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Book Review

Developmental Systems and Animal Behaviour

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A review of Susan Oyama, *Evolution's Eye: A Systems View of the Biology-Culture Divide*, Duke University Press, Durham, NC, 2000, 272 pp. (Pb) ISBN 0-822-32472-5, US $19.95.

What *is* developmental systems theory?

Susan Oyama published *The Ontogeny of Information* in 1985, offering a sustained criticism of gene-centrism in psychology and biology and positing an alternative – developmental systems theory (DST). DST is not so much a single theory as a set of theoretical and conceptual perspectives, emanating largely from comparative psychology (see references in Johnston 1987; Gottlieb 1992, 1997; Oyama 1985, 2000a,b) but having precursors of various sorts in biology, too (for instance, in Hogben 1933; Waddington 1953). Given the currency of debates over the role of development in explaining evolution and the role of genes in explaining both ontogeny and phylogeny, and the perennial character of debates over nature and nurture, it is fitting that Duke University Press should have issued a revised edition of *The Ontogeny of Information* in 2000, along with a collection of Oyama's essays, *Evolution's Eye*. The latter is the subject of this essay review.

According to Oyama's account in *Evolution's Eye*, which both reiterates and elucidates her other work, DST holds that development is not the execution of a pre-existing program located in the genes or, for that matter, anywhere else. Development is rather "a contingent series of constructive interactions, transformations, and emergences" (136).[1] That phenotypes emerge from the interaction of genes and environments is an apparent platitude granted by all biologists and most psychologists. But developmental systems theorists, uniquely, it seems, take seriously the logical implication of this seeming platitude, namely, that it is impossible *a priori*, and often enough impossible *a posteriori*, to assign causal primacy to either genes or environment for a particular phenotypic outcome. Consequently, the usual hierarchical dichotomy between internal and external causes of development cannot be sustained.

For developmental systems theorists, genes must be *deeply* contextualized. DST holds that "if development is to reenter evolutionary theory, it should be development that integrates genes into organisms, and organisms into the many levels of the environment that enter into their ontogenetic construction" (113). Hence, the central, fundamental, construct of DST: the *developmental system*. For Oyama, a developmental system is "a mobile set of interacting influences and entities" comprising "all influences on development, at all levels of analysis", including the molecular, cellular, organismal, ecological, and biogeographical (72). "The developmental system includes not only the organism but also the features of the extraorganismic environment that influence development" (82). Developmental control is therefore not centralized but rather dispersed and fluid; accordingly, "a gene is a resource among others rather than a directing intelligence that uses resources for its own ends" (118).

So, according to DST, genes are but one of many inherited developmental resources; in assessing the roles of interactants in development, we must draw our causal arrows in multiple directions, as DNA sequences and other resources interact in complex ways as components of and processes in time-sensitive intercellular feedback and feedforward loops. DST therefore attempts to refocus biological inquiry on both genetic and nongenetic factors, forces, and mechanisms in development, without insisting that genes are somehow ontogenetically primary.

Moreover, according to DST, evolutionary processes work at all levels of the developmental manifold, for "what is transmitted between generations is not traits, or blueprints or symbolic representations of traits, but developmental *means* (or *resources* or *interactants*)" (29). Oyama contends that 'transmission', as usually understood by biologists, both presupposes and requires reliable development: in order for some genetic or phenotypic feature to recur in the next generation, parents and offspring must both have developed to viability and also be relevantly similar (199). Regarding evolution, then, DST holds that multiple means are 'transmitted' between generations; that the very stability of genetic inheritance depends on nongenetic transmission; and that each of the inherited means may be subject to selection (and other evolutionary) pressures.

Nature and nurture

The essays reprinted in slightly edited form in *Evolution's Eye* appeared between 1981 and 1999 in a disparate range of venues – *South Atlantic Quarterly*, *Journal of Social Issues*, and *Theory and Psychology*, to name a few; these are not exactly the usual places for developmental and evolutionary biologists to track down references. Few biologists have seen Oyama's work; in part, this may be due to the cryptic title of the first book, in part to the relative obscurity of her publication fora. It may also be due to the prejudice that developmental systems theory has nothing of value to offer to practicing biologists. The publication of *Evolution's Eye* resolves the first two possibilities; what of the third?

