Developmental Systems Theory as a Process Theory

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Abstract and Keywords

Paul Griffiths and Russell D. Gray have argued that the fundamental unit of analysis in developmental systems theory should be a process—the life cycle—and not a set of developmental resources and interactions between those resources. The key concepts of developmental systems theory, epigenesis and developmental dynamics, also suggest a process view of the units of development. This chapter explores in greater depth the features of developmental systems theory that favour treating processes as fundamental in biology and examines the continuity between developmental systems theory and ideas about process in the work of several major figures in early twentieth-century biology, most notably C. H. Waddington.

Keywords: C. H. Waddington, developmental dynamics, developmental systems theory, epigenesis, genidentity, life history theory, process biology

(p.225) 1. Introduction

Developmental systems theory (DST) builds on a long tradition of ideas about the systems nature of development among biologists and psychologists, predominantly ideas from workers in the field of developmental psychobiology. Elements of DST are derived from C. H. Waddington's views on developmental systems (Waddington 1952) and on the 'epigenotype' (Waddington 1942), from Daniel Lehrman's influential critique of the concept of innate behaviour (Lehrman 1953), from Gilbert Gottlieb's theory of probabilistic epigenesis (Gottlieb 2001), and from Susan Oyama's book *The Ontogeny of Information*

(Oyama 1985). Developmental psychobiologists Donald Ford and Richard Lerner integrated many of these ideas into a formal framework in their book *Developmental Systems Theory* (Ford and Lerner 1992).

DST analyses development, heredity, and evolution in a way that avoids dichotomies such as nature versus nurture, genes versus environment, and biology versus culture. In this framework, *development* (ontogeny) is the reconstruction of a life cycle using resources passed on by previous life cycles. DST takes *heredity* to encompass both the stability and the plasticity of biological form, which are complementary aspects of the recurrence and modification, in each generation, of a system of genetic, epigenetic, and exogenetic developmental resources (Stotz and Griffiths 2017). The prime focus of a DST account of *evolution* is the life cycle—the series of events that occurs in each generation of a lineage. The process of evolution is the differential reproduction of variant life cycles. The end of one life cycle and the beginning of the next is marked by the reconstruction of the various mechanisms that allow the life cycle to reproduce itself from relatively simple resources. The replication of genes is simply one aspect of the replication of a life cycle. Many classes of developmental resource are replicated: genes, methylation patterns, membrane templates, cytoplasmic gradients, centrioles, nests, parental care, habitats, and cultures are all at least partly constructed by past generations and interact to construct future generations.

DST attracted the interest of philosophers of biology in the 1990s, mostly in response to the work of Susan Oyama (Godfrey-Smith 2000; Gray 1992; Griffiths and Gray 1994; Moss 1992; Robert et al. 2001). However, while most scientific work **(p.226)** in the developmental systems tradition was on behavioural development, including child development, philosophical discussion of DST focused on its implications for 'gene-centred' views of molecular developmental biology and evolutionary biology. In this vein, Kim Sterelny, Michael Dickison, and Kelly Smith (1996) proposed to assimilate developmental systems theory to the replicator/interactor view of evolution put forth by Richard Dawkins (1976) and David Hull (1988). They suggested that the evidence and arguments used to support DST could be accommodated by the concession that there are some non-genetic replicators in addition to the genetic ones. Evolution is the result of competition between members of an *extended* class of replicators.

The 'extended replicator' approach was rejected by developmental systems theorists Griffiths and Gray (1997), who pointed to some paradoxical consequences of trying to describe developmental systems and their evolution in a replicator framework. A developmental system includes a 'developmental niche' that contains the reliably inherited developmental resources needed to reconstruct that developmental system—or to modify it, in the case of phenotypic plasticity. Some of the resources that make up the developmental niche are actively constructed by the parents—for example breast milk, or the

incubation mounds built by male brush-turkeys (Goth 2004). Others, such as the flock structure required for normal behavioural development in cowbirds, are constructed through the activity of many conspecifics, and not only by the parents (West and King 2008). But some merely persist, independently of the activities of previous generations in the developmental systems—for example the territories inherited by male scrub jays from their fathers (West et al. 1988: 49). All these resources are potentially part of the evolved developmental system:

> There is a fundamental similarity between building a nest, maintaining one built by an earlier generation, and occupying a habitat in which nests simply occur (for example, as holes in trees). In all three cases, there may be an evolutionary explanation of the interaction of the nest with the rest of the developmental system.
>
> (Griffiths and Gray 1994: 291)

Griffiths and Gray used examples of habitat and host imprinting to show that one lineage can outcompete another even when the feature in which the two lineages differ falls into the category of 'merely persistent' resources (ibid., 288–90). They reiterated this point in 1997, in order to rebut the objection that habitat and host associations themselves do not evolve by natural selection; only the behaviours that *produce* habitat and host associations do. This objection fails because populations with exactly the same behavioural mechanism for habitat or host imprinting may differ in their level of fitness as a result of the specific persistent resource with which they (re-)establish a relationship: 'In cases of host imprinting in parasitic insects or cuckoos…much of the rest of the parasite group's evolution may result from the success of lineages with one relationship rather than another' (Griffiths and Gray 1997: 485).

