

## Discussion: Three ways to misunderstand developmental systems theory

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**Abstract.** Developmental systems theory (DST) is a general theoretical perspective on development, heredity and evolution. It is intended to facilitate the study of interactions between the many factors that influence development without reviving ‘dichotomous’ debates over nature or nurture, gene or environment, biology or culture. Several recent papers have addressed the relationship between DST and the thriving new discipline of evolutionary developmental biology (EDB). The contributions to this literature by evolutionary developmental biologists contain three important misunderstandings of DST.

### Introduction

Developmental systems theory (DST) is a general theoretical perspective on development, heredity and evolution. It is intended to facilitate the study of interactions between the many factors that influence development without reviving ‘dichotomous’ debates over nature or nurture, gene or environment, biology or culture. A general introduction to the range of work that falls under the umbrella of DST is the edited volume *Cycles of Contingency: Developmental Systems and Evolution* (Oyama et al. 2001). Several recent papers have addressed the relationship between DST and the thriving new discipline of evolutionary developmental biology (EDB) (Robert et al. 2001; Jablonka and Lamb 2002; Gilbert 2003; Griffiths and Gray 2004). The contributions to this literature by evolutionary developmental biologists contain three important misunderstandings of DST.

### Philosophy, biology and developmental psychobiology

The first misunderstanding is the idea that DST consists of ideas produced by philosophers of biology and unrelated to any actual observational or experimental tradition (Robert et al. 2001; Gilbert 2003). This misunderstanding seems to have arisen because a philosopher of science (Griffiths) has

been active, along with a behavioral biologist (Gray), in arguing the merits of DST in the philosophical literature (Griffiths and Gray 1994, 1997), and perhaps also because of the philosophical nature of psychologist Susan Oyama's influential book *The Ontogeny of Information: Developmental Systems and Evolution* (Oyama 2000 [1985]). Nevertheless, neither the 'developmental systems' label nor the work that falls under it have their disciplinary home in philosophy, but instead derive from research traditions in biology and psychobiology. The effects of this misunderstanding can be quite dramatic. For example, in Robert et al.'s (2001) comparison between DST and EDB they note, correctly, that EDB focuses almost exclusively on morphological development: 'EDB has yet to draw extensively from behavior/psychology' (Robert et al. 2001, 958). However, they go on to cite the work of the eminent developmental psychobiologist Gilbert Gottlieb as an exception to this rule. But Gottlieb is one of the seminal figures in DST, describing his own work as the 'developmental-psychobiological systems view' or 'probabilistic epigenesis' (Gottlieb 2001, see also Bjorklund and Pellegrini 2002, 5). Gottlieb's work dates back to the early 1960s, well before EDB emerged as a discipline, and he is centrally concerned with the role in development of highly structured, species-specific environments, something that has only just begun to be considered as a theoretical possibility within EDB (Gottlieb 1992, 1997).

Rather than being a philosophical offering to biology, recent philosophical work on DST has drawn on a research tradition in developmental psychobiology whose core ideas can be traced back at least to the comparative psychologist Daniel Lehrman's influential 1953 essay on the concepts of instinct and innateness (Johnston 2001), and arguably through Lehrman and Gottlieb to the comparative psychologists T.C. Schneierla and Z.-Y. Kuo. Whilst empirical work in this research tradition continues (Michel and Moore 1995; Bjorklund and Pellegrini 2002), many authors agree that its lessons have been largely forgotten in the evolutionary study of mind and behavior and that modern evolutionary psychology would benefit from their revival (Bateson and Martin 1999; Moore 2001).

Another important source for DST is the series of seminal papers in which Richard Lewontin criticized the so-called 'lock and key' model, according to which organisms (keys) are adapted to their ways of life because they were made to fit those ways of life (locks) (Lewontin 1982, 1983a, b). In place of the traditional metaphor of adaptation as 'fit' to a pre-existing niche, Lewontin suggested a metaphor of construction. Organisms and their ecological niches are co-constructing and co-defining. Organisms both physically shape their environments and determine which factors in the external environment are relevant to their evolution, thus assembling such factors into what we describe as their niche. Organisms are adapted to their ways of life because organisms and their way of life were made for (and by) each other. DST has drawn on Lewontin's writings to construct a representation of evolution as change over time in the compo-

sition of populations of organism–environment systems (Griffiths and Gray 2001, 2004).

