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Book Review

Cycles of Contingency: Developmental Systems and Evolution. Edited by Susan Oyama, Paul E. Griffiths and Russell D. Gray. Cambridge, MA: The MIT Press. ISBN 0-262-165063-0.

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Introduction

Genetics is a hugely successful science in its own right, and statistical approaches to genetics are credited with the revival of Darwinism in the modern evolutionary synthesis (Depew and Weber, 1995). But the nature of the basic entity in genetics, the gene, and the role it plays in development are becoming less clear. This is a consequence of the understanding that molecular biology has given us of the complexity of gene structure and action. Alongside this contribution from molecular biology, new conceptual work has been ongoing and some of this is collected in this volume.

Cycles of Contingency (CC) describes, extends and criticizes a body of ideas referred to as developmental systems theory (DST). DST aims to provide a holistic and epigenetic view of development. In epigenesis, the developing organism begins in an undifferentiated state and gradually changes to a more complex state through multiple interactions (after Waddington, 1940). This view was originally contrasted with classical preformationism (*sensu* Aristotle), which held that development proceeded simply by the enlargement of pre-differentiated structures. The contemporary picture of development incorporates elements of both views, but epigenesis dominates. For example, the imaginal disc gives rise to an insect limb or wing largely by growth and unfolding of a pre-patterned epithelial layer, but, during early development the disc is created by means of multiple, complex interactions.

In DST, epigenesis is broadened and contrasted with the view that genes control development. This view is thought to pervade the modern sciences of development and evolution, which often employ metaphors, in reference to genes, that are thought to assign them undue causal influence. This idea is explored in CC and in this review, in the context of "genetic information."

The book also explores the impact that gene-centrism has on our understanding of evolutionary dynamics. In population genetics, for example, evolution is construed only in terms of genetic change and, since environmental contingencies cannot be obviously affected by genes, evolution is seen to arise largely from external and autonomous selection pressures. DST redefines evolution as change in lineages of developmental systems. These systems are beyond "the organism" and comprise "cycles of contingency" operating between various "developmental resources" (including genes and "environmental" influences). Cycles are contingent because the impact one resource has, is, in part, a function of the other resources within the system. Developmental systems, in this sense, are not just read-outs of a genomically encoded developmental program. So, DST contains a strong notion of epigenesis, which moves beyond its traditional conception and has broad implications for many areas in biology.

The implications of DST

What are the consequences of this rearrangement of traditional notions? One answer is offered by Peter Godfrey-Smith (chapter 20), who suggests that a new framework of explanation may prove useful for developing a coherent account of biology across its diverse scientific disciplines. He characterises DST, in this sense, as a "philosophy of nature" compatible with, but not a replacement for, current notions. But, DST might reveal new kinds of developmental and evolutionary dynamics because factors formerly regarded as mere "contingencies" move onto the main stage.

One example of this is niche construction. This is presented, in this volume, in a classic paper by Richard Lewontin, for which he gives a new introduction (chapters 5 and 6), and it is also the subject of chapter 10 by Kevin Laland, John Odling-Smee and Marcus Feldman. Niche construction is the process by which organisms determine and construct their environments. This means that evolution involves reciprocal exchanges between organism and environment, which Lewontin contrasts with the conventional "lock and key" notion of adaptation whereby the environment poses a problem for the organism (the lock), which the adapted organism overcomes (the key). In chapter 10, the beaver's dam is given as an example. The dam is "inherited" by the beaver's offspring and it can affect the evolution of other species because it creates and sustains riverside wetlands. Laland et al. argue that organism-environment exchanges cannot be understood fully in terms of the extended phenotype (Dawkins, 1982) because they include the intergenerational effects of ecological modifications (*viz*. "ecological inheritance").

Another example is the evolutionary phenomenon introduced by William Wimsatt (chapter 17) as "generative entrenchment" (GE). GE is an inevitable or "generic" property of evolving developmental systems whereby certain elements of these systems contribute disproportionately to the developmental process. As a result, these elements become entrenched or "frozen" over evolutionary time. For example, the mechanisms underlying cell division are unlikely to change in evolution because a modification, genetic or otherwise, in any part of this interdependent system will likely have severely deleterious effects. Broadly, GE and its consequences are to seen as statistical generalities that emerge during development and/or evolution and are self-reinforcing. Although this chapter is largely conceptual, the roles of GE in gene networks and the evolution of culture, for example, are explored.

The phenomena of niche construction and GE force us to acknowledge a broader range of interactions than traditionally accommodated. But, DST aims to be more inclusive and one aspect of this is the reluctance in DST to "privilege" genes over other "developmental resources".