The relationship between a developmental system and a persistent resource can explain aspects of both development and evolutionary success. But the persistent resource itself is not replicated in development, nor does it increase its representation relative to alternatives as a result of the evolutionary success of the system, so the persistent resource cannot be treated as a replicator. What is replicated, and may increase in representation, is the *relationship* between system and resource. Griffiths **(p.227)** and Gray (ibid.) argued that treating these relationships as replicators independent of their relata would be a *reductio ad absurdum* of the replicator concept. DST offers a less paradoxical treatment of persistent resources:

> We conceive of an evolving lineage as a series of cycles of a developmental process, where tokens of the cycle are connected by the fact that one cycle is initiated as a causal consequence of one or more previous cycles, and where small changes are introduced into the characteristic cycle as ancestral cycles initiate descendant cycles. The events which make up the

developmental process are developmental interactions—events in which something causally impinges on the current state of the organism in such a way as to assist production of evolved developmental outcomes.

(Griffiths and Gray 1994: 291)[1]

A process ontology for DST allows it to reconcile two otherwise paradoxical facts: some components of the evolved developmental system persist without reference to the rest of the system, but the presence of these components in the system can be explained by natural selection. These facts cease to seem paradoxical if we focus on how life cycles—processes rather than systems of entities—reproduce themselves and on how variant life cycles reproduce themselves more or less effectively. It is the developmental *process* that replicates itself across the generations, making use of persistent resources as well as of resources created by earlier cycles of that process. Re-establishing or breaking a relationship with a persistent resource, for example by becoming imprinted on a new habitat, is an event that is part of a developmental process.

2. Process Biology

Griffiths and Gray argue that the fundamental unit of analysis in DST is a developmental process. This process is better described as a *life cycle*, since it encompasses the entire period between conception and death. Does this mean that DST is a form of process biology? In this chapter we will argue that it does. As a first step, we discuss the inspiration that many early twentieth-century biologists drew from process philosophy, and we ask which if any of their ideas correspond to those found in DST. A direct link between DST and these earlier thinkers is the embryologist, developmental geneticist, and theoretical biologist Conrad Hal Waddington (1905–75), whose ideas have been cited by many advocates of DST.[2] In *The Evolution of Developmental Systems*, Waddington describes his understanding of physiology, development, and evolution as nested processes:

Biologists have always been forced by their subject matter to take time seriously. But it is only gradually that they have realised to the full the necessity always to consider living things as essentially processes, extended in time, rather than static entities.

 (p.228) The day-to-day activities of living things are carried on by processes which occur anything from a fraction of a second to an hour or two…[the organism] is gradually carried along through another series of processes, those of development, each phase of which occupies a time which is fairly long compared with the life-cycle. Each life-cycle is again nearly circular, and gives rise to new animals, the descendant generation… The accumulation of such changes gives rise to the slow process of

evolution, which is on a still larger scale than either the physiological or developmental ones.

(Waddington 1952: 155)

Waddington was deeply influenced by the process philosophy of Alfred North Whitehead, as were many of his British contemporaries, for instance the biochemist Joseph Needham, the theoretical biologist J. H. Woodger, and the leading Cambridge behavioural biologist W. H. Thorpe (see chapter 1 here and Abir-Am 1987; for Thorpe's views, see Thorpe 1956). Whitehead's influence on biology was equally strong in Australia, where it extended to the Nobel Prize-winning immunologist Frank Macfarlane Burnet (Anderson and Mackay 2014), to the geneticist and ecologist L. Charles Birch (Birch 1965; see also chapter 15), and to the geneticist Wilfrid E. Agar. It was Agar (1882–1951) who introduced Australian biologists to process philosophy, through works such as 'Whitehead's Philosophy of Organism: An Introduction for Biologists' (Agar 1936). Agar sought to convince his fellow biologists that Whiteheadian process philosophy was a good framework for biological research, and so his work is particularly useful when we ask what aspects of this older enthusiasm for process thought are relevant to DST.

There are some aspects of Whitehead's thought that were important to these biologists but have little relevance in the current context. Whitehead rejected the idea that the mental must be explained in physical terms, insisting instead on a monistic 'panexperientialism'. Agar noted that '[t]he conception that the world, including the physical world, is composed of entities which are "drops of experience" or feelings will seem to many people a strange one' (ibid., 18). He hastened to reassure biologists that '[w]e must bear in mind that "feeling" is here used throughout as the purely general term for any kind of acting or being acted upon, in such a way that the make-up of the subject is affected' (ibid., quoting Emmet 1932: 142). Through these aspects of his system, Whitehead offered biologists a way to make room for consciousness in the physical world, as well as a route to reconcile science and religion; and, for some biologists, this was an important source of their attraction to Whitehead (Bowler 2014).

However, as historian Peter Bowler has noted, 'Waddington had no interest in encouraging scientists to revive an interest in religion' (Bowler 2014: 80). His interest in Whitehead's metaphysics was strictly biological. The lessons he derived from Whitehead were that biological phenomena should be explained at the level of the whole system and that the reconstruction of form in development should be explained dynamically, not as a result of the transmission of something that concretely embodies that form. In his autobiography he outlined some specific impacts on his work in embryology and genetics:

> In the late '30s I began developing the Whiteheadian notion that the process of becoming (say) a nerve cell should be regarded as the result of the activities of large numbers of genes, which interact together to form a unified 'concrescence'....Again a few years earlier it had become **(p.229)** apparent that the 'gene-concrescence' itself undergoes processes of change; at one embryonic period a given concrescence is in a phase of 'competence' and may be switched into one or other of a small number of alternative pathways of further change—but the competence later disappears and if you've missed the bus the switch won't work....If I had been more consistently Whiteheadian, I would probably have realized that the 'specificity' [the fact that the switch sends the cell down a particular developmental pathway] involved does not need to lie in the switch at all but may be a property of the 'concrescence' and the ways in which it can change. Because of course what I have been calling by the Whiteheadian term 'concrescence' is what I have later called a *chreod* [canalised developmental trajectory]. (Waddington 1975: 9–10)

As we will see in this chapter, what makes DST a process theory is that it seeks to explain developmental outcomes as the result of a dynamic process in which some of the interacting factors are products of earlier stages of the process, rather than as the result of the arrangement of preexisting factors into a static mechanism. Even when factors exist independently of the developmental process, they are drawn into it and made part of a developmental 'system' by the unfolding process, as we have already discussed above. It is the process that defines the system. In these respects, DST is the direct inheritor of Waddington's process biology.

