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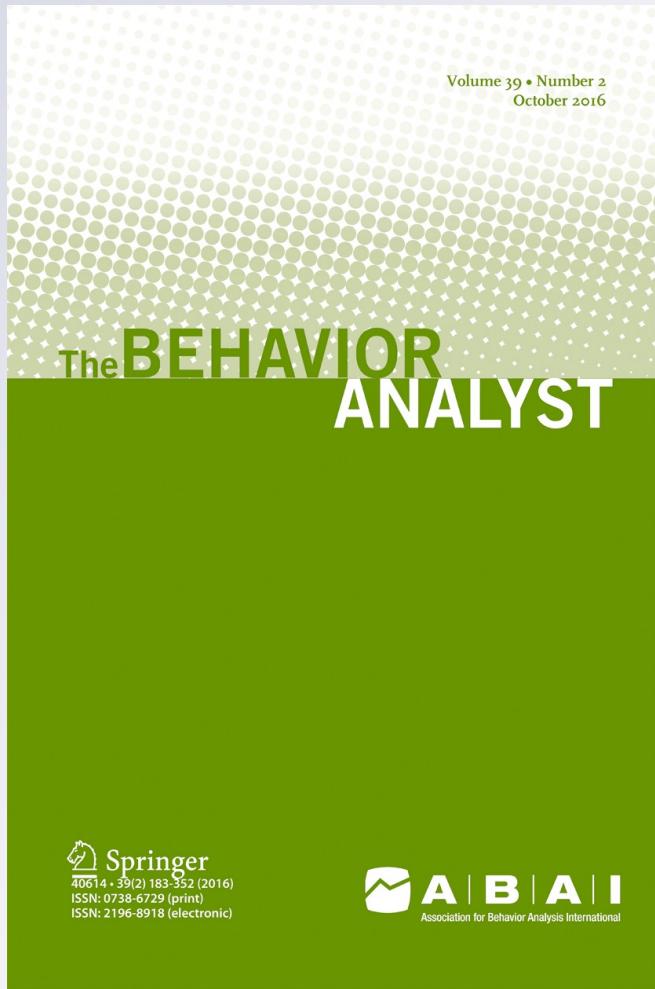
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The Behavior Analyst

An Official Journal of the Association for
Behavior Analysis International

ISSN 0738-6729
Volume 39
Number 2

BEHAV ANALYST (2016) 39:243-258
DOI 10.1007/s40614-016-0068-3



 Springer

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The Developmental Systems Approach and the Analysis of Behavior

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Published online: 11 August 2016
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Abstract The developmental systems approach is a perspective that has been adopted by increasing numbers of developmental scientists since it emerged in the twentieth century. The overview presented in this paper makes clear that proponents of this approach and proponents of modern behavior analysis should be natural allies. Despite some distinctions between the two schools of thought, the essential ideas associated with each are compatible with the other; in particular, scientists in both camps work to analyze the provenance of behavior and recognize the central role that contextual factors play in behavioral expression.

Keywords Developmental systems · Nature-nurture · Phylogeny fallacy · Instincts

In the second half of the twentieth century, a new approach to the analysis of behavior began to emerge in the scientific and philosophical literatures, an approach that emphasized both the developmental history of an organism and the complex relations that give rise to organisms' behavioral and biological traits (Ford & Lerner, 1992; Gottlieb, 1991a, 1992; Johnston, 1987; Lickliter & Berry, 1990; Oyama, 1985; West & King, 1987). Emerging from work in developmental psychology (Thelen & Smith, 1994), philosophy of science (Griffiths & Gray, 1994), developmental biology (Gilbert, 1992; Nijhout, 1990), and interdisciplinary fields related to these subjects (Michel & Moore, 1995), this approach grew out of ideas that had been advanced in earlier decades (e.g., by Kuo, 1967; Lehrman, 1953; Schneirla, 1957) and was initially called “Developmental Systems Theory;” it has sometimes been known by its acronym, DST (Ford & Lerner, 1992; Griffiths & Gray, 1994; Griffiths & Tabery, 2013; Johnston, 2010; Johnston & Lickliter, 2009; Oyama, Griffiths, & Gray 2001). By the early 1990s,

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researchers interested in behavior analysis were already attending actively to the growing DST literature (Midgley & Morris, 1992; Morris, Lazo, & Smith 2004; Schneider, 2003, 2007).

