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Essay review

Dissecting developmental biology

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Towards a Theory of Development, Alessandro Minelli, Thomas Pradeu (Eds.). Oxford University Press, Oxford (2014). 304 pp., Price GBP 37.50 paperback, ISBN: 978-0-19-967143-4

1. Introduction

Minelli and Pradeu have assembled a stellar list of authors, including many of the main scientific contributors to evolutionary developmental biology, as well as some of the leading philosophers of science who have written about that field. Whether or not there really is a theory of development, this volume leaves little doubt about the value of theoretical biology in general.

Despite the title of the book there is no consensus among the authors regarding the feasibility and desirability of a general theory of development, or about how to understand the two terms 'theory' and 'development'. Although the editors do a good job of weaving the themes of the several contributions together in their introduction, those contributions are wide-ranging and thought provoking rather than providing elements of a single approach to the question of a theory of development. Our discussion will focus on three themes that can be found in many of the contributions.

1. What is a scientific theory and what is the significance of having a theory for the scientific status of a research area, such as developmental biology? Answers to these questions would seem to be presupposed in asking if developmental biology should want or need an overarching theory? After all, instead of promoting research an overall theory might constrain it, and even be an obstacle to innovative research.
2. A more substantive question concerns the concept of development and what a theory of development should cover. Is there a consensus about what development is? What is development's temporal dimension: when the organism is able to reproduce a new organism, or is it instead the whole life cycle, no matter how simple or how complex and expanded that may be? What does development include spatially: a single organism, a group of organisms, extended 'hybrids' such as an organism including its symbiotic microorganisms or an organism within its developmental environment (such as the mother or parents, a nest or a womb, siblings, extended resources such as sustenance, warmth, protection and stimulation), or any other system imaginable or as yet unimaginable? If we include within the scope of development a whole life cycle unfolding in its developmental environment—its developmental niche (Stotz, 2008, 2010, 2014a, 2014b; West & King, 1987)—then the relationship between two generations and the modes and mechanisms of the transmission of developmental resources would come into focus. Processes of heredity would then appear as deeply coupled to the process of development. This leads to the question of how should we delineate development from other dynamical processes, such as metabolism, self-organisation, regeneration, and even behavior, or the more overarching dynamical processes of heredity and evolution? Minelli asks if only functionally adaptive aspects of change merit the name development, or possibly any changes (pp. 228, 235). Many authors touch on one or more of these issues.
3. Several authors also address a further question, namely the causal structure of development and the kinds of causal processes that we find in development. The role of genetic causation and its relationship to other causes is obviously of particular interest here, but the more general issue of what kind of causal networks we find in development, how to distinguish between causes and whether they can be modeled, is also debated.

Clarifying these more general issues may, as interesting as they are in their own right, at first lead us away from the question

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regarding a theory of development, but on second thoughts may be an important prerequisite for the development of such an elusive theory.

2. A theory of development?

Textbook philosophy of science contrasts two views of what ‘theories’ are, the syntactic and the semantic conceptions. On the older, syntactic conception a scientific theory is a claim about how the world works, a claim that would ideally be stated as a set of axioms in which all terms would either be defined in terms of observation, or implicitly defined by their role in the axioms. A theory of development would thus be a set of axioms about development from which the development of an individual system could be predicted by specifying the initial conditions of that system. On the alternative, semantic, view a theory is a family of models, which gain empirical content when we add the claim that some real world system is similar enough to the model that we can reasonably use the model to understand that system. Important issues about the nature of scientific representation have been canvassed in these very abstract terms, but it seems clear that the question of a theory of development will not be usefully approached in this way. The idea of an axiomatic approach to developmental biology seems quite hopeless, and the claim that developmental biology contains a set of models that can be used to understand the development of particular organisms, and that it hopes one day to have more and better models, seems true but unhelpful. It seems that a majority of contributors to this volume would endorse a looser, but in this context probably more helpful, conception of a scientific theory as any form of *systematic* representation of scientific knowledge.

