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COMMENT

Exploring the Dynamics of Development and Evolution: Comment on Blair and Raver (2012)

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Blair and Raver (2012) have provided an organism-in-environment conceptualization of the development of stress response physiology and its relation to the development of self-regulation. They argue that we must consider the context in which self-regulation and stress reactivity occur to understand their implications for developmental outcome. More generally, they present a cogent argument for why it is necessary to think developmentally when considering the effects of early experience on subsequent physical, emotional, cognitive, and social development. Blair and Raver's article also highlights a persistent challenge for developmental theory—how to make sense of the relationship among the various timescales over which phenotypes develop and change occurs. Their efforts to identify the factors involved in the variability and stability of self-regulation over different timescales demonstrate the dividends of integrating developmental and evolutionary perspectives to better understand the malleability of phenotypic development.

Keywords: probabilistic epigenesis, self-regulation, development and evolution, plasticity

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Most accounts of development and evolution across the 20th century focused on partitioning an individual's phenotypic traits into those that are genetically determined and those that can be attributed to the environment. We now know such partitioning is not biologically plausible, even in principle (Johnston & Edwards, 2002; Keller, 2011; Lickliter & Honeycutt, 2003). Modern developmental science has provided abundant examples that development is always the result of interacting processes occurring at multiple levels and multiple timescales. Blair and Raver (2012) provide an integrative overview of how the development of self-regulation is best understood as the result of these reciprocal interactions among developing systems. Their empirical findings suggest that environmental adversity associated with poverty can affect the development of self-regulatory competence, with cascading consequences for cognitive and behavioral development.

Self-regulation is a fundamental capacity for adapting to variation in contextual conditions (e.g., Gestsdottir, Urban, Bowers, Lerner, & Lerner, 2011; McLelland, Cameron, Wanless, & Murray, 2007), and it is clear that successful self-regulation is a crucial factor contributing to healthy development (Blair & Diamond, 2008). Blair and Raver (2012) have made significant headway in providing a neurobiological framework for how this capacity is achieved across individual ontogeny. Animal-based research has consistently documented that early experience can influence stress response systems to make them more or less sensitive to stress hormones (i.e., Lyons, Parker, & Schatzburg, 2010; McEwen, 2000; Champagne & Meaney, 2001). Following up on and extending these findings, Blair and Raver have provided an organism-in-environment conceptualization of the development of stress response physiology and its relation to the development of self-regulation. Their approach emphasizes the coactions between the individual and his or her context—the physical and social ecology in which the individual develops. Blair and Raver effectively argue that we must consider the context in which self-regulation and stress reactivity occur to understand their implications for developmental outcome. More generally, they provide a cogent argument for why it is necessary to think developmentally when considering the effects of early experience on subsequent physical, emotional, cognitive, and social development.

Recognizing development as a process that is situated, contingent, and experience dependent (as Blair and Raver clearly do) represents a major shift in thinking in the life sciences from the prespecified view of development that was widespread for most of the last century. This shift is having far-reaching effects on how we approach the processes of development and evolution and is raising new questions about the importance of experience, the nature and extent of heredity, and the sources of phenotypic stability and variability. For example, the last several decades have seen a different account of phenotypic stability and variability take shape in developmental biology, evolutionary biology, and developmental psychology. This new account is based on a relatively simple but profound insight: Given that all phenotypes arise during ontogeny as products of individual development, it follows that a primary basis for both phenotypic stability and variability must be the process of development itself.

The thread of this insight can be traced back to several pioneering embryologists and developmental biologists working in the

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first half of the 20th century, including Walter Garstang (1922), Edward Russell (1930), Gavin de Beer (1940), Richard Goldschmidt (1940), Conrad Waddington (1942), and Ivan Schmalhausen (1949). Although each of these biologists had a distinctive perspective on the links between development and evolution, they all promoted the notion that changes in individual development were an important basis for evolutionary change. This view was well outside mainstream 20th-century thinking about evolution but is being reconsidered across the biological and psychological sciences. Indeed, the relevance of development to evolution has received increasing attention over the last several decades across multiple disciplines (Gottlieb, 1992; West-Eberhard, 2003), and evolution is now more often discussed in terms of changes to developmental processes rather than simply in terms of changes in gene frequencies (Oyama, Griffiths, & Gray, 2001; Robert, 2004). This shift has involved moving beyond the notion of genes as the fundamental cause of phenotypic traits, thereby allowing for the consideration of a variety of extragenetic factors that are essential to the emergence and maintenance of phenotypic traits. Blair and Raver's emphasis on taking development seriously in discussions of the evolutionary basis of reflective versus reactive phenotypes is a valuable addition to this ongoing change in perspective.

Of particular importance to their concern with the links between development and evolution is the relatively recent insight that variability across individuals is generated by genetic and nongenetic means. The complex web of temporal and spatial interactions among genes, their products, and the internal and external environment of an organism is the focus of epigenetics, a rapidly growing field within the biological sciences that is typically defined as the study of change in gene expression and function that cannot be explained by changes in DNA sequence (Richards, 2006) or, more broadly, as 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 genes (Crews, 2008). Consistent with the probabilistic epigenesis view promoted by Blair and Raver (2012), there is now considerable evidence that parents transfer to their offspring a variety of nongenetic factors in reproduction that can directly influence phenotypic outcomes, including DNA methylation patterns, chromatin marking systems, cytoplasmic chemical gradients, hormones, and a range of sensory and social stimulation necessary for normal development (reviewed in Harper, 2005; Jablonka & Lamb, 2005; Lickliter, 2005; Mameli, 2004).