Another reason why biologists were drawn to Whitehead was his *organicism*— the idea that collectives have an enduring identity that cannot be reduced to the continuity of their parts.[3] This was at the heart of Agar's interest in Whitehead:

> It is in [Whitehead's] conception of the unity of a nexus that we strike the main idea of theories of organism as usually understood by biologists, namely, the idea that the whole is more than the sum of its parts, and indeed imposes its own character on its parts. As Ritter puts it, the whole acts causally on its parts, as well as being acted on causally by its parts. This is only understandable if we get away from the idea of substance and fix our attention on process. We must not think of the molecule as composed of ultimate particles of matter in motion. But the molecule is a pattern of processes, and each constituent process conforms to its place in the pattern, and resists factors tending to alter it.
>
> (Agar 1936: 29; see also Agar 1943)

Agar finds in Whitehead an account of the identity of an organism that is reassuringly Darwinian: 'It is cardinal to Whitehead's philosophy that the subjective aim of an actual entity is not merely at self-realization, but at self-realization as an agent creative of other entities like itself, or at least of the production in other actual entities of feelings like its own' (Agar 1936: 22). Elsewhere Agar identifies 'subjective aim' with final causation, so part of what he is saying here is that the *telos*[4] of an organism is to reproduce itself.

We do not think that the details of Agar's Whiteheadian organicism contain much that is of relevance to DST, but the issue he is addressing—the identity of processes through time and their distinctness from one another—is a vital one for DST. A biological individual is a process that may intersect with other organismic processes, but it has a principle of identity that marks just this series of events out as **(p.230)** one biological individual. DST thus requires an account of what is known in process philosophy as 'genidentity' or identity as continuity of organization. This principle of identity also determines, by identifying a process, the boundaries of the developmental system—the matrix of resources required for that process to proceed to completion. We return to this issue in section 6, where we will see that the identity of a developmental process and its distinction from other individual processes are indeed given by its *telos*, although not in the exact sense envisaged by Agar.

3. Process in the Developmental Systems Tradition

An animal is, in fact, a developmental system, 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: 155)

Waddington's idea of a developmental system and his early attempt to explain development as the result of the dynamic structure of that system are important precursors to DST (Griffiths and Tabery 2013). However, he remained a profoundly gene-centred thinker. The dynamic structure is an 'epigenotype'—the global expression of all the organism's genes—and it explains, through the presence of 'chreods', the resistance of some developmental trajectories to environmental perturbation. Waddington does not embrace the idea that the evolved developmental system actually *includes* aspects of the environment rather than merely being designed to function in an environment and cope with its variations.

For this central theme in DST we must turn to the comparative psychologist Daniel S. Lehrman, perhaps the single most important figure in the development of DST, and indeed of the scientific field of developmental psychobiology:

Natural selection acts to select genomes that, in a normal developmental environment, will guide development into organisms with the relevant adaptive characteristics. But the path of development from the zygote stage to the phenotypic adult is devious, and includes many developmental processes, including, in some cases, various aspects of experience.

(Lehrman 1970: 36)

Lehrman was not a Whiteheadian, and so it is all the more significant that his efforts to place development at the heart of the study of animal behaviour led him to adopt a process view of the organism:

The use of 'explanatory' categories such as 'innate' and 'genetically fixed' obscures the necessity of investigating developmental *processes* in order to gain insight into the actual mechanisms of behavior and their interrelations. The problem of development is the problem of the development of new structures and activity patterns from the resolution of the interaction of *existing* structures and patterns, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the *current* stage and between the *current* stage and the environment. 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 different stage of its development.

(Lehrman 1953: 345)

 (p.231) Lehrman is not merely being pedantic in insisting that organisms, not genes, interact with environments. The impact of a genetic or environmental factor at some point in development depends on how the organism has developed up to that point. It is an organism at some stage of development that interacts with both genes and environment to produce the next stage of development. Development is essentially a dynamic process in which, as Waddington insisted, we need to take account of time, as well as of a list of ingredients.

