



Developmental Systems Theory: What Does It Explain, and How Does It Explain It?

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We are indebted to Susan Oyama for reading and providing very useful feedback on an earlier version of this article. Griffiths’ work on this paper was supported as part of an Australian Research Council Discovery Project DP0878650.

Abstract

We examine developmental systems theory (DST) with two questions in mind: What does DST explain? How does DST explain it? To answer these questions, we start by reviewing major contributions to the origins of DST: the introduction of the idea of a “developmental system”, the idea of probabilistic epigenesis, the attention to the role of information in the developmental system, and finally the explicit identification of a DST. We then consider what DST is *not*, contrasting it with two approaches that have been foils for DST: behavioral genetics and nativist cognitive psychology. Third, we distill out two core concepts that have defined DST throughout its history: epigenesis and developmental dynamics. Finally, we turn to how DST explains, arguing that it explains by elucidating mechanisms.



1. ORIGINS OF DEVELOPMENTAL SYSTEMS THEORY

Developmental systems theory (DST) emerged in the 1990s, building on earlier developmental systems perspectives. In this section, we consider several such contributions to the wider developmental systems perspective that eventually turned into DST: Conrad Hal Waddington’s introduction of the “developmental system”, Gilbert Gottlieb’s concept of probabilistic epigenesis, Susan Oyama’s attention to the role of information in the developmental system, and finally Donald Ford and Richard Lerner’s explicit identification of a “DST”.

1.1. Waddington and the “Developmental System”

Conrad Hal Waddington was a true British polymath, spending portions of his career devoted to ammonite paleontology, Whiteheadian process philosophy, embryology, biochemistry, developmental genetics, population genetics, and theoretical biology (Robertson, 1977; Slack, 2002). Waddington used the phrase “developmental system” in a sense that has much in common with current usage in an address to the 1951 Australian and New Zealand Association for the Advancement of Science (Waddington, 1952). Waddington contrasted preformationist theories of development (the characters of adults are present in the fertilized egg) with the theory of epigenesis (the characters emerge from causal interactions between simpler components in the fertilized egg). “There can be no doubt nowadays that this epigenetic point of view is correct. ... An animal is, in fact, a developmental system,” Waddington continued, “and it is these systems, not the mere adult forms which we conventionally take as typical of the species, which becomes modified during the course of evolution” (Waddington, 1952, p. 155). To help convey the idea, Waddington also provided a “mental picture of the developmental system” (Fig. 3.1). Waddington later termed this image the

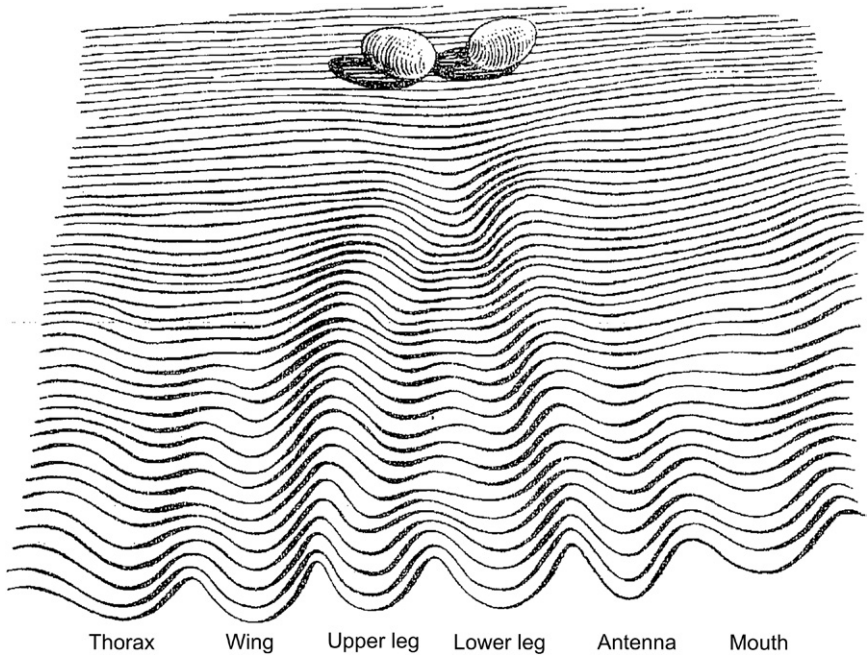


Figure 3.1 A representation of the developmental system of an animal as a grooved surface over which biased balls are free to roll. (From *Waddington (1952), Fig. 1*).

“epigenetic landscape” (*Waddington, 1957*), and it is this idea for which he is perhaps best known. But it is worth recognizing that this well-known concept and image was originally conceived of as a *developmental system* by *Waddington*, and he emphasized this concept of a developmental system late in to his career (*Counce & Waddington, 1972, 1973*).

Studying the developmental system, *Waddington* pointed out, was not the same thing as studying heredity: “For the purpose of a study of inheritance, the relation between phenotypes and genotypes can be left comparatively uninvestigated; we need merely to assume that changes in the genotype produce correlated changes in the adult phenotype, but the mechanism of this correlation need not concern us. Yet this question is, from a wider biological point of view, of crucial importance, since it is the kernel of the whole problem of development” (*Waddington, 2012 [1942], 10*).¹ In contrast to identifying correlations between inputs (genotype) and outputs (phenotype), the “whole problem of development” required

¹The *International Journal of Epidemiology* conveniently reprinted *Waddington’s* “The Epigenotype” along with commentaries by *Gilbert (2012)*, *Haig (2012)*, and *Jablonka and Lamm (2012)*. Page references are to the 2012 reprint.

elucidating the *mechanisms* that causally linked inputs to outputs. We will return to Waddington's focus on mechanisms later, as the nature of mechanisms and mechanical explanation is now a major topic in the philosophy of science.

Waddington's attention to developmental systems was progressive for its day. Still, his vision was quite gene centric. Indeed, the quote just given concerning the whole problem of development was from an article titled "The Epigenotype" (Waddington, 2012 [1942]). In this article, Waddington emphasized that, "...the genotype is [in] continual and unremitting control of every phase of development. Genes are not interlopers, which intrude from time to time to upset the orderly course of a process which is essentially independent of them; on the contrary, there are no developmental events which they do not regulate and guide" (Waddington, 2012 [1942], p. 12). In the same way that an individual has its genotype, then, Waddington's developmental system had its epigenotype.

