

Eric Davidson, his philosophy, and the history of science

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Abstract Eric Davidson, a passionate molecular developmental biologist and intellectual, believed that conceptual advances in the sciences should be based on knowledge of conceptual history. Convinced of the superiority of a causal-analytical approach over other methods, he succeeded in successfully applying this approach to the complex feature of organismal development by introducing the far-reaching concept of developmental Gene Regulatory Networks. This essay reviews Davidson's philosophy, his support for the history of science, and some aspects of his scientific personality.

Keywords Mechanistic biology · Popper · Loeb · Neo-Darwinism · Eric H. Davidson

Our advice is that every man should remain in the path he has struck out for himself, and refuse to be overawed by authority, hampered by prevalent opinion, or carried away by fashion. (Goethe 1906, aph. 537, 188–189)

I met Eric for the first time in 2001, during my visit at Caltech, when Eric wanted to talk to me about my first book, *Biologists under Hitler* (Deichmann 1996). We have remained in touch ever since, and I am deeply grateful for his encouragement, criticism, numerous stimulating discussions, and for his friendship. I here reflect on Eric's support for the history of science, his philosophy, and his scientific personality, frequently quoting from his letters and the interview that I conducted with him in 2014 (Deichmann 2016).

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1 Support for the history of science and the Jacques Loeb Centre

A passionate exact scientist, Eric was deeply convinced that reflections on the history and philosophy of science were not only an intellectual challenge but also highly relevant to research; he believed that conceptual advances in the sciences, and conceptual history, can never truly be separated. This is most clearly expressed in his reverence of Theodor Boveri and Edmund B. Wilson, whose concepts of the chromosomal, as opposed to cytoplasmic, control of heredity and development inspired greatly his own research (Davidson 1968; Laubichler and Davidson 2008). His conviction of the importance of historical and philosophical reflections manifested itself also in the moral support and help that he granted, for example, to the Jacques Loeb Centre that I had founded as a center for an intellectual encounter of working scientists and people who comment on science like philosophers of science, historians of science, and science journalists.

His support for the Centre began shortly after it was founded in October 2007 and ended only with his death on 1 September 2015. His appreciation, as well as skeptical attitude, are revealed in correspondence by e-mail that I had with him: “I looked at the Loeb Center announcement,... And knowing you there will be extremely interesting projects happening there. If you were to invite me to one of the workshops there I would come, and I hope someday you do! I know that working scientists are not usually among those whose profession it is to consider the nature of scientific process and event, past and present, but one reason for that is that many wonderfully effective scientists are distinctly not also intellectuals” (e-mail of 27 January 2008). After attending our workshop in April 2009, he wrote: “I want to thank you for a most interesting and rewarding experience. We did truly enjoy many different aspects of our time there, not the least the warm and wonderful hospitality of your friend Dany [Lachish]. I found the meeting itself most interesting, which I did not entirely expect, and hope I shall have a chance to participate in more of such subjects...” (e-mail of 14 April 2009). He did have plenty of these chances. He participated in almost every one of our workshops until 2014. He also encouraged many of his colleagues to participate and gave me suggestions and advice.

Eric engaged in many discussions with fellow scientists as well as historians and philosophers of biology, critically commenting on tendencies he considered detrimental for current research. To mention here only one example (more examples follow later): While he was critical, on the one hand, of holistic, anti-mechanistic views in science, he also fought the narrow-mindedness he perceived in attitudes of his fellow molecular biologists, or of historians who had not realized the limitations of classical molecular biology in regard to explaining complex phenomena such as development. He wrote to me about the changes he perceived in biology,

Of course science IS changing and re-orienting. It IS true that this reorientation, in some of the most rapidly advancing areas of bioscience, slices across disciplinary lines. In my area of gene regulatory networks for example, structure/function relations between many regulatory genes are studied together experimentally, not built up from individual gene studies; and

math and biochemical and genomics and embryological issues are intertwined and deployed en suite. But it is just as causal and exact as any earlier bioscience and the fault in the current popular argument is the persistence of the 70's idea that only research that deals with a single moving part (hard nosed reductionism) is capable of getting a hard answer (to the wrong problem) and that all other research must have some fuzzy unscientific core. I've been fighting that attitude for about 40 years. (e-mail of 22 January 2008, emphasis in the original)