Before proceeding, it is important to be clear about what the acronym DST refers to. Keller (2005) has distinguished at least three different ways in which DST has been used in the past 20 years (see also Pradeu, 2010). In particular, she noted that while Ford and Lerner's (1992) book on DST focused on the importance of temporal dynamics in the *development* of an individual organism's behavior, Griffiths and Gray's (1994) treatment of DST focused on the important roles of non-genetic factors in the *evolution* of behavioral and biological phenotypes. Thus, Keller identified an important difference between two schools of thought, both of which used the same acronym: "Where one version of developmental systems theory [Griffiths and Gray's] emphasizes the multiplicity of resources employed in heredity, development, and evolution, the other [Ford and Lerner's] emphasizes the critical importance of temporal dynamics in the dialectics of individual development" (p. 412). To make matters more confusing, another closely related literature used DST to refer to *dynamic* (rather than "developmental") systems theory (Thelen & Smith, 1994), an approach that explored the development of human behavior using the mathematics of nonlinear systems, which had been pioneered by theorists who were attempting to explain the emergent behavior of self-organizing systems like stars, hurricanes, and ecosystems (Kelso, 2000; Stewart, 1989). Regardless of these differences, all versions of DST appear to share some central ideas (Keller, 2005).

One of the essential ideas shared by the various forms of DST is that all phenotypes—including both biological and behavioral traits—emerge spontaneously from the mechanical interactions of a large number of factors that together constitute a single complex system (Griffiths & Gray, 1994; Noble, 2006; Pradeu, 2015; Thelen & Smith, 1994). Such a system normally comprises influential factors such as DNA, cytoplasm and its contents, cell membranes and their embedded proteins, hormones, neurotransmitters, other organ systems, other individual organisms, societal factors, and physical features of the environment. In addition, at any given moment, a system's components are as they are in part because of historical factors, including the system's own behavioral history. Importantly, the emergent products of these mechanical interactions are novel, in the sense of being qualitatively distinct from the system components that give rise to them; accordingly, phenotypes cannot be reduced to any of the components at lower levels of the system (Witherington & Lickliter, 2016) and they are not contained in any way in any of these lower-order components (Johnston & Gottlieb, 1990; Johnston & Lickliter, 2009).

Therefore, this "systems view" carries with it a second essential idea: genes cannot be considered the primary determinants of any phenotype (Griffiths & Tabery, 2013; Lickliter, 2013; Oyama 1985/2000) because contextual factors always play indispensable, informational roles in phenotype development (Griffiths & Gray, 1994; Thelen & Smith, 1994). In fact, DST proponents have concluded that genes are no more foundational than any of the other system components that contribute to phenotype development (for a detailed exploration of this point, see Moore, 2002). Given these essential ideas, all forms of DST recognize development as epigenetic (discussed below) and probabilistic rather than predetermined (Godfrey-Smith, 2001; Gottlieb, 1991a, 1992, 1998, 2007; Pradeu, 2010); predetermination is impossible in such systems in part because the contextual factors that contribute to development are, themselves, not invariably predictable. And because organisms are responsive to contexts that have the

features they do in part *because* of those very organisms' behaviors (Lewontin, 2000), all forms of DST reject as inherently flawed the traditional view that nature and nurture can contribute in independent ways to development (Lewkowicz, 2011; Overton, 2006; Stotz, 2012). Developmental systems theorists in psychology, philosophy, and biology have focused on different kinds of phenomena or have advocated the use of different kinds of methods, but they all share these overarching perspectives on the developmental origins of behaviors and other biological phenotypes. In addition, like behavior analysts, these theorists are all committed to elucidating the *mechanisms* through which phenotypes arise, because such an approach promises to yield interventions with the potential to improve the human condition (Moore, 2009, 2015a, 2015b).

As the worldview shared by these theorists is better thought of as a *perspective* than a formal theory, a number of writers (e.g., Lickliter, 2013; Moore, 2002; Spencer, Blumberg, McMurray, Robinson, Samuelson, & Tomblin 2009) have begun referring to this collection of ideas as the developmental systems (DS) *approach*, rather than as DST. I will be using this terminology henceforth in this paper.