### Development and evolution

The second misunderstanding of DST is that it involves a ‘developmental,’ as opposed to a selective, theory of evolution. For example, Gilbert (2003) lists the developmental biologist Brian Goodwin as a supporter of DST. In his evolutionary writings, Goodwin has called for the replacement of the ‘evolutionary paradigm’ with a ‘generative paradigm.’ He interprets evolution as the unfolding of the potential for variation implicit in the developmental biology of the organism, and assigns natural selection a relatively a minor role (Goodwin 1984; Goodwin and Saunders 1989). But as other commentators have pointed out, this ‘developmental’ approach to evolution emphasizes the sources of biological form ‘inside’ the organism, and particularly inside the genome, and the resistance of form to perturbations by outside factors (Griffiths 1996; Van der Weele 1999). In precise contrast, DST stresses the delicate dependence (‘contingency’) of development on a rich matrix of factors ‘outside’ the genome. Moreover, advocates of DST who have discussed its implications for evolutionary theory have stressed the importance of selection in designing developmental systems that can assemble the same matrix of developmental resources in each generation (Griffiths and Gray 1994, 2001). In fact, the idea of ‘developmental evolution’ is more akin to radical interpretations of EDB and of contemporary developmental genetics than to any version of DST. The biologists who contributed to *Cycles of Contingency...* do not advocate ‘developmental evolution’ or the ‘generative paradigm’ (see especially Bateson 2001), and the philosophers who comment on DST in that volume all take its central ideas to be compatible with a range of more or less adaptationist approaches to the explanation of form.

The source of this second misunderstanding of DST is hard to locate. The only context in which DST is associated with a rejection of selectionist explanations is when these are offered as a *substitute* for developmental explanations. A central part of Lehrman’s critique of the ethological concept of instinct was that it conflated the *evolutionary* question of whether a trait is an adaptation with the *developmental* question of whether that trait is insensitive to environmental variation in ontogeny (Lehrman 1953, 1970). In what developmental psychologist Robert Lickliter has called the ‘phylogeny fallacy’ (Lickliter and Berry 1990), the fact that a trait is ‘innate’ in the sense that it is an evolved feature of normal development was taken by the young Konrad Lorenz and his followers to *exclude* the possibility that the trait develops through an interaction with the normal developmental environment. Rejecting this view, Lehrman argued that the evolutionary result leaves the developmental question wide open.

Advocates of DST have argued that certain standard uses of the idea of genetic information embody the ‘phylogeny fallacy.’ This concern dates back

to the 1960s. In response to Lehrman's critique, Lorenz offered a new definition of innateness in terms of developmental information (Lorenz 1965). Lorenz accepted that the environment played a much more constructive role in the development of evolved traits than he had previously allowed, but argued that no matter how complex and highly specific the environmental requirements for normal development may be, the simple fact that the outcome is adaptive as a result of evolution is enough to show that the organism had 'innate information' about the demands of the environment. Innate traits, then, are those whose adaptiveness is largely or wholly explained by natural selection and thus by 'innate information.' However, it takes considerable intellectual effort to use terms like 'genetically programmed' and 'innate information' without falling into assumptions about the pattern of gene-environment interaction in development! So it has been necessary to constantly reiterate Lehrman's response to Lorenz 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, 35) The persistent misuse of the ideas of genetic and developmental information to support overly simple, 'preformationist' views of the relationship between genes and phenotypes is a central theme of Oyama's *Ontogeny of Information...* (Oyama 2000 [1985]), and Scott Gilbert has noted that a similar critique is part of contemporary EDB (Gilbert 2003).