The historical contingency of individual development was at the heart of what developmental psychobiologist Gilbert Gottlieb, another major source for DST, called the 'developmental psychobiological systems view' (Gottlieb 1970). Gottlieb contrasted what he called 'probabilistic epigenesis' with what he saw as the prevailing view of 'predetermined epigenesis'. The latter concept, he argued, covered up the persistence of preformationist thought in modern biology (Gottlieb 2001; see also Robert 2004). According to Gottlieb, 'the cause of development—what makes development happen—is the relationship of the components, not the components themselves' (Gottlieb 1997: 91). The impact of

any causal factor depends on the order in which the system is exposed to that and other factors. This places limits on our ability to predict the results of development from a list of measured factors. Gottlieb's influence lives on in DST's emphasis on contingency.[5]

The idea of a formal developmental systems *theory* is due to Donald Ford and Richard Lerner (1992), who identify two core theses of DST. The first, which they call 'developmental contextualism', is derived from Gottlieb's concept of probabilistic epigenesis. Development proceeds at several levels—for example gene expression, the formation of tissues, and the state of the environment—and the interactions between levels are the prime focus of research, rather than one level being focal and the others being background against which the former unfolds. Developmental contextualism is a modern version of the epigenetic—as opposed to predeterminist—view of development. Ford and Lerner's second core thesis is 'dynamic interactionism', which they contrast with conventional, 'static interactionism'. This reflects Lehrman's distinction between organism-environment and gene–environment interaction mentioned earlier. Ford and Lerner regard interaction as an ongoing process that can transform the interactants themselves. In other words, the parts that interact with one another and with the developmental system are products of the developmental system. Overall, Ford and Lerner present a thoroughly processual view of the developmental system: a view in which we can see the same ideas that we encountered in Waddington and that he claimed to have derived from Whitehead.

This process view of development led to the radical reformulation of the distinction between nature and nurture proposed by Susan Oyama (2002). In the conventional picture of (static) gene–environment interaction, nature and nurture are simply interacting causes. Genes, or genes plus 'epigenes', represent nature. The environment represents nurture. Added together, they cause development. In DST, however, nature and nurture are product and process. Nurture is the interaction between the current state of the organism and the resources available to **(p.232)** it—environmental *and* genetic. The nature of the organism at each stage is simply the state of the organism—including the modified state of its genome and of its developmental niche, both of which have been transformed by earlier processes of nurture. Oyama rejects the very idea that nature exists separately from, and before, nurture. One way she conveys this is by insisting that the developmental information expressed in the organism is not present in the starting point of development, but is itself created by the process of development, through feedback from the current state of the organism to the states of the resources that will influence future development. This is what she means by the 'ontogeny of information'.

In *The Ontogeny of Information* Oyama pioneered the parity argument, or the 'parity thesis', concerning genetic and environmental causes in development (see also Griffiths and Gray 1994; Griffiths and Gray 2005; Griffiths and Knight 1998; Stotz 2006; Stotz and Allen 2012). Oyama relentlessly tracked down failures of parity of reasoning in earlier theorists. The same feature is accorded great significance when a gene exhibits it, only to be ignored when a non-genetic factor exhibits it. When a feature thought to explain the unique importance of genetic causes in development is found to be more widely distributed across developmental causes, it is discarded and another feature is substituted. Griffiths and Gray (1994) argued in this spirit against the idea that genes are the sole or even the main source of information in development. Other ideas associated with 'parity' are that the study of development does not turn on a single distinction between two classes of developmental resources, and that the distinctions useful for understanding development do not all map neatly onto the distinction between genetic and non-genetic. Ulrich Stegmann has argued that, because DST has not identified a single, essential way for genetic and non-genetic resources to be treated with parity of reasoning, the idea of parity is too vague to be useful (Stegmann 2012). It is hard to know what to make of this criticism. Other critics of DST have dismissed parity as the wildly holistic view that no distinctions of any kind can be made among developmental causes: 'Parity arguments then claim that picking out one cause, when in fact there are many, cannot be justified on ontological grounds because, after all, causes are causes' (Waters 2007: 533).[6] Developmental systems theorists have repeatedly rejected this interpretation and provided examples of how one developmental cause can be more significant than another in ways that are consistent with DST (Oyama 2000; Griffiths and Knight 1998; Griffiths and Gray 2005). In recent work, Griffiths and colleagues have constructed a quantitative measure of relative causal contribution and used it to assess the parity thesis in specific cases (Griffiths et al. 2015).

As we have seen, the ideas that Waddington derived from process philosophy can be found in all the major figures who inspired and developed DST. In the next section we discuss in more detail two core ideas that define DST as a distinctive approach to development and we argue that both support the notion that the fundamental unit of analysis for DST is the developmental process or the life cycle.

(p.233) 4. Core Ideas in DST: Epigenesis and Developmental Dynamics
Two ideas recur in all the authors presented above and are at the heart of DST: *epigenesis* and *developmental dynamics* (Griffiths and Tabery 2013). Both of them support the view that the central focus of DST should be on developmental processes rather than on sets of objects (developmental resources).

4.1. Epigenesis

The term 'epigenetics' derives from the much older word 'epigenesis'. 'As a continuation of the concept that development unfolds and is not preformed (or ordained), epigenetics is the latest expression of epigenesis' (Hall 2011: 12). It was coined by Waddington as a fusion of 'epigenesis' and 'genetics', to refer to the processes by which genotype gives rise to phenotype and to the study of those processes (Waddington 1942). Waddington suggested that existing knowledge from experimental embryology supported a view of how genes are connected to phenotypes that is broadly in line with the older idea of epigenesis. The interaction of many genes produces an emergent level of organization that Waddington called the 'epigenotype', and development is explained by the dynamics of the developmental system at this level.

Waddington's 'epigenotype' is a global expression of the genetic causal factors that influence development. The effect of changing any one gene depends on how that gene interacts with the rest of the system. The epigenotype as a whole interacts with the environment to determine the phenotype. DST expands this vision to include non-genetic factors that influence development. The epigenotype is replaced by a more inclusive vision of a developmental system, a global expression of all the causal factors that influence development. The developmental system still does not determine a unique phenotype, both because development is a probabilistic process, as Gottlieb emphasized, and because development is plastic by design. The environment provides many requirements for normal genome expression (the 'ontogenetic niche' of West and King 1987), and thus partly constitutes the developmental system; but the environment also determines the specific values of variables in an individual life cycle and thereby selects the particular course that development will take from those available to the system. The genome also plays these two roles, as some variables are determined by genetic individual differences (see Tabery 2009).