What is the function of a theory? For some of the authors, such as Thomas Pradeu, a scientific theory is a useful thing to have because a systematization of knowledge allows explanation, prediction and understanding, rather than mere local descriptions. The function of theories is foremost to provide “novel, daring, testable, and hence often wrong” statements or hypotheses (p. 23). Such ‘how possible’ answers therefore “stimulate challenges” (p. 24). Unification—providing a unifying framework for heterogeneous phenomena—is a second function for theories that Pradeu identifies.

For Alan Love, however, scientific theories are valuable because they provide a useful guide for future research. Love denies that a theory of development would or could do that. He argues that what organizes and guides research in developmental biology is not a theory, but a set of core problems or problem agenda; developmental biology is erotetically organized. Developmental biology is not guided in its approach to new questions by an overarching theory that systematizes our understanding of the nature of development. Instead, future research is guided by what has been learnt about the best questions to ask.

Griesemer agrees that a science may not need “a formalized, exact theory to be successful” (p. 200), particularly an inexact science such as developmental biology. While Griesemer does not see the need for a theory of development for the “conduct of inquiry into development per se” (p. 184), he argues that such a theory will be needed for an extended evolutionary theory that integrates developmental biology. He proposes a plurality of theories with the aim of articulating, “a set of core principles, a family of models, and a theoretical perspective” (p. 199). All three ingredients are necessary for a theory for description, explanation and prediction on the one hand and to guide future empirical inquiry on the other. Many contributors seem to agree that a plurality of theoretical perspectives would not be to the detriment of developmental biology.

3. The conceptual boundaries of development

The relationship of development to heredity and evolution, and possibly even to fields like ecology and immunology as some contributors argue, points to another topic touched on by most contributors to the volume: where are the conceptual boundaries of development? There are several reasons for relating a theory of development to a more general theory of “ecological, evolutionary developmental biology” (Griesemer p. 183) or a theory of “developmental evolution” (Moczek p.218). For Moczek the most important reason is “the role of phylogeny in shaping organismal development” (p. 219). An equally important reason would be that understanding phenotypic evolution requires understanding development. But most importantly, we would argue, is that the very existence of the process of evolution relies on there being developing, reproducing systems. Hence Griesemer argues that concepts of development and reproduction, and also of inheritance, should be “conceptually *prior* to a concept and principle of evolution” (p. 190). These key concepts should be able to be defined without reference to the process of evolution to which they give rise.

But how can we delineate development from other dynamical processes such as metabolism or regeneration, or, we argue, even behavior, if the very meaning of development as preformed ‘unfolding’ is in question? A recent survey article defined behavior, as opposed to development, as the “internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes”. They excluded development on the ground that “developmental processes are … generally much slower than phenomena considered as behavior, and are primarily *based on ontogenetic programmes specified by the individual's genetic makeup* (Livitis, Lidicker, & Freund, 2009, 108, emphasis added). We are still a long way from any unbiased characterization of development, but several chapters of this volume provide food for thought about possible avenues in this direction.

The conceptual boundaries of development are contested on at least three axes, temporal, spatial and phylogenetic. The temporal dimension is perhaps the simplest. At what point in the life of an organism, if any, does ‘development’ end? Developmental biology grew out of embryology, which by definition restricted the temporal dimension of development to the egg and fetus. Developmental biology widened this to include all processes that lead from the fertilized egg to reproductive maturity. Some of the contributors think, as we do, that development must in principle include the entire life-history of an organism. Gilbert and Bard see development as the process which creates the whole life cycle rather than just a sexually mature adult.[1] While the editors acknowledge this as an “extreme position” developmental systems theorists have promoted this view for quite some time.

The phylogenetic and spatial dimensions of development are equally important and equally contested. The editors point out in their introduction that developmental biology has always been “biased by the idiosyncratic properties of the most fashionable model species on which observation and experiments are performed” (p. 2). It is evident how much more challenging it becomes to conceive of a general theory of development if we wish to include plants and fungi as well as animals. But the potential scope of developmental biology is even wider, including microbes and

[1] Interestingly, in *Ecological developmental biology* (Gilbert & Epel, 2009) the authors still distinguish between developmental and phenotypic plasticity, a distinction that would be problematised under the whole life-cycle view.