2 Philosophy

Eric was guided by a clear and explicit philosophy, namely that of mechanicism. For him, the modern mechanistic view was the current criterion in experimental molecular biology for successful scientific analysis, "one that succeeds in explaining with good causal evidence how something works and why". That is, his idea of mechanism included the search for causes. He was dealing with one of the most complex biological systems, that is animal development, in particular the early development of sea urchins. Therefore, he explained, a causal-mechanistic explanation could be only achieved in a systems approach in which almost all components and their interactions were included: "The fundamental premises of experimental systems developmental biology are that all processes that can be defined as observable episodes of development are generated through multiple interactions of multiple biologically active components, and that all these components, and all (or almost all) their interactions, must be included in an analysis in order to solve a mechanism that has sufficient predictive explanatory power". (Davidson 2016, 173) In this way he succeeded in pushing back non causal-mechanistic, purely phenomenological research in his field.

Experimental perturbation and predictions were essential: "Only by deliberate experimental perturbation and predictive challenge of the system can the mechanisms by which it operates be revealed". However, since systems developmental biology produced extremely complex constraints, secondary and tertiary effects had to be considered as well, "perturbation analysis in systems developmental biology demands the intellectual guidance provided by the use of hypothesis at every step" (*ibid.*, 175).

His strong emphasis on hypothesis, predictability, and hypothesis-testing is reminiscent of Karl Popper. Eric's outlining of a complete mechanism that took care of any possibility, or, as he put it, without leaving any room for the appearance of 'black swans', may have been also inspired by his wish to overcome Popper's prohibitions: Popper, as is well known, excluded the question of hypothesis-creation from philosophical analysis and banned the use of induction from testing hypotheses because the appearance of one 'black swan' could always prove an inductive idea (such as that all swans are white) wrong. Though indirectly relating to Popper and agreeing with him with regard to the central importance of hypothesis testing, Eric would not have agreed with Popper that all experimental tests of hypotheses were attempts at falsifying them, no matter what scientists consciously think they were

doing. Eric created his own semi-Popperian epistemology. He believed in the correctness of those of his hypotheses that were corroborated by experimental and computational methods and would therefore have strongly disagreed with Popper's conviction that, by force of 'verified' conclusions, theories can never be established as 'true', or even as merely 'probable' (Popper 2002 [1959], 33). Unlike Popper, Eric put emphasis on the *creation* of ideas and hypotheses, not only on *testing* them, and here he considered induction essential. Eric's beliefs in the high relevance and basic correctness of his theories was preceded by manifold exact testing, but certainly his beliefs were so strong that at times he was not ready to acknowledge that other questions in his field might be important as well.

3 Ethics

Eric claimed to dislike ethics, which he considered unnecessary. But a moralist agenda can be found throughout his work. An example is his fight for a mechanistic understanding of development and evolution, which for him was not only the only way to conduct science in these fields fruitfully, but also a bulwark against any irrational views of life, such as creationism. He displayed his moral attitude when he pointed to what he considered bad science, which according to him led to a waste of time, energy, resources, and constituted an attack on generally accepted, successful scientific epistemology.

The huge, well funded, and *Nature* magazine supported ENCODE program (Encyclopedia of DNA Elements) was one of Eric's targets. While ENCODE's provision of large amounts of data for scientists have been widely appreciated, methods, significance, and interpretation of ENCODE's own scientific research have been strongly criticized by many scientists and philosophers, including by Michel Morange, Ford Dolittle and Dan Graur. Eric focused his criticism on ENCODE's epistemology:

It is indeed essential to have a parts list. But note that the list of approved approaches excludes any perturbations, such as changing a sequence experimentally to test a functional prediction,... In the world of ENCODE genomics, the analysis is to be published on the basis that the measurements... were made and analyzed using sophisticated mathematical statistics; whether the result has any power of predictability is not relevant. In science, conceptual predictability accruing from an analysis is the golden criterion of value, of progress in understanding. Predictability is the lynchpin of scientific knowledge. (Davidson 2016, 169)

Using a semi-Popperian criterion of good science by exchanging Popper's falsifiability criterion by predictability, Eric criticized ENCODE's epistemology as essentially unscientific. Eric was also aware and concerned about the devastating effects of Lysenkoism, and the related Michurinism, that has remained influential in China until today, long after it disappeared in the Soviet Union, and he urged me to write about it.