A recent exchange in *BioEssays* highlighted key aspects of DST in relation to the question of its possible value to practicing biologists. Robert et al. (2001) explored DST and contrasted it with the emerging synthesis of developmental and evolutionary biology known as evolutionary developmental biology (EDB – for reviews of EDB, see Hall (1998), Raff (2000), and Robert (2002)). We reached several conclusions: from a scientific perspective, DST's criticisms of gene-centrism are worth making and well-taken, but DST has not afforded a new research programme for biologists interested in evolution and development; meanwhile, EDB does offer new research programmes, but also runs the risk of gene-centrism – especially in insisting that biological inheritance is exclusively gene-based. Jablonka and Lamb (2002) responded to Robert et al., picking up primarily on this latter claim; they urged biologists to take seriously the phenomenon of epigenetic inheritance, and argued that this emphasis on expanding inheritance is an important lesson for evolutionary developmental biology from developmental systems theory.

It is evident, then, that broader scientific deliberations regarding the value of DST in explaining development and evolution are already underway. But discussing developmental systems theory primarily in relation to evolutionary developmental biology has important limitations. Significant among them is that such a discussion picks up only on DST's prospects for providing a systems-based perspective on *morphological* development and evolution (as in Gray 1992, 2001; Griffiths and Gray 1994, 1997, 2001; Oyama et al. 2001a), without attending to DST's other central preoccupation: to provide a non-gene-centric perspective on *behavioural* development and evolution and, specifically, the traditional nature-nurture dichotomy in psychology and biology (as in Lehrman 1970; Johnston 1982, 1987, 2001; Bateson 1987; Johnston and Gottlieb 1990; Lickliter and Berry 1990; Gottlieb 1992, 1995, 1997, 1998; Wahlsten and Gottlieb 1997; Lickliter 2000; Oyama et al. 2001a; and Johnston and Edwards 2002).[2] Note that no strong distinction between morphology and behaviour can always, or even often, be consistently maintained; the distinction implied here is rather a weak one. Note further that evolutionary developmental biology, though by no means ignorant of behavioural development and evolution, tends to focus considerably less on *human* behavioural development and evolution than does developmental systems theory. Here, then, I focus more closely on DST's prospects in the human behavioural realm, a focus made all the more appropriate by the particular substance of Oyama's papers in *Evolution's Eye*.

The traditional disputants in the nature-nurture debates are hard-line genetic determinists and hard-line environmental determinists. One would be hard-pressed to find a serious exemplar of either position in contemporary biological or psychological literature. Long-gone are the days in which it was easy to identify one's opponents in the nature-nurture disputes, the days in which genetic determinists proudly proclaimed the futility of environmental interventions in human genetic fate, while environmental determinists just as fiercely decreed the inefficacy of genes in fashioning the human story. In fact, the nature-nurture debate has been proclaimed dead time and time again. Behaviour geneticists, for instance, claim to have no interest in resurrecting nature-nurture 'cold wars', that biologists and psychologists have moved well beyond the nature-nurture debates, resolving in favour of a compromise: not nature *versus* nurture but rather nature *and* nurture (e.g., Plomin and McLearn 1993; Goldsmith et al. 1997). "Nowadays," as Russell Gray (1992: 172) has observed, "it seems that everybody is an interactionist".

Among others, Philip Kitcher (2001) has defended this putative "interactionist consensus", which refers to the truism that phenotypes emerge from interactions between genes and environments. At some level, everyone accepts this claim: we can all agree that interactions determine phenotypes (that's why it is a truism). Yet despite (sometimes rhetorical) protestations to the contrary, there is indeed evidence that the nature-nurture debates live on – consensus interactionism notwithstanding. For instance, behaviour geneticist David Lykken maintains that "a better formula than Nature versus Nurture would be Nature via Nurture. . . . The genetic influences are strong and most of us develop along a path determined mainly by our personal genetic steersmen" (Lykken 1998); evolutionary biologist John Maynard Smith underscores a strong and irreducibly important distinction between nature and nurture – though nurture is required to trigger nature, nature is primary and necessarily so, given that nature is inherited and nurture is not (Maynard Smith 2000). But neither Lykken nor Maynard Smith is a hard-line genetic determinist; both could, and should, be characterized as 'interactionists'. It is thus evident that DST is correct in asserting that the nature-and-nurture compromise only *apparently* resolves nature-nurture disputes.