In 1958 the biologist David L. Nanney introduced another sense of 'epigenetics': the sense in which it is primarily used in molecular biology today (Haig 2004). Epigenetics in this sense is the study of mechanisms that determine which genome sequences will be expressed in the cell. These mechanisms control cell differentiation and give the cell an identity that is often passed on through mitosis. Writing in the year in which Francis Crick first stated his 'sequence hypothesis' that the order of nucleotides in DNA determines the order of amino acids in a protein and thus encodes the biological specificity of the protein (Crick 1958), Nanney wrote:

> 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 **(p.234)**

specificities are to be expressed in any particular cell....[T]hey will be referred to as 'genetic systems' and 'epigenetic systems'.

(Nanney 1958: 712)

Epigenetics in this narrower, modern sense allows a major role for the environment in development: '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 extracellular] context, and others by external and/or environmental factors' (Hall 2011: 12). The regulated expression of the coding regions of the genome depends on mechanisms that differentially activate and select the information in coding sequences, depending on context. Biological information is distributed between the coding regions in the genome and regulatory mechanisms, and the specificity manifested in gene products is the result of a process of 'molecular epigenesis' (Stotz 2006; Griffiths and Stotz 2013).

So the idea of epigenesis is alive and well in contemporary biology. As Waddington argued, developmental outcomes are to be explained at the level of the whole system, and not by single causes that 'encode' or 'instruct' that outcome (for an influential restatement of this view, see Noble 2006). Developmental outcomes are also explained dynamically, as trajectories in a space of possible states of genome expression. The role of epigenetic marks in development is to successively differentiate cells as a result of earlier stages of development, making genome expression in one tissue at a time a function of the history of these cells. The complexity of biological networks makes it plausible that in many cases this process will display emergent dynamics that can only be studied through simulation, a point we expand on in the next subsection.

DST adds to this modern epigenetic vision of development the same element that it added to Waddington's original vision of epigenetics, namely a constructive role for the environment. The networks that regulate gene expression extend outside the cell and outside the organism. Evolution designs developmental processes that draw these wider resources into the developmental system by re-establishing relationships with them. The presence of suitable external resources is in many cases explained by the activity of parents and of conspecifics more generally ('developmental niche construction', see Griffiths and Stotz 2013), and sometimes by the feed-forward effects of earlier stages of the developmental process itself.

4.2. Developmental dynamics

The idea that development is a dynamic process is central to DST. Ford and Lerner contrast 'dynamic interaction' with a more conventional conception of interaction associated with analysis of variance techniques, such as those used

in behavioural genetics (Ford and Lerner 1992). In this 'static interaction' the values of two variables measured before development, such as shared genes and shared environment, are shown to interact with each other. In contrast, dynamic interaction must be studied as a temporally extended process. For example, in Celia Moore's iconic 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 this response of the mother to male pups depends on differences in their urine, which are the result of earlier **(p.235)** processes of sexual differentiation (Moore 1984, 1992). The presence of this environmental influence is a feed-forward from earlier development in the pup itself. The patterns of gene expression that underlie sexual development in the rat arise through interaction with an environment that has been partially structured by an earlier stage of the rat's development. The notion of developmental dynamics embodies one of the basic ideas of process biology, namely that the developmental system is defined, and in part physically produced, by the process of development.

If interaction is a dynamic process, then the temporal dynamics of the interaction may play an independent role in explaining the outcome. This is why many DST advocates have also been attracted to explanations of development that draw on dynamical systems theory (abbreviated here DyST, to avoid confusion). Griffiths and Tabery (2013) argue that there is nothing about the basic idea of dynamic interaction found in DST that *requires* the use of DyST. The example of rat development just given, for example, is a sequential mechanism that can be described without using DyST. But in other cases DyST provides additional explanatory resources (Thelen and Smith 1994; Bechtel and Abrahamsen 2013). DyST exemplifies, even more strongly than the bare notion of developmental dynamics, the idea that developmental outcomes should be explained at the level of the whole system (see chapter 12 for a detailed discussion of DyST).

In this section we have argued that the core principles of DST, epigenesis and developmental dynamics, embody the very same ideas that featured in Waddington's process biology. Developmental outcomes are explained at the systems level, and in identifying the components of a developmental system we start with the developmental process, not the other way around. In the next section we develop these thoughts further by examining how DST has conceptualized the constituents of developmental systems.

5. An Ontology for DST: Genomes, Epigenomes, and Developmental Niches
One of the most controversial features of DST is its conceptualization of the developmental system as an organism–environment system. Rather than it being the case that an organism develops in an environment, aspects of the developmental environment are part of the developmental system. As well as talking of developmental systems, advocates of DST have talked of sets,

collections, or matrices of developmental resources—and, more recently, of ontogenetic or developmental niches that provide the developmental context for organisms or genomes.

