

they see too much continuity between human and non-human animals and attribute human-like conscience, morality, and mental life to monkeys and other non-human animals. Rejecting both views, Kagan suggests that there is no non-human animal model for human pride, shame, and guilt, because the presence of the concern with right and wrong and the desire to feel virtuous are "like the appearance of milk in mammalian mothers, a unique event that was discontinuous with what was prior." In other words, "Not even the cleverest ape could be conditioned to be angry upon seeing one animal steal food from another."

In the end it appears that Kagan is quite prepared to defend, on scientific and secular grounds, the dualistic Cartesian claim that human beings have a soul, and non-human animals do not. That message may be out of favor these days, or against the current. It may surprise Darwinians, materialists, and reductionists of all sorts. At the very least, however, it calls for a deep reading of this rather courageous book. The idea of the duality of human nature (of meaning over and above mechanism, of mind over and above body, of angel over and above beast), and of the remarkable discontinuity of human nature from everything that came before, is alive and well for Kagan precisely because he has such high regard for facts. What exactly was "Descartes' error" anyway?

## BOOKS: DEVELOPMENT

## A View from Switzerland

Claude Desplan

Describing the intellectual lineage of an eminent scientist is as difficult as tracing the events that led to a major discovery. In his book, *Master Control Genes*, Walter Gehring gives a precise personal view of his own lineage and of the process that led to the discovery of the homeobox, the "Rosetta stone of developmental biology." The book is in part a textbook and in part a historical perspective. Its overview of biology in general and of developmental biology in particular emphasizes Swiss contributions over the last century.

Gehring's chronology of important steps towards understanding the genetics of development begins with Friedrich Miescher's 1871 discovery of nucleic acids, which he

called "nuclein." In letters to his uncle Wilhelm His, a famous embryologist, Miescher formulated ideas about nuclein as the hereditary material. He proposed the very interesting model that hereditary information is stored in the particular stereochemical forms of a given molecule. His contributions are slowly being rediscovered, and this book will help this revival. A century later, molecular biology has established many more principles of genetics. The molecular era of developmental biology, however, had to await the advent of recombinant DNA technology and the realization that homeotic genes were the "key to understanding development."

The author provides colorful examples of *homeosis* (the "change of something into the likeness of something else"), ranging from early discoveries of William Bateson and Edward Lewis (1) through his own findings on the molecular aspects of the homeotic genes. Gehring's mixture of scientific facts and history, with his very personal interpretations, will interest developmental biologists. In particular, his account will help them relive the very exciting time that preceded the discovery of the homeobox, which is portrayed more as a revolution that came with the development of the techniques of molecular biology than as a race between rival teams. One feels the excitement in the lab where much of this happened and sees how, in retrospect, things could have been predicted; this is science with passion. Scientists working in developmental biology will recognize the characters and interactions in this story, and will be able to follow the events that led to identifying the homeobox. Readers from other fields will enjoy this first part for its personal character and its historical perspectives.

The second part of *Master Control Genes* will reach a different audience. It is a more detailed and difficult survey of the different modes of development in a series of organisms, from worms (the "European mode of development," where lineage is critical) to mice (the "American mode of development," where who you know matters more). This survey leads to a description of research that followed the discovery of the homeobox, especially the major contributions that came out of Gehring's lab. The focus on *fushi tarazu* (*ftz*) neglects much of the work on the identification and molecular studies of other segmentation genes, but it is clear that *ftz* is a powerful paradigm. Through the descriptions of the technical advances that were used to study *ftz*, we can recognize how

much of that period's progress was achieved by adapting to higher organisms techniques developed for bacteria. Even structural studies of the homeodomain were then at the forefront of technology. Ten years later these procedures may seem routine; these chapters help explain how many of the tools of modern molecular genetics (promoter fusions, mis-expression experiments and, most importantly, enhancer traps) were developed.

The phrase "master control genes" in the book's title may irritate some developmental biologists. Gehring's description of the genesis of the experiment "redesigning the body plan of the fly," where mis-expression of the homeotic gene *Antennapedia* (*Antp*) led to the transformation of an antenna into a leg, and his conclusion from that experiment that *Antp* is "a master control gene for leg morphogenesis," may enhance their annoyance. Separated from all the hype, however, the experiment shows that homeotic genes confer identity to the cells, even if this is "only" a positional identity. Thus, the results represent a landmark, despite not providing a molecular explanation for transdetermination, which remains the holy grail for Walter Gehring.

Although *Antp* may not be the holy grail of the leg, *Pax-6* comes close to exhibiting the effects expected of a "master regulator of eye development." Gehring's account in the final chapter is surprisingly modest, considering that the ability to induce ectopic eyes in *Drosophila* by mis-expressing the *Pax-6* gene from any species still remains one of the most striking experiments in biology. Whether *Pax-6* is the "master gene," or is only a critical regulator sitting near the top of a hierarchy of genes, its potency and its conservation demonstrate its critical importance in eye morphogenesis.

*Master Control Genes* offers a vivid introduction to recent findings on how genes control development. In reading it, the layperson will also learn a great deal about the process of discovery through Gehring's particularly warm and personal perspective. Developmental biologists might not care as much about the technical descriptions, but they, too, will enjoy Gehring's accounts, which may seem like looking back at old family movies from their youth.

## Notes

1. Bateson described a large collection of homeotic variations, including transformations of antennae into legs or hind legs into hind wings (in insects), and eye into antennae in crabs. Lewis devoted most of his career to an extensive genetic analysis of the *bithorax* complex in *Drosophila*.

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The author is at the Howard Hughes Medical Institute, Box 151, The Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, USA. E-mail: desplan@rockvax.rockefeller.edu