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viruses, which until recently only entered into view as far as their relationship to multicellular organisms was concerned. Several contributors to this volume explicitly demand that a theory of development include the life cycles of these organisms. Griesemer's discussion of the plasmodium bacterium and HIV virus life cycles, as well as Nyholm and McFall-Ngai's description of microbial influences on animal development, dramatically highlights how complex, multi-generational and multi-genomic are the life cycles of some of these supposedly simple organisms. Minelli targets a "framework of developmental biology broad enough to apply, if possible, to every form of life on Earth" (p. 228).

The case of hybrid lifecycles that include more than one organism extends the boundary discussion from the temporal to the phylogenetic and spatial dimension. The development of literally all life forms is influenced by microbes, with which every organism is more or less tightly associated, as Nyholm and McFall-Ngai's chapter illustrates. Griesemer's molecular conceptualization of the life cycle of malaria parasites or the HIV virus shows its dependence on many features of their respective hosts that 'scaffold' their development. The term 'scaffolding' was first introduced in developmental psychology for temporary features in the child's environment that support and guide the development of slowly developing capacities. Child-directed speech (Motherese), for instance, provides them with the clues needed to help them develop their own language skills. Recently Kim Sterelny and others have introduced 'scaffolding' as a supplement to the idea of 'extended cognition', using it to label environmental resources which support, complement, and amplify the operation of cognitive capacities, as well as supporting their development (Sterelny, 2010).

Griesemer approaches the question of a theory of development from the perspective of a spatially broad, or 'ecological' evolutionary developmental biology, as several authors in this volume do one way or another, particularly Armin Moczek, and to a certain degree Michel Morange. This approach is particularly associated with Scott Gilbert, although his contribution to this volume does not primarily address this aspect of his work. There is also Jean-Jacques Kupiec's approach, although it is somewhat debatable to what extent applying a Darwinian selection principle to cell differentiation amounts to an "ontophylogenesis" (Kupiec, p. 156). From this term one may rather expect something like a real mapping of ontogenesis to phylogenesis within a unified naturalist metaphysics of complex adaptive and regulatory systems, as for instance Cliff Hooker has envisioned (Hooker, 1995, 51). There could very well be quite different mechanisms of selection at work between entities of different levels of organisation at different time scales. Natural selection by definition selects for reproductive fitness. Selective processes at work within a self-organizing system may select for stability, effectiveness or whatever attributes of the parts are of relevance to the survival and reproduction of a system as a whole.

One well-known example of a very spatially broad approach to development is 'developmental systems theory' or DST (Oyama, Griffiths, & Gray, 2001). This has at its core the idea of an organism-environment system that includes environmental features that are reliably transmitted to offspring and provide necessary resources for development. Griesemer criticises DST's lack of clarification of "how the expanded mechanisms figure as part of the system that must not only develop but reproduce" (p. 193). However, to be fair DST has devoted significant attention to extended heredity, seeking to show that the genetic material is not the sole hereditary unit. Instead, heredity is more widely understood as processes providing transgenerational stability and plasticity through the reliable transmission or reproduction of developmental resources to and for the next generation. This includes epigenetic germline inheritance but also transgenerational epigenetic effects and more generally maternal and paternal (parental) effects that are transmitted behaviorally, culturally, or even symbolically (Jablonka & Lamb, 2005).

Some of Griesemer's concerns can be met by focusing on the idea of the 'developmental niche', a concept first introduced by developmental psychobiologists Meredith West and Andrew King (1987) to conceptualize the inherited developmental environment (see Griffiths & Stotz, 2013; Stotz, 2008, 2010, 2014a, 2014b). Griesemer himself uses the term 'developmental niche' several times without reference to its origin (pp. 186, 192, 197, 199). This is unfortunate, because people unfamiliar with the history of this idea in theories of behavioral development often conflate the developmental niche, as Moczek does, with the *selective* niche made famous by niche construction theory (Odling-Smee, Laland, & Feldman, 2003): "Niche construction theory thus makes room to understand the immediate developmental environment experienced by individuals …. Instead what is passed on to the next generation is the selective environment as generated by individuals and as experienced by descendant generations" (p. 224). Despite their reference to the developmental environment, what niche construction theory in the sense made famous by Odling Smee and others makes clear is how past generations (with no special focus on parents) influence the selection pressures acting on later generations. This is not the same thing as how past generations—with a very strong focus on parents—help to create the normal environment that is needed for development. This distinction is as important for evo-devo as it is for DST, since it is also a distinction between two complementary drivers of evolution: the production of new heritable variation through construction of new developmental environments, and the selection of heritable variations by construction of new selective environments.