And there's the rub. As Oyama asks, if we're all interactionists, then "why the fuss" (2000b: 5)? The problem is that, as different notions of 'interaction' are on the table, our putative consensus rests on the shaky ground of equivocal and sometimes idiosyncratic definitions of 'interaction' (see discussion in Robert 2000a: 198–199); just as shaky are the characterizations of *what* exactly is supposed to be 'interacting'. What are 'genes' and 'environments' such that organisms 'emerge' from their 'interactions'? Answering such a loaded question requires at least a book-length treatment (see, e.g., Gottlieb 1997; Robert 2000b). The essays collected in *Evolution's Eye* offer some hints as to how DST intervenes in the debate over nature and nurture.

Oyama rightly observes (154) that the dynamic of the nature-nurture debate is a matter of trap-setting and -tripping: the debate is gerrymandered such that critics of genetic determinism open themselves to the charge of environmental determinism, while critics of environmental determinism risk exposing themselves as supporters of genetic determinism. Oyama further notes that merely conjoining 'nature' and 'nurture' will not work, given that both of these are flawed constructs in the first place; conjunction simply compounds the problem in a debate that was misguided from the very outset. "What we need is *not* ever more sophisticated ways to prize them apart [as reviewed, for instance, in Schaffner 2001], but rather a view of life and history that is rich enough to integrate the genetic, morphological, psychological, and social levels (each 'biological', each with a history) in such a way that we are not tempted to indulge in phenotype partitioning at all" (94).

This rich view of life and history requires reconceptualizing both 'nature' and 'nurture'. "Nature," according to Oyama, is "not properly contrasted with nurture in the first place; it is the product of a continual process of nurture" (72). With the idea of a developmental system, of which genes and cells and ecological elements are part, in mind, Oyama reconceptualizes 'nature' as phenotypic rather than genotypic; 'nurture' as developmental interactions; and so 'nature' as the product of 'nurture' rather than a competing (or conjunctive) explanation for developmental outcomes (48–49). 'Nature' is no longer the stable reality behind phenotypic illusions, no longer the engine of phenotypic change, but rather the changing phenotype as such; 'nurture' actively creates, maintains, and alters emergent 'nature' (181). Nature via nurture indeed, but not in the way Lykken and others have imagined; for nature is not given but gotten.

In Oyama's vision, there are no "personal genetic steersmen" or selecting environments operating on passive standers-by; there are, rather, "organisms assimilating, seeking, manipulating their worlds, even as they accommodate and respond to them" (95). "What comes of the chemical, mechanical, and social-psychological resources an organism inherits depends on the organism and its relations with the rest of the world. It makes its own present and prepares its future, never out of whole cloth, always with the means at hand, but often with the possibility of putting them together in novel ways" (*ibid.*).

Aside from the focus here on the behaviour of the organism in its own (behavioural and morphological) development, notice as well the expanded notion of inheritance proposed and exploited within DST. As Gabriel Dover (2000: 1154) has recently emphasized, "DNA is a far more unstable molecule, on an evolutionary scale, than is conventionally thought". But whatever stability genetic inheritance enjoys, even on a much shorter timescale, depends critically on the inheritance of non-genetic developmental interactants. Oyama et al. (2001b: 4) note that "some of these resources are familiar – chromosomes, nutrients, ambient temperatures, childcare". Less familiar inherited resources include the chromatin marking system, chemical gradients in the cytoplasm, and the altered environments (and associated altered selection pressures) generated through niche construction.[3] Accordingly, DST reinterprets hereditary transmission as *contingent but reliable reconstruction of resources-in-interactive-networks in the next life cycle*.

In support of this conceptual innovation, it is worth citing Oyama's discussion at length (199):

> if transmitting or 'passing on' means 'delivering materially unchanged', then few if any developmental resources are transmitted across evolutionary time, depending on how one measures material change. If transmission means 'reliably present in the next life cycle', which is the biologically relevant meaning in DST, then an indefinitely large set of heterogeneous resources or means is transmitted. They are sought or produced by the organism itself, supplied by other organisms, possibly through social processes and institutions, or are otherwise available. Although many developmentally important environmental features are exceedingly stable, others are noncontinuous, perhaps varying seasonally or geographically. Any definition of inheritance that doesn't privilege the nuclear or cell boundary a priori will be applicable to other constituents of the system. . . . The developmental systems perspective stresses the processes that bring together the prerequisites for successive iterations of a life cycle.[4]

These 'transmitted' processes, all of which are natural, are 'nurture'; their emergent products, all of which are nurtured, are 'nature'. There is thus, within DST, no nature-nurture debate of the traditional sort – no submission to the primacy of the genes, of course, but also no claim that genes are less important than environmental factors in development. But neither is there, within DST, acceptance of the now-common resolution of the traditional nature-nurture debate – no acquiescence to the interactionist consensus, but also no refusal of the importance of interaction (*contra* Kitcher 2001).