### **Genes and genocentrism**

The third misunderstanding identifies DST with the thesis that 'genes are not important' or 'genes are less important than people think.' This results in the view that DST is a simply another critique of overly simple 'bean bag genetics' and that this critique has been rendered irrelevant by the sophistication of modern developmental genetics (Gilbert 2003). This, however, is fundamental misunderstanding of DST's 'parity thesis,' according to which the roles played by the many causal factors that affect development do not fall neatly into two kinds, one exclusively played by DNA elements the other exclusively played by non-DNA elements (Griffiths and Knight 1998). Instead, there are numerous important distinctions to be drawn amongst the causal roles played by developmental factors. Some of these are useful for thinking about development itself. For example, Gilbert stresses a distinction between 'instructive' and 'permissive' causal factors in the development of phenotypes, and suggests that the instructive factors in morphological development are usually genes, although sometimes, as in sex determination in turtles or crocodiles, non-genetic factors play this role (Gilbert 2003). Other distinctions are useful for thinking about evolution, such as Kim Sterelny's distinction between 'informational' and 'sample based' heredity systems (Sterelny 2001). Still further distinctions

are needed to think about the evolution of heredity and development, although which these are has been the subject of much recent debate (Jablonka and Lamb 1995; Maynard Smith and Szathmary 1995; Sterelny 2001). The ‘parity thesis’ points out that these distinctions do not map neatly onto one another and that none of them neatly map onto a distinction between DNA elements on the one hand and all other causal factors in development on the other. Thus, for example, developmental psychobiologists since Lehrman have been engaged in documenting the ‘instructive’ role of experiential inputs to the development of ‘instinctive’ behavior. There are non-genetic examples of Sterelny’s ‘informational heredity.’ Work on ‘epigenetic inheritance systems’ is precisely the expansion of the cast of hereditary material beyond DNA elements. The parity thesis derives its name from Oyama’s earlier call for ‘parity of reasoning’ when thinking about the roles of DNA elements and other developmental resources. She argued that if one of the above distinctions applies to some but not all DNA elements and also applies to some non-DNA influences in development, we should treat both the DNA and the non-DNA factors alike in the area of theory where the distinction is useful. In order to be able to follow this principle of parity it is essential not to build grand, metaphysical distinctions, like that between form and matter or information and matter, on top of the many empirical differences between the roles of DNA elements and the roles of other causal factors in development (Griffiths and Knight 1998). DNA does play a distinctive set of roles in development, but it does not play just one role (partly because DNA elements are themselves so diverse) and the important roles those various DNA elements plays are sometimes played by non-DNA factors in development.

The real differences between DST and EDB over the role of DNA elements in development arise because of their two different visions of the limits of the developmental system. DST and EDB share the view that development must be understood as a ‘system’ from which adaptive phenotypes emerge through the interaction of many factors, rather than by assigning responsibility for specific phenotypic features to one or a small number of genes interacting in a simple, additive fashion. However, DST, drawing on psychobiological research on ‘experiential’ factors in behavioral development, has sought as inclusive a definition of the developmental system as possible. In attempts to relate this vision of the developmental system to evolution, DST has found itself converging with independent research traditions that explore the evolutionary potential of epigenetic inheritance and organism–environment co-evolution. In contrast, EDB, whose growth as a discipline has been closely tied to discoveries in developmental genetics, has embraced a conception of the developmental system as an emergent feature of the genome.<sup>1</sup> The differences between DST

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<sup>1</sup>The phrase ‘developmental system’ was used in much the same sense by Conrad H. Waddington to refer to the system of genes and their interaction viewed globally and with the understanding that the system has many emergent dynamical features that cannot be understood at the level of the individual genes (Waddington 1952).

and EDB emerge when we start to expand the developmental system beyond those limits, something as follows:

1. The developmental significance of individual DNA elements is a function of their context. This is agreed on all hands as long as ‘context’ is restricted to the genome.

