply put, evolutionary novelties largely originate in the process of development.

This idea of the importance of development to evolution has a long, complex history in both biology and psychology. Following the thread of an idea proposed by French naturalist Etienne Geoffroy Saint-Hilaire in the early 1800s, the embryologist Gavin de Beer[13] proposed that evolutionary change can only come about by changes in development. However, for de Beer et al. working on the relation between development and evolution during the first half of the 20th century, modifications in development that could initiate evolutionary changes were thought to be the result of random genetic mutation, genetic drift, or genetic recombination. Environmental factors were not typically considered in discussions of evolutionary change (even by those focusing on the importance of development) because it was thought that nongenetic factors could not be reliably replicated across generations and therefore could not provide a basis for the heritable variation upon which natural selection could act. However, individuals of most animal species are typically raised by parents of the same species, in an environment or developmental niche that has been occupied by that species for many generations. This continuity of early experience across generations serves to surround the developing organism in a physical, biological, and social environment that is as characteristic of its species as is its genotype. Gottlieb's[14] decades of research on the development of species identification in ducklings provides an elegant example of how nonobvious this continuity of early experience can be. His program of research in behavioral embryology documented how the features and patterns of transgenerationally recurring prenatal sensory experience, including self-stimulation, both guide and constrain young ducklings' attention, perception, and learning during the prenatal and postnatal periods of development. This species-typical experience effectively ensures successful species identification after hatching, without appeals to 'instinctive,' 'innate,' or 'genetically determined' behavior (see Blumberg, *Development evolving: The origins and meanings of instinct*, *WIREs Cogn Sci*, also in the collection *How We Develop*).

MOVING ON FROM NARROW VIEWS OF EVOLUTIONARY CHANGE

Missing the importance of development to evolution in biology and psychology during most of the 20th century came largely from a narrow definition of evolution as *a change in the genetic composition of populations*.[15] In this framework, development was seen as the process by which genotypic specification was translated into the phenotypic traits of individuals, including their anatomy, physiology, and behavior. This narrow perspective on both development and evolution was promoted by several generations of biologists, and was based on three widely held underlying assumptions regarding development and heredity:

1. Instructions for building organisms reside in genes.
2. Genes are the exclusive means by which these instructions are faithfully transmitted from one generation to the next.
3. There is no meaningful feedback from the environment or the experience of the organism to its genes.

These three assumptions fit neatly within the conceptual framework of population genetics, which is concerned with how genetic mutation, genetic recombination, and natural selection could lead to changes in gene frequencies in a population. In the mid-20th century, the architects of the 'Modern Synthesis' of evolutionary biology (including Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, and George Gaylord Simpson) promoted these three assumptions and saw no need to integrate development into their collective attempts to synthesize the tenets of Darwinism and Mendelism.[16] The gene-centered framework of the Modern Synthesis of evolutionary biology effectively sidestepped the issue of development while also downplaying any role of the environment in the evolutionary process. If genes contain all the necessary information for phenotypes and if events and experiences during individual development could not directly influence the phenotypic traits of offspring, then internal factors (genes) clearly had to have priority over external factors when attempting to explain both development and evolution.

In recent decades, these assumptions about development and heredity have all been called into question. Specifically, growing evidence from molecular biology, neuroscience, and behavioral ecology, among others, indicates that genes are *not* the only source of inheritance across generations. In addition to genetic inheritance, epigenetic inheritance, behavioral inheritance, environmental inheritance, and cultural inheritance are increasingly recognized as contributing to transgenerational phenotypic stability.[12,17]