The DS Perspective on Nature and Nurture

By explicitly rejecting the traditional nature-nurture dichotomy, the DS approach forces a reconsideration of earlier ways of thinking about behavior. One important consequence of adopting the DS perspective is the need to relinquish the older idea that behaviors can be categorized as having roots in *either* phylogeny *or* ontogeny. This idea, which was a conventional viewpoint through much of the twentieth century, held that some behaviors reflect learning that occurs during an individual's lifetime (i.e., nurture) whereas other behaviors reflect evolutionary processes (i.e., nature). This viewpoint supported a sharp distinction between species-typical behaviors that appear unlearned—so-called instincts—and other behaviors that emerge following specific experiences, such as classical or operant conditioning. Because unlearned, species-typical behaviors were understood to require explanations in terms of natural selection operating on an evolutionary timescale—and because the modern evolutionary synthesis of biology held that evolution results *only* from changes in the frequencies of *genes* in a population (Gottlieb, 1992; Wereha & Racine, 2012)—such “instinctive” behaviors were effectively regarded by many writers as genetically determined. However, because DS theorists understand all phenotypes to emerge from numerous interactions among components that constitute a single, complex, integrated system, they argue that there are no behaviors that can be attributed directly and exclusively to genes. In fact, molecular biologists have known for some time that DNA cannot single-handedly specify behaviors (more on this below). Therefore, no behaviors can be dismissed as instinctive (in the sense of “genetically determined”); instead, behaviors that seem instinctive—just like behaviors observed after operant or classical conditioning—require analysis to discover the factors and mechanisms that give rise to them.¹

¹ It is certainly reasonable to distinguish between categories of behavior based on other factors, such as whether or not the behavior is species-typical (for instance). The point here is that a comprehensive understanding of *any* behavior—however, it might be categorized in another scheme—requires a developmental analysis of its emergence.

In a seminal 1990 article, Lickliter and Berry explicated this argument by identifying a misconception they called “The Phylogeny Fallacy.” This fallacy holds that there are two different causes of phenotypes: proximate (developmental or ontogenetic) and ultimate (evolutionary or phylogenetic). In rejecting this fallacy, DS proponents hold that when it comes to analyzing the origins of a behavior, no principled distinction can be made between “inherited” and “acquired” behaviors, because *all* behaviors emerge in real time from the same kinds of interactions, interactions that occur between components of developing systems. As most twentieth-century scientists saw things, “innate” or “unlearned” behaviors could be accounted for by phylogenetic contingencies, whereas “acquired” or “learned” behaviors could not; but according to Lickliter and Berry, this conceptualization accepts a false dichotomy. And one unfortunate effect of uncritically accepting this false dichotomy is an openness to the idea that events that occurred prior to the conception of an organism can be responsible for that organism’s later behaviors, as if behaviors can somehow emerge in real time without any *proximate* causes being responsible for their emergence. Although events in the distant past can *contribute* to behaviors in real time via their influences on the state of some of the components comprising a developing system, the behaviors themselves are always influenced by proximate factors, regardless of whether those behaviors are learned or unlearned.

Prior to the ascendance of DS thinking in some branches of the behavioral sciences, it was generally assumed that nature and nurture could be disentangled using particular methodological approaches. One of these approaches controls for genetic factors, either by studying research participants who are monozygotic twins or by using subjects that come from isogenic, inbred strains of laboratory animals. Another of these approaches attempts to control for experiential factors, either by studying newborn research participants, or by using animals raised in controlled environments; the idea here is to study organisms that either have had no experiences at all with certain classes of stimuli, or have had nearly identical upbringings. As explained in the next section, DS proponents have rejected both of these approaches as being unable to disentangle phylogenetic and ontogenetic contributions to behavior. In fact, these theorists have concluded that it is not possible *in principle* to untangle these contributions to behavior.

Insights from Developmental Science

As far back as the mid-1950s, scientists such as Lehrman (1953), Schneirla (1957), and Kuo (1967) had argued that a truly developmental approach to the study of behavioral phenotypes would always reveal proximate causes of behavior; in contrast, viewing so-called instinctive behaviors as “immanent, preformed, [or] inherited” (Lehrman, 1953, p. 359) would be a mistake, because doing so would interfere with genuine analysis of the development of those behaviors. From the perspective of developmental science, the question of interest is how a behavior emerges, regardless of whether that behavior is species-typical and seemingly unlearned, or idiosyncratic and obviously influenced by the organism’s past experiences. That is, all complex behaviors must be understood

to emerge from developmental processes, and it is the job of the developmental scientist to explore these processes.