1.2. Gottlieb and Probabilistic Epigenesis

Gilbert Gottlieb, recalling his preparations for a 1970 Festschrift devoted to Theodore Schneirla, noted that, "In my literature review, I found two rather different conceptualizations of behavioral embryology, one I called predetermined epigenesis and the other probabilistic epigenesis" (Gottlieb, 2001, p. 42). Despite the passage of decades since Waddington championed epigenesis, Gottlieb saw the persistence of preformationism in biology beneath a superficial layer of epigenetic clothing. Predetermined epigenesists, according to Gottlieb, understood behaviors to arise from invariant schedules of neural growth and maturation; moreover, they believed that the environment played little role in this maturational process. Probabilistic epigenesists such as Schneirla, in contrast, understood behaviors to arise probabilistically; moreover, they believed that the environment was critical in the probabilistic process. Where the predetermined epigenesist saw invariance along a set course, the probabilistic epigenesist saw inherent uncertainty due to factors such as neurochemical stimulation or the musculoskeletal effects of use during development. And, where the predetermined epigenesist saw a unidirectional relationship between structure and function, wherein the former dictated the latter, the probabilistic epigenesist saw a bidirectional structure–function relationship wherein the former not only directed but also received direction from the latter (Gottlieb, 1970). Gottlieb's attention to complex interactions and bidirectional relationships apparently developed as an undergraduate when he read John Dewey and Arthur Bentley's

Knowing and the Known (1949), which envisioned interaction superseding unidirectional self-action and then transaction superseding interaction. “I got really excited about transactionalism,” Gottlieb recalled just a month before his death, “the idea that you didn’t just have interactions going in one direction, but you had them going in both directions so you needed a new word. You needed transaction, so you can go across, and that just excited me” (Miller, 2006, p. 3).

Importantly, Gottlieb recognized early in his career that the assumptions dividing the predetermined and probabilistic camps were empirically testable (Gottlieb, 2001). This recognition set Gottlieb on a course of innovative experimental research that lasted for decades. In an early experiment, Gottlieb found that ducklings hatched in incubators with no exposure to maternal calls could still identify their maternal call after hatching and could distinguish that maternal call from the maternal call of a chicken (Gottlieb, 1965). Robert Lickliter and Christopher Harshaw have noted, “Had Gottlieb taken the path favored by most nativists, that of proclaiming the behavior in question to be ‘instinctive’ or the product of some ‘innate module’ and then moving on to other topics, developmental science would have been deprived of one of its most interesting series of discoveries” (Lickliter & Harshaw, 2010, p. 503).² Gottlieb did not take that path. Instead, he devised a method of devocalizing the avian embryos in a way that did not interfere with the otherwise healthy development of the birds (Gottlieb & Vandenberg, 1968). The completely devocalized ducklings that were not exposed to maternal calls could not distinguish their maternal call from that of a chicken, while ducklings that were devocalized only after being able to hear their own vocalizations could distinguish the duck call from the chicken call (Gottlieb, 1971). This was a win for probabilistic epigenesis, and Gottlieb noted as much, writing, “The present results indicate that the epigenesis of species-specific auditory perception is a probabilistic phenomenon, the threshold, timing, and ultimate perfection of such perception being regulated jointly by organismic and sensory stimulative factors” (Gottlieb, 1971, p. 156).

The experiments described above, although genuinely innovative, ignored the role of genes in the phenomenon, thus leaving genetic activity out of the bidirectional relationship. Gottlieb sought to correct for this by collaborating with neurologists who had expertise with protein synthesis in the nervous system. Gottlieb prepared three groups of duck embryos: the

²See also Batson and Logan (2007) for another tribute to Gottlieb’s innovative experimental legacy.

first group was exposed for several days to species-specific vocalizations, the second group was exposed for several days to extravisual stimulation via a lighted incubator chamber, and the third group was incubated in acoustic isolation and in the dark. Gottlieb delivered the three groups of duck embryos to his collaborators, and they found enhanced protein synthesis in the auditory nuclei and the optic lobes in the first two groups. Gottlieb saw in this result yet another win for probabilistic epigenesis, recalling, “This, of course, implied a bidirectional S[tructure]–F[unction] relationship all the way to the genetic level during the embryonic period, and it meant that genetic activity could be influenced by normally occurring exteroceptive sensory stimulation and thus result in an enhancement of neural maturation” (Gottlieb, 2001, p. 46). Unfortunately, one of Gottlieb’s collaborators was overburdened by other commitments, and these results never reached a peer-reviewed journal. Still, Gottlieb brought genes into the bidirectional relationship in 1976, contrasting the predetermined “older view” inspired by the central dogma of molecular biology (DNA → RNA → Protein) with the probabilistic “newer view” (Fig. 3.2(a)). Gottlieb eventually developed this

(a)

Older view: Unidirectional structure–function relationship

Genes → Structural maturation → Function.

Newer view: Bidirectional structure–function relationship

Genes ↔ Structural maturation ↔ Function

(b)

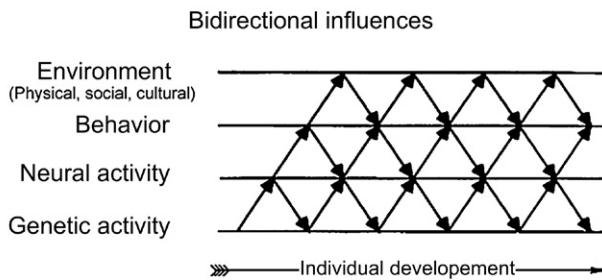


Figure 3.2 (a) The predetermined unidirectional versus the probabilistic bidirectional structure–function relationship (Reproduced from Gottlieb, 1976, p. 218). (b) The bidirectional and coactional relationship. (From Gottlieb (1992), p. 186).

early representation of the bidirectionality between genetic activity, structure, and function into his mature vision (Fig. 3.2(b)) of the “completely bidirectional and coactional nature of genetic, neural, behavioral, and environmental influences over the course of individual development” (Gilbert, 2001, p. 50), which pervaded in his later works (Gottlieb, 1992, 1997).

1.3. Oyama and the Ontogeny of Information

DST has been extremely skeptical of the concept of a genetic program and the idea that either the development of behavior or that behavior itself represents “the decoding of the programmed information contained in the DNA code of the fertilized zygote” (Mayr, 1961, p. 1502). One of the founders of developmental psychobiology (a disciplinary precursor to DST), Daniel S. Lehrman, summed up this skepticism by saying that, “although the idea that behavior patterns are ‘blueprinted’ or ‘encoded’ in the genome is a perfectly appropriate and instructive way of talking about certain problems of genetics and evolution, it does not in any way deal with the kinds of questions about behavioral development to which it is so often applied” (Lehrman, 1970, p. 35).