The developmental niche framework is a useful way to try to accommodate the complex multi-genomic and multi-generational features of the 'simple' life cycles of microbes and viruses. Just as the rat pup passes through a series of consecutive developmental niches (the uterine niche, the dam, the huddle and the coterie (Alberts, 2008), which provide sustenance, warmth, protection, and necessary experiences for learning), so does the HIV virus or the plasmodium pass through a series of different 'niches' that support different stages of development. This is particularly the case if we take Minelli's conceptual clarifications regarding the terms 'individual' and 'generation' into account. In a chapter exploring the disparity of development the author divides the traditional concept of generation into two separate concepts (p. 229–231). He links the more common-sense meaning of demographic generation to a physically distinct object—the reproducing individual, while a genetic generation, where individuals may be produced through sexual reproduction or just mere sexuality, decouples reproduction from sexuality. He likens this move to the recognition of multiple notions of individuals—e.g., historical, functional or genetic.

4. The causal structure of development

Given the extent to which development, at least in the last century, was explained in terms of the genetic constitution of the organism, one theme touched on by several authors is the causal role of genes in development. However, no proponents of a strong gene-based account of development can be found in this volume, as Brian Hall remarks in his foreword, and the editors note in their introduction. In a discussion of the dichotomy between the theories of preformation and epigenesis, however, Minelli and Pradeu quote Lewontin complaining that even though epigenesis supposedly has "decisively defeated preformationism … it is really preformationism that has triumphed" (p. 4). What Lewontin has in mind can

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perhaps be seen in Arthur Wallace's description of epigenesis as the idea that there is "information of some sort that could be interpreted as a set of instructions about how to build an adult of the species concerned" (p. 146). The concept of information is something of an anachronism when applied to the thought of the major epigenicists in the history of biology, but leaving that aside, the idea that the egg contains instructions for development is far closer to classical preformationism than to classical epigenesis. An eighteenth century epigenicist like Denis Diderot would have been horrified by the idea, fearing that these 'instructions' would reintroduce God as the immediate author of development, and a preformationist like Charles Bonnet would have been quite content, for the same reason. As Kenneth Schaffner has remarked, simplistic views of the causal role of genes in development substitute many 'traitunculi' for the single 'homunculus' of classical preformationism (Schaffner, 1998).

The strongest defense of a gene-based theory of development can be found in Michel Morange's historical and philosophical reflection on a theory of development (and evolution) in terms of gene regulatory networks. He does give some thought to what kind of ingredient might be missing in this framework, particularly to an integrated theory of evolution, such as possibly a more general theory of innovation; still, Morange doesn't seem to share Gilbert and Bart's view that much of development *is not* determined by the genome. In contrast, Moczek criticises the uselessness of program and blueprint metaphors forcefully in his contribution.

Later in his chapter and in line with developmental systems theorists and modern epigenesists, Wallace dismisses the strict dichotomy between genes and environment when he discusses the theory of cell differentiation in terms of 'variable gene activity'. He instead points to the permanent interplay of genes with a variety of factors that include other molecules but often also environmental factors (p. 147). His hope for a much broader and more general theory of development in its totality, however, lies in the search for subtle patterns of causal connections, that go beyond the abstract description of such patterns as either hierarchical, modular, combinatorial or negative feedback. Such a search, and most importantly in our view, "combined with a mathematical modeling approach in which causal interactions are quantified rather than being simply labeled as activating or repressing, might yet produce a theory of development" (p. 153).