Interactions, though, are not always additive, and certainly not always 'genes-*plus*' something else (usually some environmental trigger). The non-additivity of interactions has been long recognized; DST was 'scooped' on this count by Hogben (1933), for instance (see Sarkar 1996, 1998; see also Lewontin 1974; Wahlsten 1990). For DST, though, a strictly additive account of interaction is too unidirectional, failing to recognize the bidirectional character of co-determining influences in development (see, e.g., Gottlieb 1970; Johnston and Edwards 2002). Such an account of interaction is also too atomistic: anti-atomism is characteristic of all systems perspectives, from at least von Bertalanffy (1933) onward. The interdependence of causal factors in development rules out attempts to tease apart the relative contributions of nature and nurture, the very substance of nature-nurture disputes. Dealing with this interdependence, scientifically and politically, requires a systems perspective.

Modeling behaviour

As noted above, behaviour geneticists are the first to decry any attempt to reopen the traditional nature-nurture disputes. Behaviour geneticists are also, nevertheless, prone to attempt to statistically separate genetic and environmental causes of particular traits into precise numerical fractions (as in Plomin 1994). From the perspective of Oyama and other developmental systems theorists, this lack of consistency, this lip service to interactionism, is deeply problematic.

The appropriate response, though, is not to throw up one's hands and conclude that development is too complex to be analyzed. That this is supposed to be DST's response is implied in critical reviews of DST (e.g., Schaffner 1998) and of systems-based or methodologically anti-reductionist theories more generally (e.g., Roll-Hansen 1984; Rosenberg 1997). Allow me to suggest otherwise.

In a commentary on Gottlieb's (1995) criticisms of behaviour genetics, Turkheimer et al. (1995) agreed that a systems approach to development is both desirable and, at least in theory, analytically tractable – but bidirectional causal models are very difficult to build. To their mind, the most promising exemplar of such a model was developed by Sing and colleagues (1992, 1993) in their work on coronary heart disease. Within this model, an investigator engages in both 'top-down' (behavioural phenotype → organismal phenotype → physiological endophenotype) and 'bottom-up' (genes → gene products → physiological endophenotype) analysis of causes, in an effort to identify factors and pathways involved in the development, over time, of the trait of interest.[5] But Turkheimer et al. are well aware that the complexity of behavioural phenotypes (and their development) is of a greater order of magnitude than that of heart disease, and are consequently at a loss as to how to formulate sufficiently complex models of human behavioural phenotypes (1995: 149–152). More recent work, though, has begun to shed light on this vexing problem.

Johnston and Edwards have just published a series of increasingly specific (or "unpacked") representations of a model of the development of behaviour. Johnston and Edwards' model is not meant to specify every molecular or cellular aspect of the complex interactions comprising development, but is rather designed to provide "a useful intermediate level of detail that captures that complexity while at the same time rendering it reasonably comprehensible" (Johnston and Edwards 2002: 31). For these authors, genes are not to be considered "carriers of information or repositories of plans and blueprints" (*ibid.*: 27) somehow both separate from and yet also directing development, but instead as molecules that are biologically active within the developmental system and have only indirect reciprocal effects via mRNA synthesis (*ibid.*: 26, 28; see also Lickliter 2000). Experience, too, has indirect and reciprocal effects on the development of behaviour, mediated through multiple levels of biological, ecological, and social organization. The model is meant to focus investigative attention on developmental interactions and specific mechanisms, beyond metaphor and shorthand formulations that have the effect of "side-stepping the task of *developmental analysis*" (Lickliter 2000: 324).