The influential work of Susan Oyama, and especially *The Ontogeny of Information* (1985), was a systematic development of this idea. Her work demonstrated how the idea of information was deployed to background the role of nongenetic factors in development and to minimize the impact of accepting that phenotypes develop through the interaction of genes and environment. Oyama pioneered the “parity argument”, identifying the criteria used to assign the central causal role in development to genes and showing that these criteria were ignored when they applied to nongenetic factors in development (Oyama, 2000).

The positive aspect of Oyama’s program was the idea that developmental information is actually produced during development: information has an ontogeny. Developmental scientists have often compared nativist views of development to the doctrine of preformationism in early modern biology. Instead of a tiny homunculus, the genome contains little “traitunculi” (Schaffner, 1998). Oyama identified the concept of information as the last bastion of preformationism. The causal connections between genes and complex phenotypic traits were indirect and contingent upon many other causal factors. Treating genes as representations of traits, or instructions for making them, reduced the role of these other factors to providing nonspecific support for reading that information. In contrast, Oyama argued that the phenotypic significance of a single developmental factor, genetic or

otherwise, was always contextual, conferred upon it by its role in the system as a whole. Locating developmental information in the genome confused a contextual property with an intrinsic property.

The ontogeny of information produced a radical reformulation of the distinction between nature and nurture (Oyama, 2002). Nature and nurture were not interacting causes, as in the conventional idea of gene–environment interaction. They were process and product. Nurture was the interaction between the current state of the organism and its environment: the *organism–environment* interaction of Gottlieb and Lehrman. The nature of the organism at each stage was simply the state of that organism and of its developmental environment, both of which were products of earlier processes of nurture.

1.4. Ford, Lerner, and a “DST”

The phrase DST came from Ford and Lerner (1992), who set a systematic research agenda for developmental psychology that incorporated many of the themes introduced earlier. They defined development itself in a way that placed organism–environment interaction at its core. Development consisted of a series of functional transformations of the organism produced by the interaction of the current state of the person with their current context.

One of the core theses of Ford and Lerner’s DST was *developmental contextualism*, which they recognized as closely related to Gottlieb’s concept of probabilistic epigenesis (Ford & Lerner, 1992, p. 11). Rather than reduce one level of causal analysis to another, or treat one level as focal and the others as background against which it unfolds, contextualism treated development as a process that proceeded at several levels and treated interaction between levels as the prime focus of research. Another core thesis was *dynamic interactionism*, as opposed to static interactionism. This contrast was closely related to the contrast between organism–environment interaction and gene–environment interaction mentioned earlier. Ford and Lerner stressed that interaction was an ongoing process in which the interactants were themselves transformed, so that what was interacting later in the process depended on the earlier phases of interaction.

Ford and Lerner linked the idea of a developmental *system* to systems theory and cybernetics. The dynamics of the system played an important role in explaining development. This emphasis on a systems level of explanation provides a link back to the ideas of Waddington, with whom we started. Because Waddington’s approach was more internalist than contextualist, it may seem odd that he has been regarded so positively by DST. What

Waddington shared with Ford and Lerner, however, was their dynamic interactionism and the realization that this form of explanation depended on a rigorous theory of systems.

Starting in the 1990s, there was an explosion of interest in DST in the philosophy of science, mostly in response to the work of Susan Oyama (Gray, 1992; Griffiths & Gray, 1994; Godfrey-Smith, 2000; Moss, 1992; Robert, 2001). However, this interest was aroused by the implications of DST for causation and explanation in genetics. So while most scientific work in the DST framework has been on behavioral development, and much of it on human development, philosophical discussion of DST has focused on its application to molecular biology, or to developmental biology with its traditional emphasis on embryology (Robert, 2001, 2003, 2004; Stotz, 2006, 2008).



2. WHAT DEVELOPMENTAL SYSTEMS THEORY IS NOT

Our review of the contributions of Waddington, Gottlieb, Oyama, and Ford and Lerner provides a sense of what DST is. It is also instructive, however, to focus on what DST is not. And indeed, many of the contributions from the developmentalists discussed earlier took shape in response to other disciplines that they saw as fundamentally flawed. We discuss two such disciplines that were foils for DST: quantitative behavioral genetics and nativist cognitive developmental psychology.

2.1. Quantitative Behavioral Genetics and Its Developmental Critics

A discipline such as quantitative behavioral genetics may be defined either methodologically or sociologically (Hull, 1988, p. 393). Methodologically, quantitative behavioral genetics consists of the application of quantitative genetic methods to behavioral phenotypes. In 1918, Ronald A. Fisher published “The Correlation between Relatives on the Supposition of Mendelian Inheritance” (Fisher, 1918). In the process of demonstrating the compatibility of Mendelian and biometrical models, Fisher also introduced a new statistical concept—variance (Box, 1978, p. 53). In contrast to previous methods of measuring similarity, variance was a measure of difference. The concept was of interest to Fisher because it offered him a means of quantifying genetic and environmental differences and establishing how much each contributed to the total phenotypic variation for a trait in a population. Much of Fisher’s career was spent developing statistical methods

such as the analysis of variance, tests of statistical significance, and the design of experiments, all with the goal of answering this *how-much question* about the *relative contributions of nature and nurture*. This focus on relative contributions would become a defining feature of quantitative behavioral genetics (Griffiths & Tabery, 2008; Tabery & Griffiths, 2010).

From a more sociological perspective, the emergence of behavioral genetics can be dated to around 1960 (Fuller & Simmel, 1986; Whitney, 1990). This date is chosen to recognize the publication of John Fuller and William Thompson's *Behavior Genetics*. "The time seems ripe", the authors began, "for a modern treatment of the division of knowledge we have called 'behavior genetics'" (Fuller & Thompson, 1960, p. v). A textbook-style treatment, *Behavior Genetics* introduced readers to the basics of genetics and population biology, the methods of analysis of variance and twin studies, and the application of these methods to personality and mental disorders. The pivotal disciplinary event occurred a decade later, in 1970, with the creation of the journal *Behavior Genetics*, along with the founding of the Behavior Genetics Association with Ukrainian-American geneticist Theodosius Dobzhansky as its first president (Griffiths & Tabery, 2008; Tabery & Griffiths, 2010).

In later years, advances in molecular biology facilitated the investigation of the role that genes played in the development of a phenotype at the molecular level. When the focus was on humans, however, ethical considerations largely confined behavioral geneticists to traditional quantitative genetic methods. Thus, classical twin and adoption studies continued to be employed to evaluate the relative contributions of different sources of variation, along with gene-hunting studies, that tracked the distribution of genetic markers in families (linkage studies) or populations (association studies) in an attempt to seek out candidate genes associated with behavioral traits (Griffiths & Tabery, 2008; Tabery & Griffiths, 2010).