This insight illuminates a problem with research methods designed to identify “instincts” by studying newborn animals, or animals raised in highly controlled environments. The classic example of such a method is the so-called isolation experiment, in which the behaviors of animals are deemed instinctive if those behaviors emerge even when opportunities to learn them seem to have been eliminated. Most mid-century behavioral scientists considered such behaviors to be inherited. However, developmentalists like Lehrman argued strenuously that we cannot know *prior to developmental analysis* what the relevant antecedent experiences are for the development of a behavior, so it is never appropriate to assume that such proximate causes do not exist (i.e., that the behavior has merely been inherited via some unspecified mechanism). Instead, proponents of the DS approach recognize that factors present at one point in time are themselves the products of earlier developmental events (Griffiths & Tabery, 2013), so developmental analysis always requires a search for antecedent factors as well as experimental elucidation of how those factors interact mechanistically.

In part to demonstrate the importance of the developmental approach, Gottlieb (1991b, 1997) sought to discover the proximate causes underlying the consistent preference that *newborn* Mallard ducklings exhibit for their mothers’ species-typical assembly calls. Even when duck embryos (in eggs) are raised in incubators where they are prevented from hearing maternal vocalizations *and* from hearing the vocalizations of nearby siblings, the ducklings still hatch already exhibiting a preference for the maternal call. At first glance, this seems like a behavior that has been inherited. However, Gottlieb’s (1991b) research revealed that *experiences* with the embryos’ own vocalizations—vocalizations that, to the human ear, do not sound at all like the maternal assembly call (Gottlieb, 1991a)—are essential in the development of the newborns’ preferences. Thus, an experiential factor is crucial in the development of the behavioral preference, even though the behavior certainly *appears* (at first glance) to develop independently of experience (because it emerges even in animals whose sensory experience has been severely limited).

This finding lends credence to an understanding Lehrman highlighted in 1953: “The isolation experiment [in which an animal is deprived of normal experiences] ... provides at best a negative indication that certain specified environmental factors probably are not directly involved in the genesis of a particular behavior. However, the isolation experiment by its very nature does not give a positive indication that behavior is ‘innate’ or indeed any information at all about ... [the] development of the behavior ...” (1953, p. 343). Studies other than Gottlieb’s have likewise revealed that experiences that are not *obviously* related to specific behaviors can nonetheless be crucial antecedents of those behaviors (Alberts & Ronca, 2012; Goldstein, King, & West 2003; Wallman, 1979). To provide a single example from a primate species, Masataka (1993) found that squirrel monkeys can learn to fear snakes as a result *not* of exposure to snakes (or other snake-like stimuli), but as a result of exposure to organisms like grasshoppers or crickets that have been placed in their food! And although studies involving newborn organisms might seem useful when trying to make a point about unlearned behaviors, the fact remains that newborn animals have many sorts of prenatal experiences that influence their postnatal behaviors (e.g., see Alberts &

Ronca, 2012). To provide a single example, human fetuses hear their mothers' voices, an experience that influences some of their auditory preferences shortly after birth (DeCasper & Fifer, 1980; DeCasper & Spence, 1986). Similarly, animals raised in controlled environments have *some* experiences that likely influence their subsequent behaviors. A DS approach encourages investigations of the development of such behaviors by insisting that researchers continue to seek the proximate causes of those behaviors rather than simply declaring behaviors without *obvious* experiential causes to have been inherited or somehow shaped by "phylogenetic contingencies."

Of course, some of our behaviors reflect specific experiences whereas others seem only to reflect the basic structures of our bodies (e.g., swallowing, waste elimination, etc.). But as proponents of the DS approach see it, such a distinction masks critical similarities in the development of all of our behaviors. In fact, while the species-typical structures of our bodies might *seem* to be genetically determined, this illusion fades once we begin to study the emergence of these structures in development. Behaviors that reflect the basic structures of our bodies—no less than behaviors that obviously reflect our experiences—must still be subjected to developmental analysis if we hope to understand them. The precise point DS proponents seek to make is that it is conceptually problematic to draw sharp distinctions between behaviors that obviously reflect experiences and behaviors that appear to emerge independently of experiences, because *all* phenotypes depend on both genetic and non-genetic factors for their development. Conceptualizations that permit different modes of explanation for learned versus unlearned behaviors risk underestimating *both* the extent to which non-genetic factors contribute to bodily structures and functions *and* the extent to which genetic factors contribute to learned behaviors. Thus, from the perspective of the DS approach, we should never consider any behaviors to be inherited and exempt from further developmental analysis (Blumberg, 2005).