A growing number of biologists and psychologists are thus expanding the focus of their research attention to include not only the internal features of the developing organism (genes, proteins, cells, hormones) but also the contributions of the varied physical, biological, and social resources provided or denied the individual in its developmental context (see Bateson & Gluckman, 2011; Gilbert & Epel, 2009). Blair and Raver's research program on self-regulation serves as a first-rate example of this approach within developmental psychology and situates the topic of stress physiology and self-regulation within this rich theoretical context. In particular, their framework emphasizes that the organism–environment system is the fundamental level of analysis in our efforts to understand the links between development, heredity, and evolution.

The reliable and repeatable features of stimulation and experience occurring in an organism's developmental context were termed the *ontogenetic niche* by West and King (1987) some 25 years ago, which they defined as the set of ecological and social circumstances typically inherited by members of a given species. This ontogenetic niche is available both prenatally and postnatally and provides diverse but dependable resources and influences for the developing individual. The ontogenetic niche can be described in terms of light level and cycle, energy sources and their distribution, patterns of social interaction, and so on. These extragenetic factors are part of each organism's inheritance, and every ontogenetic cycle depends on the availability of a particular set of these developmental resources, made available in each generation (see Avital & Jablonka, 2000; Oyama, 1985, for further discussion and examples). From a developmental perspective, the recurrence from generation to generation of the specific developmental resources and interactions that make up an organism's ontogenetic niche serves as a primary basis for the development and maintenance of its species-typical behavior (see Haraway & Maples, 1998; Lickliter, 2005; Miller, 1997; West, King, & White, 2003). Although some investigators continue to view the environment as essentially supportive or disruptive to the realization of species-typical behavior and therefore a less-than-equal partner with genetic factors, Blair and Raver show us that this weak form of interactionism is not adequate to the task of making sense of the effects of psychosocial stress on the development of self-regulation across early childhood.

Blair and Raver's focus on the coactional traffic between neural function, hormones, behavior, and the environment of poverty emphasizes the difficult but critically important task of all developmental analysis—filling in the bidirectional details among the specific internal and external factors that contribute to the generation of phenotypic traits or outcomes. As outlined by Gottlieb (1992, 1997), this approach 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. Blair and Raver's multileveled, experiential canalization model of the role of stress in the development and maintenance of self-regulation enriches current accounts of the roles of early experience in physiological and behavioral development and also emphasizes the importance of a transgenerational approach to the study of these important topics. They suggest that advancing our knowledge of the dynamics of developmental processes at multiple timescales will lead to a deeper understanding of both developmental and evolutionary change.

In this light, Blair and Raver's article highlights and begins to address a persistent challenge for developmental theory—how to make sense of the relationship among the various timescales over which phenotypes develop and change occurs. These timescales include *real* time, the immediate experiences and exposure of an individual to their physical, biological, social, and cultural environments; *developmental* time, the continuing influence of prior experiences and encounters on an individual's ongoing interaction with these varied environments; and *evolutionary* time, the transgenerational effects of an individual's experiences and activities during ontogeny (Johnston & Lickliter, 2008). Integrating developmental dynamics across multiple systems and timescales is a particularly challenging task for developmental science (see Urban, Osgood, & Mabry, 2011), and Blair and Raver have provided a useful conceptual framework to address this theoretical and methodological challenge. In particular, their efforts to identify the factors involved in the variability and stability of self-regulation over different timescales demonstrates the dividends of integrating developmental and evolutionary perspectives to better understand the malleability or plasticity of phenotypic development.

It is important to note that phenotypic plasticity was long considered to be genetically determined by most evolutionary biologists during the last century (e.g., Mayr, 1942; Via & Lande, 1985). In recent years, however, a growing number of developmental and evolutionary biologists have questioned this genocentric perspective on plasticity and have focused on the complex interactions among genetics, development, and ecology to better understand the range of morphologies, physiologies, and behavioral repertoires observed across individuals and populations. Blair and Raver bring this approach to developmental psychology, emphasizing that plasticity is a developmental phenomenon that provides a potentially powerful means of adaptation to distinct environments. In particular, developmental plasticity provides a potent pathway for organisms to rapidly change structure and function in response to environmental changes. Blair and Raver extend the work of West-Eberhard (2003), a developmental evolutionary biologist who has extensively explored the relationships among plasticity, behavior, development, and evolution. West-Eberhard defined phenotypic plasticity as "the ability of an organism to react to an environmental input with a change in form, state, movement, or rate of activity" (2003, p. 34). She argued that these alternative morphologies, physiologies, and/or behaviors can evolve within a species as a result of adaptive responses to different environments and their demands. Like West-Eberhard, Blair and Raver realize that it is the process of development that produces the phenotypic variation that is screened by natural selection. This key insight provides a key rationale necessary to bridge developmental and evolutionary accounts of behavior.

In other words, in order to understand phenotypic change during evolution, we have to understand phenotypic change during development. In my view, the conceptual framework of developmental and evolutionary processes provided by contemporary evolutionary psychology is not adequate to this task (see Lickliter, 2008, for further discussion). Blair and Raver (2012) have provided an outline of a feasible alternative, one that recognizes the external environment as a source of developmental resources as crucial to the realization and modification of phenotypic outcomes within and across generations as are genes and their products. Further, their approach to development and evolution is consistent with the notion that genetic modification often follows, rather than being synchronous with, phenotypic evolution (see Gottlieb, 1992, 2002; West-Eberhard, 2003). This is a significant shift in thinking from traditional neo-Darwinian perspectives and is receiving increasing empirical support over the last several decades.

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