Also, in later years, quantitative behavioral genetics ventured into the study of development. Developmental behavioral genetics involved the application of the quantitative behavioral genetic methods to developmental data, that is, to repeated observations of the same phenotype at different stages of development—the study of "distributions of individuals developing across time," as Sandra Scarr has characterized the field (Scarr, 1995, p. 158). Scarr argued that developmental behavioral genetics should resemble traditional quantitative behavioral genetics in seeking the causes of phenotypic *differences*, rather than the causes of phenotypes (Scarr, 1992, 1993, 1995). Thus developmental behavioral genetics, according to Scarr,

was a discipline that sets out to explain how much of the observed differences between the developmental trajectories of children can be attributed to genetic differences, to differences in environment, to correlations between genes and environment, and so forth (Griffiths & Tabery, 2008; Tabery & Griffiths, 2010).

DST took shape in part as a reaction against the vision of nature and nurture espoused by quantitative behavioral genetics because it was not “truly developmental” (Gottlieb, 2003). Two features of quantitative behavioral genetics have been particularly subject to criticism: (1) its focus on *how-much* questions about relative contribution rather than *how* questions about developmental mechanisms and (2) its dichotomous view of nature and nurture rather than an interactionist view of their dynamic interplay. Waddington nicely captures the difference between quantitative behavioral genetics and the study of development when it comes to how-much questions about relative contributions versus how questions about causal mechanisms. The behavioral geneticists “assume that changes in the genotype produce correlated changes in the adult phenotype, but the mechanism of this correlation need not concern [them],” while, for Waddington, the mechanism is “of crucial importance, since it is the kernel of the whole problem of development” (Waddington, 2012 [1942], p.10). Gottlieb, likewise, argued that behavioral genetics was not truly developmental in the sense that, “[t]he population view of behavioral genetics is not developmental. It is based on the erroneous assumption that the quantitative analysis of the genetic and environmental contributions to individual differences sheds light on the developmental process of individuals” (Gottlieb, 2003, p. 338). Oyama’s demand for causal parity relied on identifying the developmental mechanisms involved in ontogeny, which would be missed if the task was statistically partitioning relative contributions to one or the other. In sum, the developmentalists directed attention to *how genes caused traits*, rather than to *how much traits genes caused*.

DSTists were also critical of the reification and dichotomization of nature and nurture inherent in the process of statistically partitioning their relative contributions. While statistically valid, in their view, this procedure utterly misrepresented the actual process of development. Gottlieb’s distinction between the unidirectionality of the predetermined epigenesists and the bidirectionality of the probabilistic epigenesists was in this vein. Oyama’s theory of the construction and contextualization of information during ontogeny rejects the very idea that nature exists separate from and before nurture. Finally, both Waddington and Ford and Lerner pointed to

dynamic interactionism as a process in which nature and nurture do not come together to create ontogeny, but are both partly products of ontogeny.

2.2. Nativist Cognitive Psychology and Its Developmental Critics

DST also defined itself against neonativist cognitive developmental psychology. A good deal of research in contemporary cognitive developmental psychology is devoted to documenting “innate” features of the mind that constrain and/or enable later cognitive development (Carruthers, Laurence, & Stich, 2005, p. 9). Chomsky’s “language acquisition device” has served as an exemplar for research on the innate contributions to other psychological domains (Chomsky, 1965). Similar to the language acquisition device, other putatively innate features are thought to embody innate “knowledge” or innate “theories” about specific cognitive domains. For example, the eminent cognitive developmental psychologists Susan Carey and Elizabeth Spelke argue that children possess four domains of innate “core knowledge” that underlies much of their later cognitive development. These domains are “objects, agents, numbers and space” (Carey & Spelke, 1996, p. 517; see also Carey, 2011).

Neonativists support their claims by presenting one or more of three kinds of evidence: (1) the putatively innate features are distinctive of one cognitive domain rather than another, (2) the environment of the child does not contain the right stimuli for the child to learn these features (poverty of the stimulus), or (3) the same features are found in many human cultures. For example, one putatively innate feature of cognition is said to be that living things are subject to a strictly hierarchical classification and that a particular level in that classification—the “generic species”—is associated with “psychological essentialism”. People make inferences about members of a generic species that embody the implicit theory that individuals have a hidden “essence” that causes them to have the typical properties of their species (Atran, 1990; Medin & Atran, 2004; Medin & Ortony, 1989; see also Gelman, 2003). To support this claim, studies are presented in which children reason in this way about living things but not about other domains and in which people in different cultures around the world reason in this way about living things.

The DST critique of neonativism is straightforward: “innate” is not an explanatory category. Neonativists simply do not have developmental explanations of the features they document. This is a modern incarnation of the critique of early twentieth century instinct theories by the

Chinese psychologist Zing-yang Kuo (Guō Rènyuǎn), whose work was later to influence [Gottlieb \(2001\)](#). Calling something “innate” or “instinctive” merely raises the question, “How are our instincts acquired?” ([Kuo, 1922](#)) For this reason, when Gottlieb identified an apparently “innate” trait in ducks’ recognition of maternal vocalizations despite being raised in isolation, he asked *how* this trait was acquired, and undertook experiments to link it back to the embryonic ducks’ own vocalizations (see discussion above). A related critique accuses nativists of conflating evolutionary with developmental explanations ([Lickliter & Berry, 1990](#)). The evidence for nativism is often evidence that the trait in question is the result of evolutionary design, and one of the many meanings of “innate” is that a trait is the result of evolution ([Mameli & Bateson, 2006](#)). So the label “innate” suggests a developmental explanation when the evidence for that label only supports an evolutionary explanation.

Neonativists think that this critique underestimates their understanding of development. They recognize that all traits, including those that they label “innate”, result from an interaction of genes and the environment and that psychological development results from the interaction of these innate features with the local developmental environment ([Carey & Gelman, 1991](#); [Marcus, 2004](#)). They define their own views against forms of environmentalism that do not recognize any specific biological contribution to psychological development. However, neonativist explanations of the development of “innate” traits engage in just the kind of backgrounding of nongenetic factors that DST sets itself against. Their development is maturational; their epigenesis is predetermined—with environmental factors only permitting the expression of genetic potential.