Just as they have questioned the value of isolation experiments, proponents of the DS approach have also rejected the idea, advanced by the authors of thousands of papers (see Plomin, DeFries, McClearn, & McGuffin 2008), that studies of identical and fraternal twins can reveal something about developmental versus evolutionary contributions to human behaviors. Francis Galton (1907) was the first to recommend the use of these sorts of studies as a way to tease apart nature and nurture, and the method continues to be implemented in the twenty-first century mostly as Galton originally envisioned it. Unfortunately, although monozygotic twins could, in theory, allow researchers to effectively control for genetic factors, there is little reason to believe that twin studies are capable of providing useful answers to questions about how evolutionary versus developmental processes contribute to phenotypes. A formal critique of twin studies is beyond the scope of this paper, but such critiques are available in numerous other locations (Burt & Simons, 2014; Chaufan & Joseph, 2013; Joseph, 2015; Moore, 2002, 2006, 2008, 2013a, 2013b; Moore & Shenk, 2016; Richardson & Norgate 2005; Shultziner, 2013a, 2013b), and these critiques have identified a variety of problems with twin studies, problems that render these methods unhelpful in studying phenotype origins.

Although twin study methods are among the most powerful tools available to quantitative behavioral geneticists (i.e., the researchers who took up Galton's goal of disentangling nature and nurture), they are not satisfactory tools for studying phenotype development because they do not actually explore biological processes. In fact, in their

authoritative textbook, *Behavioral genetics*, Plomin and colleagues (2008) noted that “quantitative genetics, such as twin and adoption studies, depends on Mendel’s laws of heredity but does not require knowledge of the biological basis of heredity” (p. 40). Because twin studies ignore the biological and behavioral processes that produce phenotypes, they are not equipped to answer developmental questions about the proximate causes of those phenotypes (behavioral or otherwise). Instead, as the DS approach insists (Griffiths & Tabery, 2008, 2013; Tabery, 2014), a *thorough* understanding of such causes requires knowledge about how it is that biological entities like DNA segments, micro-RNAs, proteins, and cell membranes physically interact with their contexts to construct nervous systems that generate behaviors *in context-dependent ways* (where “context” must be understood to include both an organism’s current circumstances and its historical experiences). Understanding something about how biological processes build the nervous systems that contribute to behavior is essential if one is to have a comprehensive understanding of behavior.

The basic facts of biology indicate that DNA is used in context-dependent ways during development to help produce RNA (Griffiths & Stotz, 2006; Lewontin, 2000; Moore, 2002, 2013a; Stotz, 2006). This is all DNA can do; it cannot single-handedly cause nervous systems to have their characteristics, let alone cause full-blown behaviors. In fact, as one early advocate of the DS approach pointed out, there is *always* “a long and tortuous developmental route” between complex phenotypes like behavior and the molecules that DNA helps to construct (Johnston, 1987, p. 160). Therefore, regardless of what twin studies might tell us about the heritability of a behavior, that behavior emerges from multiple developmental processes involving more than DNA alone (Moore, 2002); even if a behavioral characteristic were found to be 100 % heritable, a developmental analysis would still uncover non-genetic factors that contribute to the emergence of the behavior, factors that are *informative* and *constructive* regarding development, even though they are not genetic factors (Griffiths & Tabery, 2013; Lickliter & Berry, 1990; Lickliter & Honeycutt, 2015; Michel & Moore, 1995; Moore, 2006, 2013a, 2013b; Moore & Shenk, 2016). The fact that DNA cannot determine precise phenotypes independently of non-genetic factors is evident from the behavioral, physiological, and morphological differences that can be observed between identical twins or between cloned animals.

Behavioral Epigenetics: Molecular Biology’s Confirmation of the DS Approach

Although the DS approach dates to the 1980s or earlier, remarkable progress began to be made in the very late 1990s in a branch of molecular biology known as epigenetics, and the developments in this field have strongly reinforced the message espoused by proponents of the DS approach. Epigenetics is a research field that explores gene expression, that is, what it is that leads specific segments of DNA (i.e., genes) in specific cells to be transcribed into segments of RNA in specific spatial and temporal contexts. A sub-field of epigenetics, known as behavioral epigenetics (Lester et al., 2011; Van IJzendoorn, Bakermans-Kranenburg, & Ebstein 2011), is concerned specifically with how psychological processes—such as emotional reactivity, behavior, and memory—affect and are affected by gene expression (Moore, 2015b). Studies of

behavioral epigenetics have confirmed that in contrast to the traditional view of genes as capable of *actively* influencing phenotype development, DNA is actually better thought of as *reactive* to its context (Gilbert & Sarkar, 2000; Keller, 2014); as Pradeu has written, “genes in the organism are not so much activators as they are activated” (2015, p. 11). Thus, as developmental scientists have been asserting for decades, DNA should be understood to be sensitive to its context and only one of several factors in a complex, integrated system that gives rise to biological and behavioral phenotypes.