We are very much in agreement with Wallace. In reaction to the debate in the philosophy of biology about how to distinguish between more and less specific causes in developmental biology, we and our collaborators have made some preliminary steps in the direction of measuring the specificity (degree of actual or potential causal control) of a cause over its effect (Griffiths et al., in press). Our work started from James Woodward's suggestion that intervening on a highly specific cause allows us—or the system—to exercise fine-grained control over processes within the system (Woodward, 2010). Philosophers of biology Kenneth Waters and Marcel Weber have both argued that DNA has much more fine-grained control over the outcome of gene expression than do other causes that are equally necessary, as for instance the enzyme polymerase (Waters, 2007; Weber, 2006). Stotz in contrast has argued that in eukaryotic gene expression splicing and editing factors may be equally or even more specific than the underlying open reading frame (Stotz, 2006). In our recent work, we have brought a combination of information theory and causal graph theory to impose a quantitative framework on this dispute (Griffiths et al., in press). Specificity, we have argued, is *distributed* across multiple causes.

The term specificity has been of immense importance in biology over the last 150 years. Gilbert and Bart (p. 132) emphasize the continuing importance of the concept of *stereochemical* specificity:

> Two principles must be recalled in every discussion of upward causation in embryology. First, … Information is not about essence, it is about relations. … Second, development acts almost exclusively through stereocomplementarity (Gilbert & Greenberg, 1984). Stereocomplementarity is the interaction between shapes, and it is one of the great unifying principles of biology. … Thus, information in development is about the interaction of complementary shapes. Our 'information' is in-form-ation. That is, information takes shape; … we are really discussing the interaction of shaped objects.

They do not mention a second, *informational* conception of specificity, which Francis Crick introduced in 1958 with his Sequence Hypothesis and Central Dogma. Biological specificity, Crick argued, did not need to be encoded in unique three-dimensional shapes. The same 'information' could be encoded by different sequences of a simple, linear molecule. This informational conception of specificity now complements the older stereochemical or conformational conception. Both stereochemistry and sequence information allow an organism to manifest specificity.

Recently we proposed that causal relationships in biological systems should be regarded as informational whenever they are highly causally specific (Stotz & Griffiths, under review). We endorse Crick's own definition of information: "Information means here the *precise* determination of sequence" (Crick, 1958, 153, his italics). Biological specificity, whether stereochemical or informational, seems to us to be simply the application of the idea of causal specificity to biological systems. The remarkable specificity of reactions in living systems that biology has sought to explain since the 19th century can equally be described as the fact that living systems exercise 'fine grained control' over many variables within those systems.

Others have pointed out that the study of biological development requires two sources of such information. In an immediate response to Crick's new picture of sequential information encoded in DNA, David L. Nanney pointed out the need for an epigenetic control system that allows the developmental system to use this information:

> This view of the nature of the genetic material … permits, moreover, a clearer conceptual distinction than has previously been possible between two types of cellular control systems. On the one hand, the maintenance of a "library of specificities," both expressed and unexpressed, is accomplished by a template replicating mechanism. On the other hand, auxiliary mechanisms with different principles of operation are involved in determining which specificities are to be expressed in any particular cell. …To simplify the discussion of these two types of systems, they will be referred to as "genetic systems" and "epigenetic systems." The term "epigenetic" is chosen to emphasize the reliance of these systems on the genetic systems and to underscore their significance in developmental processes. (Nanney, 1958, 712)

Postgenomic biology has vindicated Nanney's vision. It has brought with it a new conception of the causal role of genes in development, replacing the active gene with a reactive genome that is regulated by cellular processes that include signals from the internal and external environment. This regulation includes not only the regulated *activation*, but also the differential *selection* and even the *creation* of genetic coding sequences, processes which one of us has labeled "molecular epigenesis" (Stotz, 2006). Informational specificity in developmental systems is distributed between coding and *cis*-regulatory sequences, *trans*-acting factors (RNA and

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proteins) such as splicing or editing factors, and environmental signals which activate or translocate these factors thereby relaying environmental information to the genome (Griffiths & Stotz, 2013; Stotz, 2006).

5. Conclusion

This highly recommended collection provides informed, rich and diverse discussion of many topics in today's developmental biology. While it can be debated to what extent it makes progress towards a theory of development—a quest that to many contributors doesn't seem too important to begin with—it clearly makes huge steps towards clarifying other pressing questions for developmental biology and for the philosophy of biology. This review has outlined some of these questions, particularly the temporal, phylogenetic and spatial dimensions of development, and the causal structure of developmental systems. Answering these questions is surely one of the steps that is needed to move towards a theory of development.

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