DST has always resisted the belief that there is a single way to divide the inputs to development that will be useful for every scientific question about development (Hinde 1968; Johnston 1987; Oyama 1985). Instead, distinctions should be introduced locally to suit the question at hand. For some purposes, as an alternative to 'organism and environment' or 'genes and environment', the resources that make up a developmental system can be partitioned into three: the genome, the epigenome (chemical modifications of DNA that are transmitted through meoisis), and the developmental niche. Since the fundamental unit of analysis for DST is the complete **(p.236)** developmental process or the life cycle, we can think of that process as occurring within, and as feeding forward into the construction of, a developmental system with these three components. Or we can think of the life cycle as consisting of the regulated expression of an epigenetically modified genome through its interaction with a developmental niche.

The genome is a familiar concept, and the epigenome increasingly so. The notion of a developmental niche will be less familiar to many readers. Developmental psychobiologists Meredith West and Andrew King (1987) introduced the term 'ontogenetic niche' to capture the idea that environmental resources form a social and ecological legacy inherited by a developing organism. We have used 'developmental niche' as a synonym for West and King's term (Stotz 2008; Stotz 2010; Griffiths and Stotz 2013). Species-specific phenotypes depend on species-typical environments of development. These are often the result of parental activities, but their construction can also involve other conspecifics, past and present, and, importantly, the offspring itself. The idea of the construction of a developmental niche answers a fundamental question about inheritance: How do parents reliably influence the phenotype of their offspring and promote healthy development? Organisms do not rely on chance to provide their offspring with the resources for normal development: they actively intervene to modify environments to this end. West and King described the ontogenetic niche as an 'information centre' in the sense that it makes the interaction between organism and environment more *specific* than it would otherwise be. The idea of an information centre was initially developed in order to capture the experiences necessary for species-typical learning (Galef and Wigmore 1983). These are the 'aspects of experience' that Lehrman identified as part of the developmental system (Lehrman 1970, 36 and quoted above). However, this idea can be applied to the much broader category of any environmental stimulus that acts as a specific cause of normal development (Griffiths and Stotz 2013).

Dividing the developmental system into genome, epigenome, and developmental niche may be useful in the study of evolution, because it parallels one way of dividing the mechanisms of heredity. It is now fairly conventional to recognize epigenetic heredity mechanisms as a genuine form of heredity alongside genetic inheritance, although arguments about whether these mechanisms have equal *evolutionary* significance continue.[7] But DST proponents, just like other recent theorists **(p.237)** (e.g. Jablonka and Lamb 2005), recognize a wider range of heredity mechanisms. It is unfortunate that this wider class of mechanisms is often also referred to as 'epigenetic inheritance', which makes that term ambiguous, as it is used more narrowly to refer only to epigenetic marks inherited through meiosis. In earlier work we have suggested keeping 'epigenetic inheritance' for the narrower class of mechanisms and using West and King's term 'exogenetic inheritance' (West and King 1987: 5) for the broader class of mechanisms. It is this broader class of heredity mechanisms that constructs the developmental niche: 'Organisms construct their life cycles through the interaction of the contents of the fertilized egg, the genome and its narrowly epigenetic surroundings, with a "developmental niche" which is the result of epigenetic inheritance in a wider sense…"exogenetic inheritance"' (Griffiths and Stotz 2013: 5).

It is worth noting that this broader exogenetic form of inheritance may be more stable than narrow epigenetic inheritance. Some exogenetic inheritance occurs through the induction of epigenetic modifications in the offspring through parental behaviour. This can have long-term, often lifelong effects on the offspring phenotype. In some known cases these offspring phenotypes include the very parental behaviour that induced them, so that the offspring reproduce the effect in the next generation, and so forth (Champagne and Curley 2009). These behaviorally transmitted but epigenetically mediated effects contribute to the long-term stabilization of aspects of the developmental niche, and hence may be more long-lived than meiotic epigenetic inheritance.

It is important not to conflate the developmental niche with the 'niche' of niche construction theory (Odling-Smee et al. 2003). Niche construction theory concerns the influence of past generations on the selective pressures that act on future generations. This activity partially constructs a *selective niche*, the set of parameters that determine the relative fitness of competing types in the population. The *developmental* niche, however, is the set of parameters that must be within certain bounds for an evolved life cycle to occur (or, in more traditional terms, for the organism to develop normally). The two niches will often share many parameters. They are, however, conceptually quite distinct. For example, signals from parent to offspring that induce transgenerational adaptive phenotypic plasticity, as when *Daphnia* signal their offspring to grow additional defences against predators, are a clear example of developmental niche construction: the parent *Daphnia* is structuring the developmental environment of its offspring. But this is no more a case of *selective* niche

construction than is the inheritance of an advantageous mutation! The *Daphnia* embryo alters itself to fit the selective environment rather than altering the selective environment.

6. DST as a Process Theory of the Organism

One reason why early twentieth-century biologists were drawn to process philosophy was that it offered a 'theory of the organism'—an account of the unity of living systems (see chapter 1). Recent interest in process ontologies for biology has revived interest in the concept of 'genidentity', or identity as continuity of organization (see Guay and Pradeu 2015, as well as chapters 2, 4, 5, and 7 here). Distinct stages are stages **(p.238)** of the same entity because one developed from the other, rather than because they share some common properties:

> [Genidentity] says that the identity through time of an entity X is given by the continuous connection of states through which X goes....In this view, the individual X is never presupposed or given initially, because the starting point is the decision to follow a specific and appropriate *process* P, and the individual X supervenes on this process....In other words, for the genidentity view, what we single out as an 'individual' is always the by-product of the *activity* that is being followed, not its prior foundation (not a presumed 'thing' that would give its unity to this activity).