Among the best-known studies on behavioral epigenetics are those conducted in the labs of Meaney and Szyf (Meaney, 2010; Meaney & Szyf, 2005; Weaver et al., 2004; Weaver, Meaney, & Szyf 2006). This work explored why rat pups that are licked and groomed frequently by their mothers in the first 10 days after birth grow up to be adults that are less reactive in stressful situations than are rats that were licked and groomed less frequently as pups. An extensive program of research ultimately revealed that the *experience* of being licked and groomed early in life led to the activation of a DNA segment in hippocampal cells that is required for the production of a stress-moderating protein, the glucocorticoid receptor. In the absence of this sort of early life maternal caregiving, rats grew up with a deactivated segment of DNA at this location, and consequently wound up with fewer glucocorticoid receptors in their brains and increased stress reactivity in adulthood.

The finding that a maternal behavior can epigenetically activate a DNA segment confirmed the DS insight that experiential factors can alter the functioning of an organism’s genetic endowment. This discovery suggests that starting at conception, nature and nurture can participate in a real-time “dialogue” that gives rise to phenotypes; this arrangement means that phenotypic outcomes can be influenced by either experiential or molecular variables (Szyf & Bick, 2013; Zhang & Meaney, 2010). Several kinds of experiences have now been found to influence the activity of a variety of DNA segments in a variety of cell types in a variety of animal species. For example, exercise (Gomez-Pinilla, Zhuang, Feng, Ying, & Fan 2011), poverty (Borghol et al., 2012), substance addiction (Maze & Nestler, 2011), or social isolation (Cole, Hawkley, Arevalo, Sung, Rose, & Cacioppo 2007) can all affect the expression of DNA; specific experiences are associated with the activation or deactivation of DNA used to construct arginine vasopressin (Murgatroyd et al., 2009), brain-derived neurotrophic factor (Roth, Lubin, Funk, & Sweatt 2009), or the serotonin transporter promoter (Devlin, Brain, Austin, & Oberlander 2010); cells in the liver (Lillycrop, Phillips, Jackson, Hanson, & Burdge 2005), blood (e.g., T cells), and prefrontal cortex (Provençal et al., 2012) contain DNA that can be affected by experiences; and behavioral epigenetic effects have been detected in mice (Murgatroyd et al., 2009), rhesus monkeys (Provençal et al., 2012), sheep (Sinclair et al., 2007), and human beings (McGowan et al., 2009), among other species. Thus, these sorts of epigenetic effects are likely the rule rather than the exception in complex animals. After considering the implications of this growing body of data, Weaver (2007) chose to subtitle a paper on the epigenetic effects of maternal behavior “Nature versus nurture: let’s call the whole thing off.”

The phenomena of behavioral epigenetics draw attention to the fact that behavior influences genetic activity, which influences behavior in a reciprocal manner, and so on. Thus, all phenotypes—adaptive and otherwise—emerge from epigenetic processes that are not predetermined by genetic factors, but are instead open to environmental/experiential inputs. As a result, it makes little sense to imagine that some behaviors can

be explained strictly with reference to “phylogenetic contingencies” whereas others can be explained strictly with reference to “ontogenetic contingencies.” Obviously, the experiences we have while we develop can influence our subsequent behavior, even behavior exhibited many years after the experience; but it has now become clear that at least in some cases, experiences have their effects by influencing the activity of biological molecules that reflect evolutionary processes. So, as Lickliter (2009) has put it, “Whereas most accounts of development and evolution embraced by 20th-century biologists and psychologists focused on partitioning the organism’s phenotypic traits among those that are genetically determined and those that are produced by the environment, the remarkable findings now available from epigenetics demonstrate that no such partitioning is possible, even in principle” (p. 144). Instead, it now appears that nature and nurture can never be partitioned (Lickliter, 2009) or treated as independent contributors to development (Lewkowicz, 2011; Overton, 2006; Stotz, 2012). Furthermore, it now appears that DNA and non-genetic factors share causal parity (Griffiths & Tabery, 2013; Oyama, 1985), and therefore, that an organism’s phenotypes cannot be predicted prior to development simply by looking at that organism’s genome (Gottlieb, 1991a, 1992, 1998, 2007).