Concerns about the role that genes play in evolutionary processes sound familiar and raise hackles for some in biology. This is because politicized and rather hackneyed criticisms of evolutionary approaches arise frequently, which take the metaphorical vocabulary used at face value. For example, talk of "genes for" a particular trait has been seen as indicative of genetic determinism, although this term is used to refer simply to variant stretches of DNA that correlate with the trait in question. Likewise, the reductionism of genetics is held to reflect a simplistic view of reality, rather it being, more minimally and realistically, the "most successful research stratagem ever devised" (Medawar and Medawar, 1983).

CC largely avoids these excesses because, while its core thesis is critical of classical gene selectionism, its approach is refreshingly constructive. For example, Lenny Moss (chapter 8), examining the gene concept as it is used in molecular biology, makes the distinction between what genes *do* and what they are *for* by dividing the concept of the gene into two new versions that reflect each of these senses. Looking specifically at what genes, or more precisely stretches of DNA, do, it becomes clear they cannot do much without interacting with other molecules, and it is not even easy to describe all the processes that go into the production of a specific polypeptide sequence. The emphasis is therefore shifted away from genes that direct the processes of development to a complex molecular developmental system that incorporates them.

Of course, genes are necessary for these processes, but do they control them? It seems that we must wait for more research into such exotic molecular processes as RNA editing. In RNA editing, specific nucleotides within the sequences of messenger RNA transcripts are modified during or after splicing. This process disrupts the one to one relation that otherwise obtains between DNA and polypeptide sequences.

Moving away from details for a moment, there is a sense in which DST's tendency to de-emphasise genes in development is a welcome change. After the hype of the human genome project, the general reader should be encouraged to be skeptical of lofty talk about the significance of the number of genes and to resist the impression that geneticists are now so well equipped that they can peer into any problem in biology using newly available sequence data alone. For those actively researching gene functions, however, traditional techniques and approaches are not likely to lose their popularity because of the criticisms in this book. Furthermore, these approaches are, in fact, uncovering further subtleties relating to, for example, epigenetic inheritance. (With epigenetic mechanisms, the patterns of gene activity that contribute to a differentiated state are established and maintained through, for example, modifications of chromatin or methylation of DNA. Some epigenetic changes, such as those involved in genomic imprinting, can be inherited. For a review of these phenomena see Li, 2002).

Holism in DST

There are also some costs associated with DST's holistic approach. The simplest is that, if we were to adopt it as the gold standard, we would be ignoring some of the great achievements of reductive biology. Take, for example, the discovery of Hox/HOM gene complexes (acknowledged in chapter 20). The arrangement of these genes along the chromosome mirrors the position of the structures they "switch on and off" along various body axes and they are conserved across a remarkably broad range of phyla. (Hox-like genes are even found in *Cnidaria*; Ferrier and Holland, 2001). But, might a holistic approach give rise to positive misunderstanding? Criticism and defense of DST's holism is offered in the last section of CC. But in what follows, I should declare that my sympathies lie very much with the critical contributors.

One risk related to holistic frameworks is that, by trying to explain so much, they may end up explaining nothing. This problem is, I believe, demonstrated by the book's treatment of conceptions of information as applied to biological systems. Specifically, it is doubtful that a notion of information compatible with DST's holism can be derived, but by discarding current conceptions, some contributors may create confusion about the roles played by genes and other resources in development and evolution.

Holism and information

It is useful to define information. Information describes the situation in which an element of a system, by inputting energy or matter into the remainder, consistently gives rise to a signal, when other elements (or channels) are fixed. This consistency in relations between input and signal allows a looser definition that does not depend on the fixity or otherwise of channels. Information, in this sense, is anything that reduces uncertainty in developmental outcomes. In normal use, however, information includes the notion of intent because of its association with language.

Any geneticist will recognize talk of genetic blueprints as misguided, but may nonetheless employ information concepts freely: RNA editing aside, genes are said to *encode* polypeptides, and genes are *expressed* during the course of development. What many contributors to this volume aver is that this kind of talk is dangerous because the colloquial concept of information also implies a subtle form of gene-centred preformationism. The mainstream geneticist might counter that these notions still allow developmental outcomes to be contingent on various environmental or extra-genetic factors (which we can call channels). But this is seen as an insufficient defense: these contingencies create more than variations upon “the intended” theme and they should instead be seen as integral aspects of the comprehensively epigenetic (*sensu* Waddington) development envisaged in DST.

Taking this one step further, some contributors (and the editors) argue that information concepts should not be used, while an enlightening chapter (9) relies on information concepts to describe, in detail, the many different systems of extra-genetic inheritance. By defining, for each mode of inheritance, the nature of the information involved and the manner of its storage (for example), Eva Jablonka clarifies the roles that these modes or channels might play in evolution. Interactions between different inheritance channels can occur in this scheme by allowing that they are not autonomous but linked. To this end, I would add that traditional approaches might benefit from a further extended notion of epistasis, one that operates between inheritance channels. (In Mendelian genetics, epistasis refers to the situation in which the genotype of a given locus interferes with the expression of the genotype from another, but the definition is extended in quantitative genetics, because any kind of interaction between loci is included). This could be useful in evolutionary studies, because it allows gene-environment correlations or interactions to be considered separately from interactions between genes and other heritable (environmental) factors (the latter interactions being classed epistatic).