> (Guay and Pradeu 2015: 317–18)

Guay and Pradeu here exemplify themes familiar from our earlier discussion of Waddington and Agar. The persistence of biological form should be explained dynamically, not by the transmission of something that concretely embodies that form. The identity of an individual through time is a dynamic continuity of form. If the fundamental unit of analysis in DST is the developmental process or the life cycle, if heredity in DST is a relation between one life cycle and another, and if natural selection occurs in populations of life cycles (Griffiths and Gray 2001), then DST needs to give an account of the genidentity of these processes. It needs to say where one developmental process ends and the next begins. This problem arises in a dramatic form when organisms have alternating haploid and diploid phases of comparable length (Godfrey-Smith 2015). Is each phase a life cycle, or is a life cycle the combination of a haploid and a diploid phase?

The principle of genidentity of a life cycle also needs to explain how a life cycle can consist of a different series of events in different generations of that cycle. This problem arises in its most dramatic form when a species has a range of substantially different ways to get from conception to death. Some newts, for example, exhibit facultative paedomorphosis, in which individuals respond to differences in their environment either by retaining the morphology of their acquatic, larval stage and becoming reproductively mature in that state or by going through metamorphosis to become a terrestrial 'adult' reproductive form

(Denoël, Joly, and Whiteman 2005). Nevertheless, the same issue arises in principle whenever an organism exhibits adaptive phenotypic plasticity, so that successive life cycles in a single lineage do not contain the same developmental events.

DST has often been criticized for replacing the common-sense idea of an individual organism with a novel and nebulous 'system' (Sterelny et al. 1996; Merlin 2010; Pradeu 2010; see also the references in n. 6). This criticism has become increasingly unfair over the past twenty years. It is no overstatement to say that conventional theories of biological individuality are in a state of crisis brought on by new empirical and theoretical developments in biology. These developments include research on evolutionary transitions in individuality, the realization of the extent to which core physiological processes in multicellular organisms are carried out by microbial commensals, the discovery of ever more complex and highly integrated functional associations between microbes themselves, as well as increased attention paid by philosophers and theoretical biologists to the full diversity of life, in all its glorious weirdness! The result has been a wave of new work in philosophy and theoretical biology on the nature of individuality, a literature that shows few signs of **(p.239)** reaching a consensus (cf. Calcott and Sterelny 2011; Pradeu 2012; Ereshefsky and Pedroso 2013; Bouchard and Huneman 2013; Guay and Pradeu 2015; see also chapters 9 and 10 here). Statements like the following are not hard to find in the recent literature:

> Individuals can be defined anatomically, embryologically, physiologically, immunologically, genetically, or evolutionarily.…[E]ach stems from the common tenet of genomic individuality: one genome/one organism. As such, all classical conceptions of individuality are called into question by evidence of all-pervading symbiosis.

> (Gilbert et al. 2012: 325)

It is not very reasonable to complain that DST has a more problematic conception of a biological individual than the traditional organism, when that traditional conception of a population of physiologically integrated cells with a single genotype is itself so widely regarded as problematic. In light of this, the initial response of Griffiths and Gray to this line of criticism continues to be effective. They argued that the idea of an individual organism was in fact quite problematic, and that DST did not need to offer a *more* watertight account of the individuality of developmental processes in order to make itself a viable competitor to conventional accounts of the units of evolution and development (Griffiths and Gray 1994; Griffiths and Gray 2001).

Griffiths and Gray sketched how DST would approach the problem, using much of the same apparatus that biologists were already using to address problems

with the traditional conception of an individual organism. They argued that a DST account of the individuality of developmental processes—what we are now calling genidentity—would define individuality in terms of the ability to act as a unit of selection (Griffiths and Gray 1994: 292–8; Griffiths and Gray 2001: 209–14). They drew on accounts of evolutionary individuality from the emerging framework of multilevel selection theory to suggest that 'an individual is a life cycle whose components cannot reconstruct themselves when decoupled from the larger cycle' (Griffiths and Gray 2001: 213) and to recognize that, just like cells, organisms, and superorganisms, life cycles might exist at several different levels of biological organization.

Looking back at theories of the organism in early twentieth-century process biology, we can see a distinct similarity between Griffiths and Gray's ideas about the identity of developmental processes and Agar's intuition that an organismic process is united by its 'subjective aim' or *telos*. A series of developmental events is a single process because those events serve a common evolutionary goal, namely to maximize the representation of cycles descended from them in future generations vis-à-vis the representation of the variant cycles with which they compete. We can draw on conventional evolutionary theory to make this suggestion a little more precise: *an individual life cycle is a token of a life history strategy, and that strategy is its* telos *and its principle of genidentity*.

Life history theory is a powerful and remarkably general framework for addressing many basis questions about organismic design (Stearns 1992; Roff 2002; see also chapter 4). In life history theory, the goal of an organism is to find the optimal way to parcel the resources available to it into offspring. This problem is modelled as the simultaneous optimization of two parameters, the probability of surviving to each age class and the number of offspring produced in each age class, integrated across all age classes. The primary constraint on this optimization problem is the quantity of resources **(p.240)** available to the organism. But the problem is also constrained by multiple trade-offs between the two key parameters: an overall trade-off between survival and reproduction; a trade-off between reproduction in the current age class and in later age classes; another between current reproduction and growth, between growth and survival to later age classes, and so forth. Solving this complex optimization problem under different sets of constraints and in different ecological settings leads to the many different life history strategies observed in nature. Since life history theory already conceives of an organism as a series of events (age classes), it is readily applicable to a life cycle that consists of a series of developmental interactions, each one of which moves the life cycle forward.