Conclusion: Why DS Proponents and Behavior Analysts Should be Natural Allies

There are good reasons to expect contemporary behavior analysts to find the DS approach to be congenial, and proponents of the DS approach should likewise be comfortable with most of the ideas that are essential to behavior analysis. One of the major objectives of those who have written in the DS tradition is to discourage references to instinctive or “genetically determined” behaviors, because such references effectively “black box” the mechanisms responsible for producing any so-labeled behaviors (Lehrman, 1953); speaking in this way permits the mistaken impression that genes can operate as agents able to independently cause behaviors. Rather than labeling behaviors in this obfuscating way, the DS approach insists on the importance of *analysis* of such behaviors, the goal being to elucidate the mechanisms by which proximate factors give rise to behaviors in real time. In the end, DS proponents are motivated by a desire to understand the provenance of behaviors, a goal that should feel quite familiar to behavior analysts.

Likewise, proponents of the DS approach maintain that context is always key. Behaviorists have traditionally recognized the important roles of contextual factors like discriminative stimuli, and proponents of the DS approach have consistently argued that contexts themselves must be recognized as *an integral part* of the system under study (Thelen & Smith, 1994). Similarly, like behavior analysts (e.g., Skinner, 1980), DS theorists believe that a thoroughgoing understanding of a given characteristic requires a *historical* analysis of the appearance of that characteristic. That is, knowing what an organism will do next is possible only if one is in possession of information about the organism’s previous states and experiences. Perhaps in part because advocates of the DS approach are concerned with both behavioral and other biological phenotypes, their focus on context is not limited to an *organism’s* context, but also includes the contexts of DNA, cells, organs, and other biological entities. Nonetheless,

their acknowledgement of the critical importance of context remains consonant with fundamental principles of behavior analysis.

Just as behavior analysts should find themselves comfortable with the DS approach, proponents of the DS approach should be comfortable with the approach honed by behaviorists. After all, the consequences of behavior at one point in time normally contribute, as antecedent causes, to later behaviors. Therefore, one of the traditional concerns of some behaviorists—that is, the effects of the *consequences* of behavior (Schneider, 2012)—are also important to DS theorists, because some of these effects influence the mechanisms that cause subsequent behaviors. In fact, recent work in behavioral epigenetics, consistent with the DS approach, has uncovered ways in which learning has molecular effects in neurons, effects that alter the structure and functioning of the nervous system in ways that influence later behaviors (Day & Sweatt, 2010, 2011; Kandel, 2001; Levenson & Sweatt, 2005).

As Todd noted astutely in this journal in 1987, “behaviorism—as a philosophy of science—neither addresses specific empirical issues nor demands the use of a specific research methodology. Rather, it suggests that behavioral questions are best resolved by the analysis of behavior on its own level as the interaction of physical events...[the] traditional research interests and methodologies [of behaviorists] do not exhaust the possibilities of behaviorism” (p. 118). Accordingly, the behaviorist approach is fundamentally consistent with the DS approach, insofar as both are concerned with the analysis of behavior, and both recognize that such analysis requires study of interactions between physical entities. From this perspective, we should recognize the DS approach as a broad paradigm (Overton & Lerner, 2012) that can *include* behaviorism; traditional behaviorism does not look exactly like the DS approach merely because the “traditional research interests and methodologies” of behaviorists have remained more narrowly focused than their underlying philosophy of science permits. Ironically, the subtitle of Todd’s 1987 article—“Behaviorism’s presumed denial of instinct”—implied that behaviorists need *not* deny instinct even as the DS approach does just that; but when the content of Todd’s paper is considered with 29 years of hindsight, it continues to look as if DS theorists and behavior analysts should be natural allies.