REASSESSING THE LINKS BETWEEN DEVELOPMENT AND EVOLUTION

Expanding the definition of inheritance to include developmental resources beyond the genes is reshaping theory and research across the evolutionary and developmental biology. For example, evolutionary developmental biology (often referred to as *evo-devo*) is a growing field of research that involves a partnership among evolutionary, developmental, and molecular biologists to better integrate our understanding of developmental processes and evolutionary change. Unlike the gene-centered emphasis of the Modern Synthesis, evo-devo views evolution as changes in developmental processes rather than simply changes in gene frequencies. Evo-devo thus deals with how developmental processes can affect and effect evolutionary change. This perspective motivates a wide range of research questions, including how modifications in developmental processes can lead to novel phenotypes, the role of developmental plasticity in evolution, and how ecological factors influence developmental and evolutionary change.[18] For example, the discovery of the homeotic Hox gene family in vertebrates in the 1980s motivated researchers to empirically assess the roles of gene duplication and gene regulation in the evolution of morphological diversity. One of the most surprising findings from this early work in evo-devo was the realization that the genes involved in the morphological form of animals as different as a fruit fly, a mouse, and a human being are fundamentally the same.[19] The differences in form across these different species turn out to be due less to differences in genes and more to how the genes are regulated during embryonic development.

Like evo-devo, the rapidly growing field of epigenetics is also leading to the reassessment of links between development and evolution (see Moore, *Behavioral Epigenetics*, *WIREs Syst Biol Med*, also in the collection *How We Develop*). Epigenetics is typically defined as changes in gene expression and function that are not due to changes in the DNA sequence. More broadly, it is the study of how the environment can affect the genome of the individual during its development, as well as the development of its descendants, without change in the coding sequence of the DNA itself. Evidence from epigenetics research is calling into question longstanding assumptions regarding the fundamental and privileged role of genes in development, heredity, and evolution. In particular, growing evidence from epigenetic research contradicts all three widely held underlying assumptions regarding development and heredity, namely: (1) instructions for building organisms resides in the genes, (2) genes are the exclusive means by which these instructions are transmitted from one generation to the next, and (3) there is no significant feedback from the environment or the experience of the organism to its genes. These assumptions have been called into question through numerous demonstrations of the environmental regulation of gene expression and cellular function, as well as the varied effects of sensory stimulation and social interaction on neural and hormonal responsiveness.[20]

The epigenetic approach to evolutionary issues is broadening our understanding of phenotypic plasticity, which may be defined broadly as the ability of an organism to modify its phenotype in response to its environment (see Bateson, *Robustness and plasticity in development*, *WIREs Cogn Sci*, also in the collection *How We Develop*). The capacity for phenotypic plasticity was long considered by most biologists to be genetically determined. However, the rich interplay between genes and their environments demonstrated by contemporary epigenetic research has revealed a range of mechanisms whereby developing individuals can modify their morphology, physiology, or behavior in response to the features of their developmental context, suggesting additional pathways to evolutionary change.

For example, timing of hormone production and the sensitivity of organs and tissues to the presence of hormones can be readily altered by features of the environment and both can result in significant changes in morphology and behavior.[21,22] Many organisms' nervous systems monitor their environment and can rapidly change or adjust the hormonal milieu within the organism. The presence and levels of hormones in turn alter gene expression patterns, which in turn contribute to the maintenance or modification of phenotypes.

Research on desert locusts provides a striking example of the links between context, gene expression, and phenotypic plasticity.[23] The desert locust (*Schistocerca gregaria*) is usually cryptic in color (green) and solitary. In this form it avoids other locusts and flies alone at nighttime. However, under certain shifts in climatic conditions that result in an increase in desert vegetation, the number of locusts can explode, triggering a rapid increase in population density that leads to transformation of their color (now black and bright yellow) and a dramatic change in their social behavior (Figure 2). With the increase in vegetation, normally solitary locusts form bands of hoppers that eventually form swarms consisting of billions of locusts; these swarms can cause catastrophic damage to agricultural crops. This transformation in color and social behavior involves morphological, physiological, and behavioral changes that have been traced to the action of numerous chemical messengers and more than 500 genes. Anstey et al.[23] have shown that a key agent in this remarkable transformation 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 population density increases rapidly. Within as little as 2 h of increased proximity to other locusts, elevated serotonin levels switch behavior from mutual aversion to mutual attraction, allowing the formation of enormous locust swarms within just a matter of days.