Life history theory embodies a powerful principle of genidentity, because the evolutionary rationale for the choice of strategy at each life history stage is conditional on what choices have been or will be made at the other stages. A life cycle conceived of as the implementation of a life history strategy is held

together by the trade-offs between its stages. If these events were not part of a single life history serving a single, Darwinian *telos*, then they would not trade off against one another in this way. It makes sense for me to accept an elevated risk of cancer in later life in return for *my* increased reproductive success, but not for *your* reproductive success, unless that is discounted by our coefficient of relationship. The life history strategy also defines where one process ends and another begins, namely at the points between which a single set of such trade-offs exists.[8] Life history theory explains how life cycles that do not contain the same developmental events can nevertheless constitute a single lineage of cycles, which succeed in reproducing themselves. Adaptive phenotypic plasticity is part of a life history strategy, and individuals who exhibit different developmental outcomes as a result of this plasticity are individuals who shared the same, plastic strategy.

Introducing a life history perspective makes it clear why it is legitimate for developmental systems theorists to help themselves to whatever is currently the best evolutionary account of biological individuality[9] and to 'processualise' that account. Evolutionary accounts of individuality seek to identify collections of biological material that are evolving as one: they are more or less successful in reproducing themselves as a whole, and that success cannot be reduced to the successes of each part of the whole, or to the success of some larger whole, of which this is a part. Admittedly, many discussions of this problem make it seem a matter of finding which *spatial* parts make a *spatial* whole. But this is an illusion; any such unit will in fact be extended in time and will embody a life history strategy. DST will use this strategy to identify the events that make up a single, processual biological individual.

(p.241) 7. Conclusions

DST has a natural affinity with process views of the organism. The theorists who inspired and created DST all shared the view that development is a dynamic process whose study requires an investigation of its dynamic form as well as of the static constituents on which it draws. In Waddington's case, this conviction was directly inspired by process philosophy. The idea of epigenesis, perhaps the single most important idea in the developmental systems tradition, is fundamentally processual. In development, something new comes into being that is not prefigured in any of the inputs to development. Developmental dynamics, another idea that has been central to all the major contributors to DST, is also essentially processual. The impact of a genetic or environmental factor at some point in development depends on how the organism has developed up to that point. Development is, essentially, a dynamic process and cannot be reduced to a list of ingredients and their interactions. The entities that make up a developmental system—which we can divide for some purposes into a genome, an epigenome, and a developmental niche—are picked out as elements of a single system by the unity of the process to which they contribute, and not vice-

versa. That principle of unity—the genidentity of a life cycle—we have argued, is simply its Darwinian *telos*: a life history strategy.

Acknowledgements

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Notes:

(1) This proposal has a parallel within the replicator tradition, namely G. C. Williams' view of the organism as a region of space–time structured by evolved information (Williams 1992). By that stage in his career Williams had abandoned the view that objects compete to replicate themselves and embraced the differential replication of information, an approach that lends itself more easily to a process perspective and that seems to accommodate the replication of relationships.

(2) Waddington's process biology is also discussed in chapter 12.

(3) On organicism in biology, see chapters 1, 7, 12, and 13.

(4) Its end or purpose; in Aristotelian terminology, 'that for the sake of which' the organism exists and acts.

(5) To the best of our knowledge, Gottlieb was not influenced by Whitehead though he did acknowledge John Dewey as a major source of inspiration (Griffiths and Tabery 2013), and Dewey was acknowledged by Whitehead as an important influence.

(⁶) For other examples, see Weber 2006: 607; Rosenberg and McShea 2008: 174; Okasha 2009: 724; Woodward 2011: 249; French 2012: 197. Okasha calls this kind of wild holism 'causal democracy', a term introduced by Philip Kitcher (2001). Kitcher's principle of causal democracy states that biology should not assume that the genes are the most significant causes but should assess the issue empirically, on a case-by-case basis. It is thus very similar to Oyama's parity thesis, and neither is committed to any kind of holism.

(⁷) It is often asserted that epigenetic change will only affect evolution if the changes themselves persist for more than one generation (e.g. Wilkins 2011). But in conventional quantitative genetics the evolutionary significance of genetics does not result from tracking individual alleles from one generation to the next—quantitative genetics does not do this. Instead, Mendelian assumptions let us work out what phenotypes (and hence fitnesses) will appear in the next generation as a function of the phenotypes in the last generation. Epigenetic and exogenetic inheritance both change this mapping from parental phenotype to offspring phenotype, and therefore affect evolution. Both epigenetic and exogenetic inheritance appear in quantitative genetics as 'parental effects': correlations between parent and offspring phenotypes above and beyond the correlations between parent and offspring genotypes, which are not the result of a shared environment independently influencing both parent and offspring. It has long been understood that one-generation parental effects can substantially alter the dynamics of evolutionary models and can change the state to which a population will evolve as an equilibrium (Lande and Price 1989; Wade 1998). The argument that epigenetic inheritance needs to be stable for several generations to have evolutionary significance appears to be a non sequitur.

(⁸) Life history theory is in practice conducted as a branch of population genetics, and we anticipate the objection that the implicit definition of the limits of an individual that we have made use of in this section is in fact derived from genetic identity. But this cannot be the case, as the theory applies perfectly well to asexual organisms where parents and offspring are genetically identical. Moreover, so far as we can see, life history theory could be extended unproblematically to cases in which heredity is epigenetic and exogenetic as well as genetic.

(⁹) For the current views of one of the present authors, see Bourrat and Griffiths (under review).