2. The context of a DNA element includes non-DNA structures in the cell and developmental influences outside the cell. EDB accepts this idea in some limited forms. For example, although Gilbert states that development is explained by ‘neither God...nor DST, but developmental genetics’ (2003, 349), he has argued at length in other contexts that EDB should embrace the study of the ecological context of development and its causal influence on gene expression (Gilbert 2001).<sup>2</sup>

3. *The elements outside the genome are part of an evolving developmental system.* This view has been strongly rejected by the leading evolutionary developmental biologist Brian Hall (Robert et al. 2001; Hall 2003). Hall treats cases of epigenetic inheritance as the environment’s release of an epigenetic potential which inheres in DNA elements and associated molecules (for a critique of this interpretation, see Jablonka and Lamb 2002). In contrast, several advocates of DST have embraced the idea that what changes over evolutionary time is a ‘developmental system’ consisting of the organism embedded in a broader developmental context, much of which would traditionally have been regarded as an ‘environment’ and hence as a source of evolutionary pressures, rather than a product of evolution. An early influence on theorists who take this view was Richard Lewontin (Lewontin 1983, 2001). Today, however, a number of young but flourishing research programs have embraced the idea that critical aspects of the environment are a product of evolution, as well as a cause of evolution. These include organism–environment co-evolution (Brandon and Antonovics 1996), multiple heredity systems (Jablonka and Lamb 1995; Jablonka and Avital 2001), and niche construction (Odling-Smee 1988; Laland et al. 2001; Odling-Smee et al. 2003). Some aspects of these research programs resonate with the DST conception of ‘extended inheritance’ (Gray 1992; Griffiths and Gray 1994), the idea that organisms inherit more than the contents of the egg-cell. For example, during primate evolution, an abundance of dietary vitamin C caused the loss of the normal mammalian pathway for ascorbic acid synthesis (Jukes and King 1975). Because this vital developmental resource could be inherited passively, rather than via the DNA elements previously involved in its synthesis, the primate lineage became dependent on this form of extra-genetic inheritance, or ‘addicted to the environment’ as Terence Deacon

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<sup>2</sup>Another theorist who draws a fairly strict line around the developmental system, a line that coincides with the membranes of the fertilized egg, and consequently rejects the DST conception of the developmental system, is Evelyn Fox Keller (Keller 2001). Her inclusion as a developmental systems theorist in Gilbert (2003) seems to reflect the view, related to the third misunderstanding, that the point of DST is to make genes ‘less important’, an interpretation that could be also be placed on some of Keller’s writings.

has phrased it (Deacon 1997). In the same way, hermit crabs are ‘addicted’ to discarded shells and almost all large organisms are ‘addicted’ to the earth’s gravity. In fact, evolved lineages are ‘addicted’ to innumerable aspects of the environment with which they have co-evolved, although most of these aspects are reproduced so reliably that this does not give rise to significant variation, and so is overlooked. Nevertheless, any account of the evolution of development that neglects these factors, and the evolutionary processes that led to their incorporation in development, is seriously incomplete. The idea that the evolution of developmental might include the evolution by natural selection of developmental factors outside the fertilized egg is perhaps the point at which DST finds itself furthest away from EDB.

### **Conclusion**

Despite the substantial differences just discussed, we believe that EDB and DST are essentially complementary. DST does not provide a theory of phenotypic integration and modular evolution, but rather stands in need of one, and EDB is beginning to supply such a theory (Griffiths and Gray 2004). Conversely, nothing in the fundamental inspiration of EDB precludes it embracing a wider conception of the developmental system, not as emerging from interactions between genes, but as emerging from interactions between the whole matrix of resources that are required for development. A major cause of the differences between DST and EDB is clearly that the discipline of EDB came together in its current form because advances in molecular biology have made possible massive advances in understanding the evolution of morphological structures whereas DST was partly inspired by work on the development of behavior, and no-one would pretend that research on behavioral development at the molecular level has made the same massive advances in recent years as research on morphological development (Schaffner 2001; Hamer 2002). This historical perspective on DST and EDB suggests that they are separated by different foci of interest rather than clashing doctrines.

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