Since evolution acts on heritable variation, must genes now take a back seat to other forms of inheritance? A mildly critical chapter (23) questions this by showing why modern day evolutionary biology is so focussed on genetic information as opposed to other kinds. Kim Sterelny invents “Hoyle’s criteria” which describe the kinds of properties replicators would need to possess if, when used to seed an empty planet, they were to create a rich flora and fauna like that on earth. It turns out that genes fulfill most of the requisite conditions while other inheritance channels are less well suited and less evolvable. As cautioned elsewhere, however, interaction between different channels of inheritance and between the organism and its environment (niche construction), have consequences for evolutionary dynamics.

Since these accounts selectively employ information concepts (for heritable factors), it might be argued that they incorporate preformationist assumptions *a priori*. With respect to the role of genetic information, it is no doubt true that nature never holds all other inheritance channels constant, but this becomes a problem only when this inconstancy covaries with the (genetic) input under consideration (see below). So, we can still benefit from information concepts when they are construed as means by which uncertainty, in development, is reduced. I would challenge contributors to develop a holistic/non-informational account that can incorporate this meaning.

There is, then, it seems to me, no knockdown argument against the use of information concepts in this volume, but Evelyn Fox-Keller, in a detailed historical analysis (chapter 21), shows that, while arguments about the necessity or sufficiency of particular developmental resources cannot be used to exclude information talk, they can ruin notions of an exclusively genetic developmental program. I would add to this that information of a non-genetic nature is not just relevant with regard to the variety of phenotypes possible (as implied by work in quantitative genetics). Environments provide information relevant in the construction of phenotype and they should be seen, therefore, as more than life-support for its invariant aspects.

Measuring information

Should we put an end to the traditional approaches employed in genetics to measure "information"? Or should we preserve them as useful parts of an expanding toolkit? Contrary to Patrick Bateson's conclusions (chapter 13), I do not think it is yet time to celebrate "the demise of heritability."

A heritability estimate is a measure of the degree of genetic determination of a phenotype within a particular population in a given and fixed environment. There should be no need to be embarrassed by the "d" word: determinism. Correlations do imply causes, but that genes may determine an outcome, when other factors are held constant, does not mean that they are the sole causes in development. Bateson describes examples of condition-dependent development such as genetically identical grasshoppers that can adopt alternate colours when young to suit their environment. He also examines the impact of birth weights on subsequent health, independent of (often) persistent socio-economic effects.

By these means, Bateson does show that heritability cannot capture the subtleties of development in full detail, but his case against heritability as a reliable measure (p155-6) flows from the observed correlation between offspring phenotypes, on the one hand, and parent-offspring phenotype-genotype differences, on the other. This seems to raise a problem with heritability measures that is perhaps worst in humans: that is, covariance between genetic values and environmental deviations cannot be elided with genetic variance because the former is affected by parental genotypes in addition to that of the focal individual (p131-2, Falconer and Mackay, 1996). The evolutionary consequences of other genotypes in the environment are addressed in a recent paper (Wolf, 2003).

It is interesting, however, that this problem with heritability estimates is revealed by a correlative analysis. This implies that this type of measure, of which heritability is an example, can reveal useful information (!) about development. This is an important point, because to the extent that heritability estimates can be of practical use to the farmer (as acknowledged by Bateson), they can also provide information about the degree of genetic determination of developmental systems in particular populations and environmental settings. When it is possible to produce animals with replicate genotypes and raise them in different environments, further information can be obtained about the extent of gene-environment interaction by means of an analysis of variance (p132-3, Falconer and Mackay, 1996) and this can perhaps be achieved in humans by including specific environmental measures in twin studies. (For an interesting further analysis of the nature and implications of heritability estimates, see Chapter 19 of *The Blank Slate* by Steven Pinker). Heritability, then, is a blunt instrument for looking into development, but it is instrumental nonetheless.

An outline

In summary, CC sometimes over-eggs the pudding, but it contains a great deal to attract and absorb those interested in the philosophy of biology. It should also engage those wishing to understand the impact of developmentalist thinking on the sciences of molecular genetics, behaviour (not addressed in the present review) and evolution. More broadly, this book should appeal to anyone, from professors to undergraduate students, who is interested in the core ideas of biology. And the practical scientist will find many important ideas, relevant to work at the coalface, brought together in this well edited book.

Sometimes the reader will need to get to grips with a difficult style of writing; however, the meaning is generally evident from the context and can be worked through by the careful reader. The book is well structured and self-critical. While I have ventured to build upon these criticisms in some places and to add further criticism in others, I do commend the editors' and contributors' interesting and constructive contributions to modern biology.

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