A striking feature of neonativism is that the innate contribution to psychological development is studied at the level of behavior with little, if any, attention to developmental processes at lower levels of biological organization ([Marcus, 2004](#) is an important exception). This has led to the suggestion that two fundamentally separate issues are conflated in the dispute between DST and neonativism ([Perovic & Radenovic, 2011](#)). The first issue is the pattern of gene–environment interaction in the development of the features documented by neonativist research. Neo-nativists claim that the pattern is maturational, with genes as specific causes and environmental factors as merely “permissive” causes ([Holtzer, 1968](#)). The second issue is the neonativist claim that later stages of cognitive development are primarily explained by these early-developing features. Most DSTists deny both these claims, but the critiques mentioned earlier only speak directly to the

first claim. Conversely, most neonativists make both claims, but neonativist research is primarily about the second claim. The potential therefore exists for a position that not only claims that some later stage in cognitive development is primarily explained by early-developing features that strongly constrain and/or enable later development but also claims that those early developing features emerge in a fully epigenetic manner, with both genetic and environmental factors playing an instructive role.



3. CORE CONCEPTS

The discussions about what DST is and is not allow us to distill out two core concepts that are integral to the DST perspective: epigenesis and developmental dynamics.

3.1. Epigenesis

The term “epigenetics” is derived from the process of epigenesis. It is a continuation of the concept that development unfolds and is not preformed (or ordained), epigenetics is the latest expression of epigenesis.

(Hall, 2011, p. 12).

The idea that development is a process of epigenesis is at the heart of DST. The term “epigenesis” was introduced by the seventeenth century anatomist William Harvey and is derived from the Greek for “upon” and “origin”. For the next century and a half, epigenesis referred to the view that the contents of the ovum are relatively simple and that the operation of natural laws on these simple ingredients leads to increased complexity. The alternative view, preformation, saw the egg as a divinely designed Newtonian mechanism that could unfold and reorganize itself to produce an animal. In the eighteenth and nineteenth centuries, epigenesis was strongly associated with the idea of spontaneous generation. If the egg contains simple physical ingredients that develop under the influence of physical laws, why cannot other pieces of matter, under the influence of physical laws, produce life? The idea of spontaneous generation was strongly rejected by nineteenth century biology, partly because of the cell theory (“cells only come from cells”) and partly because of the germ theory of disease. Preformationism was recast as the more general doctrine of predeterminism, the idea that development consists of an orderly progression of qualitative change to a predetermined end point. What predeterminism has in common with preformationism is the view that the environment of the egg and physical laws are nonspecific or permissive factors,

while all the specific or instructive factors are inside the egg, the nucleus, or the genome (Gottlieb, 2001). Ernst Mayr's view that development is guided by a genetic program is one such predeterminist view (Mayr, 1961).

The term "epigenetics" was coined by Waddington through the fusion of "epigenesis" and "genetics", to refer to the processes by which genotype gave rise to phenotype and to the study of those processes (Waddington, 2012 [1942]). Waddington emphasized that epigenetics was a search for causal mechanisms and suggested that existing knowledge from experimental embryology supported a view of how genes were connected to phenotypes broadly in line with the older idea of epigenesis. The interaction of many genes produced an emergent level of organization that he termed the "epigenotype" (Fig. 3.1) and development was explained by the dynamics of the developmental system at this level. Thus, Waddington's epigenesis was a systems view of development and was also strongly gene centered.

In 1958, the biologist David L. Nanney introduced a narrower understanding of "epigenetics" and gave the word the sense in which it is primarily used in molecular biology today (Haig, 2004). Epigenetics was the study of mechanisms that determine which genome sequences will be expressed in the cell, mechanisms that control cell differentiation and give the cell an identity that is often passed on through mitosis. In the year that Francis Crick first stated his "sequence hypothesis" that the order of nucleotides in DNA determines the order of amino acids in a protein (Crick, 1958), Nanney wrote that, "On the one hand, the maintenance of a 'library of specificities,' both expressed and unexpressed, is accomplished by a template replicating mechanism. On the other hand, auxiliary mechanisms with different principles of operation are involved in determining which specificities are to be expressed in any particular cell. ...they will be referred to as 'genetic systems' and 'epigenetic systems'" (Nanney, 1958, p. 712). This is the picture of gene expression found in contemporary molecular biology.

Epigenetics in both Waddington's and Nanney's senses created opportunities for the environment to play an instructive role in development, even if those opportunities were often ignored. Waddington's epigenotype was a global expression of the genetic causal factors that influence development. The effect of changing any one gene depended on how it interacted with the rest of the system. The epigenotype as a whole interacted with the environment to determine the phenotype. DST expanded the epigenotype to include nongenetic factors that influence development. The expanded epigenotype, or developmental system, was a global expression of the causal factors that influenced development. It still did not determine a

unique phenotype, both because development was a probabilistic process and because development was plastic by design. So the environment figured in two ways in DST: (1) first by supplying the background to normal development (the ‘ontogenetic niche’, see below) and thus partly constituting the developmental system and (2) second by supplying the variable parameters of that system and so determining which particular course development took. It is sometimes overlooked that in Waddington’s original picture genes also played two roles. Genes collectively determined the shape of the developmental landscape and gene *mutations* also threw development down one valley (“creode”) or another.

Epigenetics in Nanney’s sense also created a space for the environment: “As the past 70 years made abundantly clear, genes do not control development. Genes themselves are controlled in many ways, some by modifications of DNA sequences, some through regulation by the products of other genes and/or by [the intra- or extra-cellular] context, and others by external and/or environmental factors” (Hall, 2011, p. 9). The regulated expression of the coding regions of the genome depended on the mechanisms that differentially activated and selected the information in coding sequences depending on context. Biological information was distributed between the coding regions in the genome and regulatory mechanisms, and the specificity manifested in gene products was the result of a process of “molecular epigenesis” (Griffiths & Stotz, 2013; Stotz, 2006). It was often assumed that the additional information provided by epigenetic regulation traced back to some feature or other of the whole genome sequence. The alternative view was that the environment, acting through epigenetic regulatory mechanisms, played an instructive role in regulating gene expression.

Much of the recent interest in “epigenetic inheritance” has been motivated by the desire to document the instructive role of environmental factors in this manner (Jablonka & Lamb, 1995, 2005; Jablonka & Raz, 2009). The phrase “epigenetic inheritance” has two senses, corresponding to the two senses of “epigenetic” outlined earlier. Epigenetic inheritance in the narrow sense is the inheritance of genome expression patterns across generations (e.g., through meiosis) in the absence of a continuing stimulus (Holliday, 1987). Epigenetic inheritance in the broad sense is the inheritance of phenotypic features via any causal mechanism other than the inheritance of nuclear DNA. To avoid confusion, we refer to this broader sense as “exogenetic inheritance”. The developmental psychobiologists Meredith West and Andrew King introduced the term “ontogenetic niche” to refer collectively to the products of exogenetic heredity (West & King, 1987).