One of his long-lasting targets was neo-Darwinism, which Eric considered insufficient to explain major evolutionary questions such as the generation of new bodyplans. According to Eric it was clear, at least since his paper with Britten in 1971, that

if you want to understand evolution, you have to understand the change in genomic programs that control development. That's the only way to consider it. Therefore it has to be concerned with change in the architecture of, what we would call today, gene networks.... Darwinian evolution was of a completely different kind. It was all about small changes and they felt if you could understand changes in petunia colors, you could understand changes in whether animals have heads or not. And that's just total nonsense. But you can't really blame the Darwinians, because all of Darwinian theory, from the Neo-Darwinian synthesis of the 1930s, was built in the absence of, and ignorance of, any knowledge of how development actually works. Other than wrong theoretical ideas. (Deichmann 2016, 525)

4 Eric Davidson and Jacques Loeb—passion and mechanistic biology

Eric's commitment to biology as a mechanistic science and his moralist stance are reminiscent to some extent of Michael Polanyi's attempt to make scientists aware of their responsibility to passionately be committed to "a vision of reality" (Polanyi 1962 [1958], 64). Eric was a passionate and visionary scientist, propagating the view of which he was convinced was the right one, albeit after long testing, making it clear that passion can be immensely scientifically fruitful when combined with exact experimenting and reasoning. As other scientists were ready to acknowledge: "Eric is today the leading liberator of quantitative principles of cell regulation trapped in the qualitative, descriptive world of biology without genomic sequence" (Istrail 2006, 14).

Jacques Loeb, after whom our Centre is named, shared with Eric a love of both passion and rationality in science, as well as a critical stance towards Darwinian evolutionary biology (despite appreciating the idea of biological evolution). Around 100 years ago, Loeb passionately promoted biology as an exact experimental mechanistic science. In a collection of essays, which appeared under the title *The Mechanistic Conception of Life* in 1912, he vehemently rejected irrationalism, which he perceived as vitalism, superstition, Chauvinism, racism, and anti-Semitic writings of intellectuals such as Eugen Dühring (Loeb 1964 [1912]). As with Eric, the shortcomings of Darwinian evolutionary biology were a major concern for Loeb who (around 1900) upset colleagues who were likewise liberal but uncritical defenders of evolutionary theory when he told them that in science one could only take things to be proven when they were based on quantitative experiments and that from this point of view their era was not the era of Darwin but the era of Pasteur. He expected biologists to attempt to find the causes of the generation of new species and to experimentally create them. Eric strongly devoted himself to similar questions through his own work where he considered changes in those parts of

developmental gene-regulatory networks that control early development as mechanisms of major evolutionary changes and envisioned a new research field of synthetic experimental evolution to deal with the questions of experimentally generating evolutionary novelties such as species or higher taxonomic ranks (see the contribution of Douglas H. Erwin on Eric Davidson and deep time in this topical collection).

In his autobiography Francis Crick described his own “hubris of the physicist, the feeling that physics as a discipline was highly successful, so why should not other sciences do likewise?” He contrasted this with the “rather plodding, somewhat cautious attitude” that he encountered when he began “to mix with biologists” (Crick 1988, 13–14). Similarly, the physicist Freeman Dyson is cited to have remarked that “scientists are split into unifiers and diversifiers and that biologists tend to be the diversifiers, ‘happy if they leave the world a little more complicated than they found it’” (Whitfield 2006, 235).

Eric does not fit this picture of biologists. Early on, he took up the challenge of complexity, not to adore it or to simplify it, but to find a causal mechanistic solution to the complex old biological problem of development and its “deep time derivative”, the evolutionary biology of the animal body plan, based on the genomic regulatory code. As Eric’s colleague at Caltech Andrew Cameron wrote in his obituary in *Nature* (2015):

The best scientists, in my view, are the ones who can stand fast in the face of bewildering complexity until they see the patterns emerge. Eric was a good example of such a person. He deeply enjoyed embracing the complexity and trying to develop a cogent view. (Cameron 2015, 196)

Eric was a deep and independent thinker who, in his own way, pushed his visions ahead, sometimes inciting sharp discussions. His radical search for causal-mechanistic explanations in biology, his rejection of superficiality and vagueness, impressed and influenced not only scientists, but also other intellectuals interested in the advancement of science and the personalities and philosophies involved.

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