Such demonstrations of phenotypic plasticity in response the environmental change have led some

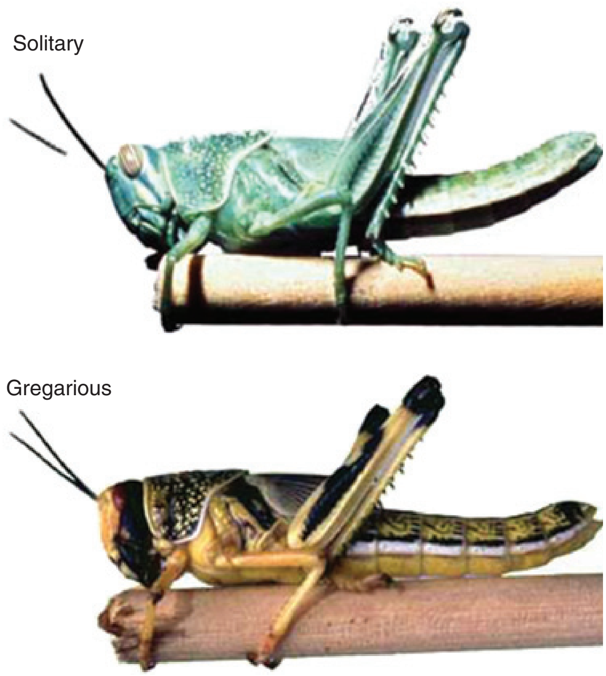

FIGURE 2 | Solitary and gregarious morphs of the desert locust. This dramatic and rapidly produced difference in both appearance and behavior is triggered by increased social stimulation.

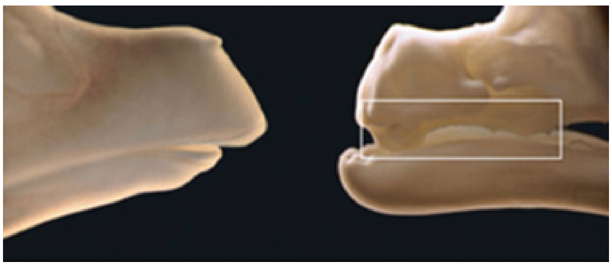

FIGURE 3 | Normal and experimentally modified beaks of chicken embryos. The presence of teeth is highlighted in the embryo on the right, an example of hidden developmental-genetic potential.

developmental and evolutionary biologists to propose the idea that an accumulation of hidden genetic variation and developmental potential can present itself when developing organisms are challenged by unusual developmental conditions.[11] A striking example of this hidden variation is the demonstration that chickens can be induced to grow teeth.[24] Under typically occurring prenatal conditions, when the chick embryo's oral epidermis and oral mesenchyme cells interact, the embryo grows the usual, species-typical chick beak (Figure 3, left). However, when the chick embryo's oral epidermis is experimentally placed in contact with mouse mesenchyme during embryogenesis, the embryo produces a mammalian tooth rather than a chick beak (Figure 3, right). This startling turn of events hints at the enormity of hidden developmental–genetic potential, which can provide developing organisms a key pathway for modulating phenotypic change in response to changing environmental conditions. Genes interact with other constituents of the cell, which interacts with other cells in the organism, which interacts with other organisms. It is out of this dynamic, multileveled process that phenotypes emerge. In other words, phenotypes are the outcomes of the whole developmental system, comprising the organism embedded within its particular genetic and cellular make-up, and in its specific physical, biological, and social environments.

CONCLUSION

Because of the variability of developmental resources available across different environments, and because only a portion of the genome is actually expressed, what is realized during the course of individual development is only one of many possible outcomes. This is a core tenet of *probabilistic epigenesis*, the view that neither physical nor behavioral development can have a predetermined outcome. Consistent with this probabilistic view of development, there is now considerable evidence that parents transfer to offspring a variety of nongenetic factors in reproduction that can directly influence phenotypic outcomes, including DNA methylation patterns, chromatin marking systems, RNA-interference, cytoplasmic chemical gradients, and a range of sensory stimulation necessary for normal development.

The realization that control for the course of development does not reside in any one factor or component, but rather in the nature and dynamics of the relations among factors *internal* and *external* to the organism, shifts conceptualizing development away from the gene-centered, prespecified framework assumed for most of the last century and toward an appreciation of development as a situated and historical process that is dependent on developmental resources distributed across the organism–environment system. Further, it is the process of development itself that produces the phenotypic variation that is screened by natural selection. This insight provides a rationale for the necessity of bridging developmental and evolutionary accounts of phenotypic change.

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