The ontogenetic niche, or developmental niche, contained the nongenetic developmental factors required for normal development. That is to say it contained the factors omitted from Waddington's original "epigenotype". The full developmental system consisted of the organism (initially the fertilized egg) and the developmental niche. Sixty years of work in developmental psychobiology documents the instructive role of the developmental niche in behavioral development (Michel & Moore, 1995). And, recent work has shown how these environmental factors operate via epigenetic mechanisms of genome regulation (Meaney, 2001, 2004).

The developmental niche concept reflects the central feature of DST that Ford and Lerner called "developmental contextualism" (Ford & Lerner, 1992). Organisms reproduce themselves by reproducing the context of development. The stability of inheritance is not only explained by the insensitivity of development to context, as Waddington's concept of canalization suggested, but also by the active reproduction of context by the parental generation. However, organisms are plastic, as well as stable. One advantage of DST over traditional interactionism is that it can recognize that the evolutionary functions of heredity systems combine the stable transmission of phenotypes across the generations and plastic responses to fluctuating environments (Bateson & Gluckman, 2011). The very same mechanisms can serve both functions, depending on the particular settings of their parameters. "Parental effects" in evolutionary ecology, for example, are mechanisms for producing both correlations and anticorrelations between parent and offspring phenotypes to match fluctuating environments (Maestriperi & Mateo, 2009; Mousseau & Fox, 1998). They are mechanisms for the intergenerational transmission of phenotypes, but they exist in the service of plasticity, not fixity (parental effects have also attracted attention in recent medical research (Gluckman & Hanson, 2005a, 2005b; Gluckman et al., 2009)).

Two themes have emerged in our discussion of epigenesis: (1) the importance of the systems level in the analysis of development and (2) developmental contextualism. Some "developmentalist" visions in biology emphasize the first of these themes more than the second. For example, the successful new discipline of evolutionary developmental biology ("evo-devo") retains a vision of development much closer to that of Waddington than that of Gottlieb. The history of life on Earth is the history of changes in gene regulatory networks via changes in the DNA sequence itself (Arthur, 1997; Carroll, Grenier, & Weatherbee, 2001). Scott Gilbert's recent call for an "ecological developmental biology" represents an attempt to introduce

something like developmental contextualism into evolutionary developmental biology (Gilbert, 2001; Gilbert & Epel, 2009).

We described earlier how Gottlieb's concept of probabilistic epigenesis added the environmental context to Waddington's vision of a developmental system. But Gottlieb also added the concept of coaction. Higher levels of developmental organization are not simply the expression of lower levels, but act on those lower levels. The organism itself is an agent in development and not just a product of development. It is to this theme that we now turn.

3.2. Developmental Dynamics

The idea that development is a dynamic process is central to DST (Kuo, 1967, pp. 55–58; Gottlieb, 1970; Lerner, 1978). In a seminal paper, Daniel Lehrman wrote that “The interaction out of which the organism develops is *not* one, as is so often said, between heredity and environment. It is between *organism* and environment! And the organism is different at each stage of its development” (Lehrman, 1953, p. 345, emphasis in original). In a dynamic approach, development at each stage builds on the results of development at an earlier stage. The components produced by interaction at one stage of development are the components that do the interacting at a later stage. Lehrman emphasizes change in the organism, but the environment can also change as a result of development. For example, in Celia Moore's well-known work on sexual development in male rat pups, male sexual development depends on differential licking of the genital area of male and female pups by the mother. But her response to male pups depends on differences in their urine, which are the result of earlier processes of sexual differentiation (Moore, 1984, 1992). The presence of this environmental influence is a feed forward from earlier development in the pup itself.

Dynamic interaction can be seen in the figure by Gottlieb depicting bidirectional influences in development (Fig. 3.2(b)). Causal influences from any one level of analysis feed forward to the other levels of analysis. The influence of one level on a second level can help to produce the later influence of the second level on the first. In his own work, Gottlieb documented the reciprocal influence of structure (e.g., morphology) on function (e.g., behavior), especially the influence of prenatal activity in birds on the development of neural structure.

Ford and Lerner contrast dynamic interaction with a more conventional conception of interaction associated with analysis of variance techniques, such as those used in behavioral genetics (Ford & Lerner, 1992).

In what we might call “static interactionism”, the values of two variables measured before development, such as shared genes and shared environment, are shown to interact with one another (there are ambiguities that we will not pursue here, see Tabery, 2007). In contrast, dynamic interaction must be studied as a temporally extended process. In the next section, we will discuss how the fact that dynamic interaction is studied over time makes it easier for a dynamic interactionist approach to recognize bidirectional influences.

If interaction is a dynamic process, then the temporal dynamics of the interaction may play an independent role in explaining the outcome. The introduction of dynamical systems theory (here written as DyST to avoid confusion) adds an additional dimension to developmental explanation. We note that there is nothing about the basic idea of dynamical interaction that requires the use of DyST. The kinds of systems pictured in Fig. 3.2(b) can be analyzed as sequential mechanisms in the sense discussed in the next section. Whether they need to be analyzed as dynamic mechanisms depends on the specific causal structure. However, some developmental psychologists have made extensive use of DyST to explain developmental outcomes by mapping the dynamics of the system as it evolves over time in multiple actual or simulated “runs” and establishing that the outcome is an attractor for the system.

This kind of explanation was used by Esther Thelen in her studies of the emergence of coordinated stepping movements in human infants. Because this behavior emerges *before* the child begins to walk, it satisfies one of the traditional criteria for innate behavior—“prefunctionality” (Mameli & Bateson, 2006). Thelen argues, however, that this behavior emerges not because it is planned or programmed somewhere in the genes, but from the previous dynamical state of the system as one of its parameters varies. This can be demonstrated in “microgenesis” experiments that bring about the emergence of a new behavior before its normal period of “maturation” by manipulating some parameter of the system. Coordinated stepping in infants results from the interaction of motor patterns present from earliest infancy but suppressed during an intermediate period by the weight of their limbs. When the available muscular force catches up with the weight of the limbs, the old pattern results in what appears as the “spontaneous” emergence of effective stepping behavior. However, this and other aspects of walking can be brought out earlier in development by removing simple physical constraints (Thelen & Ulrich, 1991).