One distinction between the DS approach and behavior analysis is that the former is concerned with the emergence of phenotypes in general rather than with behavior alone. Although many behavior analysts recognize that the category of “experience” encompasses more than learning, this point is particularly important to DS theorists, because the development of numerous phenotypes depends on non-genetic (i.e., experiential) factors other than learning. In these cases, experiences influence development in ways that influence phenotypes (including, sometimes, subsequent behavior) without necessarily producing the kinds of effects in a brain that would normally be associated with learning. For example, the physical effects of movement during embryonic development are known to influence features of tendons, ligaments, and bones in ways that have significant implications for behavior (Lickliter & Honeycutt, 2015). As Lickliter (2013) put it, DS theorists consider it “important to remember that *experience* is not synonymous with *learning* but rather refers much more broadly to function or activity, including the electrical activity of neurons, neurochemical and hormonal secretion, the use of muscles and sensory systems, and the behavior of the organism itself” (p. 84).

Some DS theorists have suggested that another difference between the approaches can be seen in their relative willingness to draw conclusions from ecologically unrealistic laboratory studies. Of course, ethologists working in the field have a long history

of using the principles of behavior analysis to understand their observations, and there is a large literature that has demonstrated that operant principles can be generalized beyond the laboratory; everyone recognizes that ecological validity is important. But because the DS approach has been concerned for decades with questions about the relationship between development and evolution (Griffiths & Gray, 1994, 2005; Keller, 2005), DS proponents consider organism-environment systems to have co-evolved, and therefore, they expect organisms to respond differently in ecologically meaningful versus ecologically arbitrary testing contexts. Lickliter and Honeycutt 2013 (p. 186), for example, were concerned with this issue when they wrote the following:

Because organism–environment systems are tuned together over developmental and evolutionary time scales, we should expect special relationships between organisms and species-typical ecological events (Johnston, 1985). In much of traditional psychological analysis, however, subjects are placed in ecologically arbitrary situations and tested for responsiveness to ecologically arbitrary events. Such artificial, simplified studies may be necessary to isolate potential mechanisms of behavior, but such studies often overstate or understate how important certain factors are in real-life situations ... [For example,] much of what we know about the acquisition of classically conditioned responses has been based on studies that involved conditioned stimuli that were ecologically arbitrary (e.g., pure tones or lights). However, when more ecologically realistic stimuli are used as conditioned stimuli in a variety of domains, the acquisition of conditioned responses are more rapid and resistant to extinction than when ecologically arbitrary (but still complex) stimuli are used (Domjan, 2005).

It can be helpful to remain aware of the different ways in which DS advocates and some behavior analysts think about “experience” in contrast to “learning,” and of their relatively different levels of tolerance for the use of ecologically valid experimental stimuli. Nonetheless, these differences do not render the two approaches at all incompatible.

Ultimately, the discovery that DNA is merely reactive to its context has strengthened developmentalists’ insistence that it is not helpful to consider any behaviors to be instinctive (Blumberg, 2005; Moore, 2002; Spencer et al., 2009). This insight means that careful analysis is required of the origins of all behaviors, origins that lie in the mechanical interactions that occur between biological entities and their contexts. The DS approach sees all phenotypes as being the product of *developmental* processes that utilize both genetic and non-genetic resources; consequently, the emergence of such traits can be understood only via developmental analysis. This means that efforts to find individual DNA segments that are responsible for particular behavioral conditions—for example, the search for “autism genes”—are doomed to failure. Instead, as behavior analysts and DS advocates agree, behaviors, including abnormal behaviors, must be understood to simultaneously reflect (1) an individual’s current environmental context, (2) the individual’s genetic state (i.e., the sequence of nucleotide bases in the DNA as well as the presence and state of numerous epigenetic factors that influence genetic expression), and (3) the individual’s developmental/experiential history (because that history has contributed to the structure and chemistry of the individual’s nervous system

as well as to numerous other anatomical, physiological, and behavioral features of the individual). Clearly, the DS approach is an interdisciplinary one that seeks to illuminate phenotype origins by integrating the findings of several branches of biology (molecular, cellular, developmental, evolutionary); several branches of psychology (developmental, behavioral, psychobiological); and emerging disciplines (epigenetics, neuroscience); the goal is then to use the insights that are generated to elaborate mechanistic explanations of development (Lickliter, 2013). By synthesizing these numerous approaches to the study of behavior—including the approaches traditionally employed by behavior analysts—proponents of the DS approach seek to obtain comprehensive, generally applicable explanations regarding the origins of behavioral phenotypes. Such explanations will be useful if they can provide information about the likelihood that a given behavior will be observed in a given context, or if they can suggest ways to helpfully intervene in behavioral development.

Compliance with Ethical Standards This article does not contain any studies with human participants or animals performed by any of the authors.

Conflicts of interest David S. Moore declares that he has no conflicts of interest.

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