Johnston and Edwards' "completely unpacked model" of behavioural development (Figure 3 in Johnston and Edwards 2002: 28) comprises fourteen boxes, each representing an interacting factor, linked together via their various bidirectional interactions (some but not all of which are causal). The fourteen boxes represent (listed in alphabetical order): Behavior, Cell Membrane, Extracellular Biochemistry, Genetic Activity, Individual Nerve Cell Activity, Intracellular Biochemistry, Neural Connectivity, Neural Growth, Non-neural Growth, Non-neural Structures, Patterned Neural Activity, Physical Influences, Protein Synthesis, and Sensory Stimulation. Any particular instantiation of the model would be only a time slice of a specific developmental moment; the model could be transformed from two dimensions to three with the addition of information regarding the timing of individual influences on development, though this would obviously make it considerably less amenable to pictorial representation (*ibid.*: 29).

The model proposed by Johnston and Edwards can be used to organize existing knowledge and also to make predictions about behavioural development that can be empirically investigated; for instance, the functions (causal or otherwise) represented by arrows or dotted lines connecting factors within the model might capture our knowledge of some developmental process (say, induction) or might "imply the existence of interactions that would, if they occurred, generate the observed changes" (Johnston and Edwards 2002: 30) – and so produce a new research programme to discover those interactions or, if unsuccessful, lead to alterations in the underlying model.

This sort of complex model, though somewhat less elegantly presented, has already been proposed for the investigation of psychopathological development, such as that involved in the aetiology of schizophrenia (Robert 2000a). As Schaffner (2001: 488) has recently noted, "it is conceivable that, as DST develops further, it will be applied more specifically to the relation of nature and nurture in a number of psychiatric disorders". Though detailed models such as that proposed in Johnston and Edwards (2002) are not to be found directly in Oyama's work, they are clearly inspired by her efforts to elucidate developmental systems theory.

Conclusion

Oyama reports in *Evolution's Eye* that a fairly common reaction to DST is " 'That's completely crazy, and besides, I already knew it' " (193). She elaborates: "theorists are exasperated to be told what they have 'always known'. Yet there is a difference between knowing in a parenthetical, 'of course it's important' way about the intimacy and reciprocality of organism-environment exchanges in development and evolution, say, and incorporating the knowledge in models and explanations, research and theory" (200–201).

One of the chief virtues of DST is the framework it offers for integrating knowledges and literatures and perspectives from multiple, disparate sources throughout the twentieth century. DST offers resources (some new, some not) for thinking seriously about science, especially, but not only, about how to interpret scientific results. Moreover, DST offers resources for designing research programmes and conducting experiments (e.g., Gray 2001; Johnston and Edwards 2002); these may not always be new insights (given, for instance, the tradition of animal ethology evident in Lehrman (1953), Gottlieb (1970), Bateson (1983, 1987), and their precursors and descendants), but DST brings these insights together in novel, even synergistic, ways.

Finally, DST forces a certain honesty in our use of concepts, given the ways that language, especially metaphorical language, impacts on the design and conduct of scientific research (see Lewontin 1996); dichotomies such as that between nature and nurture must be pressed to ensure they are not false ones; verbal models (such as 'consensus interactionism') must be tested to weed out those that prove impossible to operationalize or to be operationally impoverished; concepts (such as ‘information’) bearing significant explanatory weight must be interrogated to verify they are not made of clay. Of course, DST should be subjected to the same standards, its verbal models tested, its concepts scrutinized. *Evolution’s Eye* makes a number of these concepts widely available for inspection, and as such is a most welcome contribution to the literature on evolution and development.

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Notes

[1] All otherwise unattributed parenthetical page references in the text are to *Evolution’s Eye*.

[2] I thank Paul Griffiths and Alan Love (personal communication) for recently underscoring this point to me.

[3] On epigenetic inheritance generally, see Jablonka and Lamb 1995; Jablonka 2001; on niche construction, see Odling-Smee et al. 1996; Laland et al. 1999, 2001; Sterelny 2001.

[4] In support of these claims, Oyama cites: L.R. Caporael, “The Evolution of Truly Social Cognition: The Core Configuration Model”, *Personality and Social Psychology Review* 1 (1997), 276–298; T. Ingold, “ ‘People Like Us’: The Concept of the Anatomically Modern Human”, *Cultural Dynamics* 7 (1995), 187–214; and Griffiths and Gray 1994. See also Jablonka and Lamb 2002 for a reiteration of the importance of non-genetic inheritance.

[5] Presumably, a genuinely bi-directional model would allow for the following possible functions: behavioural phenotype ↔ organismal phenotype ↔ physiological endophenotype ↔ gene products ↔ genes.

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