Thelen summed up her DyST approach to child development as follows:

...behavior and cognition, and their changes during ontogeny, are not represented anywhere in the system beforehand either as dedicated structures, or symbols in the brain, or as codes in the genes. Rather, thought and behavior are 'softly assembled' as dynamical patterns of activity that arise as a function of the intended task at hand and an individual's 'intrinsic dynamics' [by which is meant] the preferred states of the system given its current architecture and previous history of activity...

(Thelen, 1995, p. 76; see also Thelen & Smith, 1994).

DyST explanations have often been criticized for being merely descriptive and not truly explanatory. The fact that a state is an “attractor” for the system is determined solely by observing its occurrence in multiple runs of the system but the existence of this attractor is treated as an explanation for the system being in that state (for an extended discussion see chapter six of Clark, 1997). In the next section, we will see how dynamical explanations have been incorporated into recent accounts of mechanistic explanation.



4. MECHANISMS—A PHILOSOPHY FOR DEVELOPMENTAL SYSTEMS THEORY

Waddington identified the mechanism linking genotype to phenotype as “the whole problem of development” (Waddington, 2012 [1942], p.10). Likewise, Nanney distinguished the genetic system from the epigenetic system based upon what the mechanism of each did. Why? What is it about a mechanism and mechanical explanation that scientists within the developmental perspective find so attractive?³ In this section, we introduce the philosophy of mechanism, an influential school of thought in the philosophy of science, and apply it to DST in order to characterize *how* DST explains. In particular, we apply the philosophy of mechanism to (1) Gottlieb’s concept of bidirectionality, (2) Ford and Lerner’s concept of dynamic interactionism, and (3) DST’s vision of truly developmental explanations.

4.1. The Philosophy of Mechanism

Throughout the twentieth century, the philosophy of science was dominated by a theory of scientific explanation that took explanations to consist of derivations from laws of nature. On this “deductive-nomological” account,

³For other examples of this focus on mechanism and mechanical explanation, see Feldman & Lewontin, 1975, pp. 1167–1168; Moore, 2008, p. 382.

a phenomenon was explained by deducing it from a set of premises one or more of which was a law of nature (Hempel & Oppenheim, 1948). This theory of scientific explanation seemed satisfactory in the physical sciences where laws of nature were readily available, but the theory did not apply so neatly to the biological sciences where laws of nature remained elusive. In the face of this dilemma, philosophers of science turned to the actual practice of biological science to assess how explanations worked there and what they consistently found were appeals to mechanisms (Bechtel & Abrahamsen, 2005; Bechtel & Richardson, 1993; Glennan, 1996, 2002; Machamer, Darden, & Craver, 2000).

The resulting philosophy of mechanism offers a new theory of scientific explanation: scientists explain a phenomenon by identifying and manipulating the variables in the mechanisms responsible for that phenomenon, thereby determining how those variables are situated in and make a difference in the mechanism; the explanation ultimately amounts to the elucidation of how those variables act and interact in the mechanism to produce the phenomenon under investigation. The philosophy of mechanisms is meant to capture how scientists answer questions such as the following: How do plants convert solar energy into chemical energy (Tabery, 2004)? How do rats form spatial memories of their environments (Craver, 2007)? And how does the cell produce proteins (Darden, 2006)? Such questions are answered by elucidating the mechanisms responsible for photosynthesis, spatial map formation, and protein synthesis, respectively. This theory of scientific explanation as mechanism–elucidation is very much in line with DST.

4.2. Bidirectionality

Gottlieb, throughout his career, advocated a bidirectional probabilistic epigenesis. Figure 3.2(b) shows how Gottlieb visualized this bidirectional relationship: multiple levels (genetic, neural, behavioral, environmental), with arrows pointing up and down, all moving through time to collectively constitute individual development. The arrows pointing upward and representing genetic influence on the higher levels are uncontroversial, but how should we make sense of the arrows from higher levels exerting downward influence? Such top–down causation is often dismissed as spooky because it appears to involve mysterious forces exerted by wholes upon their parts. Philosophers of mechanism Carl Craver and William Bechtel, however, disagree (Craver & Bechtel, 2007). According to Craver and Bechtel, the right way to understand top–down causation is by uniting

intralevel causal relations with interlevel *constitutive* relations. “Level”, for Craver and Bechtel, refers to a level of mechanism, so the idea is that causal relations exist within mechanisms at a given level, but mechanisms at a given level are constitutively related to mechanisms at other levels. Thus, for Craver and Bechtel, top-down causation arises via mechanistically mediated effects: “As the mechanism as a whole is put into new conditions, it is organized such that its components change with those conditions” (Craver & Bechtel, 2007, p. 561).

We can apply Craver and Bechtel’s account of top-down causation to Gottlieb’s emphasis on bidirectionality by drawing on Gottlieb’s own research. Consider his description of the duck embryos exposed to extravisceral stimulation or species-specific vocalizations, which then generated enhanced protein synthesis at the genetic level (discussed earlier, Gottlieb, 2001). The developing duck embryos consisted of many levels of mechanism: mechanisms of protein synthesis at the genetic level, mechanisms of visual and auditory perception at the neural level, mechanisms of vocalization at the behavioral level, and mechanisms of light and sound emission at the environmental level. On Craver and Bechtel’s account, there was top-down causation in this case via the mechanistically mediated effects: As the mechanism as a whole (i.e., the duck embryo) was put into new conditions (i.e., the environment with extra visual/auditory stimulation), it was organized such that its components (i.e., genes) changed (i.e., gene expression) with those conditions. The mysterious idea of downward *causation* is replaced by the very unmythical idea that large causal mechanisms are *constituted* of parts that are themselves smaller causal mechanisms. The operation of the larger mechanism produces changes in its parts.

4.3. Dynamic Interactionism

Gottlieb’s concept of bidirectionality is related to Ford and Lerner’s concept of dynamic interaction; both emphasize the reciprocal relationship between the various levels of mechanism of an organism. Ford and Lerner added to this an emphasis on the dynamic way parts interact in a system. Ford and Lerner contrasted sequential, linear causality with the idea of a causal field, wherein a change in any variable comes about as a consequence of the operation of the entire field of variables (Ford & Lerner, 1992, p. 57).

The philosophy of mechanism also has resources for making sense of this appeal to dynamical explanations. Bechtel, along with Adele Abrahamson, has advanced the philosophy of mechanism by developing it so as to capture *dynamical mechanistic explanations* (Bechtel & Abrahamson, 2010,

2011). According to Bechtel and Abrahamsen, scientists begin to explain a phenomenon by decomposing the system in order to identify the parts, operations, and organization that generate the phenomenon. Take circadian rhythm—the ability of organisms to keep track of day/night cycles—which is found in organisms across the plant and animal kingdoms. Starting in the 1970s, researchers honed in on the suprachiasmatic nucleus (SCN) as playing a critical role circadian rhythm; lesions that removed the SCN left an organism arrhythmic, and transplant experiments that moved the SCN from a donor hamster with an abbreviated rhythm to a recipient hamster with a normal rhythm led to an abbreviated rhythm in the recipient hamster. Bechtel and Abrahamsen point out, however, that scientists do not settle for decomposition; the next step is recomposition, where the task is to put the parts back together in order to produce the phenomenon to be explained. They typically do this with computational modeling that elucidates the spatial organization of parts and the temporal organization of operations. Starting in the 1990s, scientists constructed a series of computer models that identified how the circadian rhythm arose from the synchronization of individual neurons; they also explained phenomena associated with desynchronization—jet lag (Bechtel & Abrahamsen, 2010). So, for Bechtel and Abrahamsen, dynamic mechanistic explanations involve both a reductive decomposition and an integrative recomposition, and it is in the integrative recompositional phase that the dynamic interactions become apparent.

Ford and Lerner's flagship example of a dynamically interacting system is a perfect example of Bechtel and Abrahamsen's dynamical mechanistic explanation. The example is a beating heart. Each cardiac muscle, Ford and Lerner explain, is an autonomous oscillator displaying rhythmic contraction patterns, but the heart as a whole beats as a result of the synchronization of the individual cardiac cells. They also note that this synchronization can break down (fibrillation), and the organism will suffer a fate worse than jet lag if this desynchronization is not corrected—death. Ford and Lerner conclude, "As with the network of power generators, the synchronization results from the influence of the entire organization of heart muscles on component muscle cells, not from the singular influence of individual cells on one another" (Ford & Lerner, 1992, p. 58). This explanation of a beating heart involves both a decompositional identification of individual cardiac cells and a recompositional analysis of how these parts dynamically interact to synchronize such that the heart as a whole can beat and pump blood.

4.4. Truly Developmental Explanations

Gottlieb criticized quantitative behavioral genetics for its inability to provide “truly developmental” explanations. To make sense of Gottlieb’s complaint, we must first give an account of quantitative behavioral genetic explanations and then assess what those explanations lack. Quantitative behavioral geneticists, recall, seek to partition the relative contributions of nature and nurture. They do this by studying a trait in a population and determining how much actual differences in genes and how much actual differences in environment contribute to actual differences in the trait. In humans, they often study twins, adoptees, and blood relatives because then the actual differences (or lack thereof) in genes and environment can be specified. In some cases, a single actual difference in either genes or environment fully accounts for the actual difference in the trait; Waters (2007) refers to such a factor as “*the* actual difference makers”. Often, however, there are multiple actual differences in genes and the environment that account for the actual difference in the trait; Waters labels each “*an* actual difference maker”. When studying actual difference makers, the goal is linking up actual difference(s) in input with actual difference(s) in output; the mechanism linking them, however, is often left uninvestigated. Waters’ case study involves the work of Thomas Hunt Morgan and his research on the genetics of *Drosophila*, such as on the purple eye gene. “The explanatory reasoning here does not depend on identifying the material make-up, mode of action, or general function of the underlying purple gene,” Waters acknowledges (Waters, 2007, p. 558). Notice how this admission matches on to Waddington’s distinction between the study of inheritance, which “merely assume[s] that changes in genotype produce correlated changes in the adult phenotype,” and the study of development, which investigates “the mechanism of this correlation.” Quantitative behavioral genetics falls into the former category; it seeks out actual difference makers and attempts to quantify the relative contribution made by that/those actual difference makers for a given trait in a population. Thus, a quantitative behavioral genetic explanation amounts to answering a how-much question about actual difference makers.

Actual difference makers, however, are not the only causally relevant difference makers between a given input and a given output in a population. There are also what we can call “potential difference makers”. These are causes that, *had they varied*, would have led to variation in the output, but since *they did not vary* they contributed no variation. So they are difference makers, but they are only potential difference makers because there is

not an actual difference that can generate an actual difference in the population. In the mechanism between input and output, there are many potential difference makers that do not actually vary. Nevertheless, identifying these potential difference makers and elucidating how they are situated in the mechanism is crucially important for understanding how the mechanism works and which possible interventions on the mechanism would generate different outputs. Take, for example, exposure to species-specific vocalizations during embryonic development. If all the duck embryos in a clutch are exposed to the same maternal vocalizations and respond with the same vocalizations of their own, then none of the actual differences in the duck hatchlings can be attributed to the vocalizations because there was no actual difference in the vocalizations. So vocalizations would not count as an *actual* difference maker in such a scenario. What Gottlieb discovered, however, was that vocalizations nevertheless were *potential* difference makers. His experiments that isolated and devocalized the duck embryos in turn led to differences in the duck hatchlings (i.e., an inability to recognize species-specific vocalizations). Such an experiment, for Gottlieb, was one step in generating a “truly developmental” explanation of avian vocalization. Thus, a *truly developmental explanation* of a phenomenon should be understood as (1) the identification of both the actual *and* the potential difference makers in the mechanism(s) responsible for the phenomenon, (2) the distribution of the actual *and* potential difference makers in a population, and (3) the elucidation of how those difference makers make or would make their difference in the mechanism(s). Gottlieb’s criticism of quantitative behavioral genetics was that its methodologically enforced restriction to actual difference makers prevented it from generating truly developmental explanations.



5. CONCLUSIONS

DST has a rich history, and today, different researchers draw on different aspects of this theoretical tradition. But the tradition has some strong unifying themes. We have identified two core concepts of DST, epigenesis and developmental dynamics. First, development is a truly epigenetic process. The outcomes of development are explained at the systems level, and developmental is influenced by the context in which it unfolds, leading to an extensive conception of that system. Second, development is a dynamic process: the interactants at one stage are the products of earlier stages of development.

We have interpreted the explanatory structure of developmental systems using some ideas from recent philosophy of science. The “truly developmental” explanations at which DST aims are mechanistic explanations, and often dynamical mechanistic explanations, of the developmental potential of the system. They are mechanistic because they explain developmental phenomena by displaying how the components of the developmental system are arranged so as to produce those phenomena. They are dynamic mechanistic explanations when the phenomena to be explained are not the immediate consequence of the arrangements of the components but emerge from the dynamic operation of the mechanism. Finally, truly developmental explanations do not merely explain why one individual differs from another. They explain the potential of the developmental system to produce these and other outcomes.

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