

Artful Metaphors

etaphors matter. The way we picture things shapes our understanding of concepts. The more abstract the concepts are, or the more different from our daily-life experience, the more important are these mental images. Developmental biology is an area where this is especially relevant [1,2]. In *The Art of Genes*, Enrico Coen offers novel metaphors and uses them to present a fresh perspective on the facts and ideas of current developmental biology. The result is a jargon-free book that is a pleasure to read.

The argument starts with a critique of traditional metaphors for development: manufacturing and computers. The problem with the manufacturing is that humans or machines make goods, that is, the making is done by an outside agent, whereas organisms make themselves. Likewise, the analogy between developmental processes and running a computer program does not fit because there is hardware that exists from the beginning and is separate from and external to the execution of the program, whereas the organism builds itself as it progresses through the stages of development. Moreover, the interactions of DNA sequence "information" and the cellular "machinery" in development make it difficult to distinguish clearly between software and hardware or between program and data [3].

Instead of these technological comparisons, Coen uses human creativity as the central metaphor throughout most of his book. A painter working on a picture is not simply executing a fully detailed plan of the finished painting, copying a finished mental image onto the canvas. Instead, there is a constant interaction between what is on the canvas and the painter's mind. Every new brushstroke changes the painting, and the painter responds to this change in turn, progressively refining and elaborating what is already there. In a similar manner, development elaborates on preexisting patterns such as gradients or stripes of regulatory gene products to generate finer-scale and more specific positional signals.

Coen uses this central metaphor to explain development through an elaborate system of further metaphors, which constitute a sort of code for all the technical jargon that may make developmental biology seem impenetrable to the beginner. Transcription



factors conveying positional identity are "hidden colors"; for example, the Hox genes are represented by a series of greens from apple-green to herbgreen. The cells, represented by many "artists" contributing to the collective work, are able to interpret these hidden colors and respond by applying new colors. Signaling between cells is by "scents" to which cells can respond if they have the appropriate "sensitivities"; both again related to the hidden colors. This system is applied consistently throughout the book, providing the reader with a coherent account. Except for a few cases, the technical terms are not provided-perhaps a brief "dictionary" of metaphors would have been a helpful addition to the book to make it easier for the reader to access the more technical literature (but there is a glossary of the technical terms used).

In some instances, these metaphors take on a somewhat unusual form, for example, when the artists (cells) multiply or when Coen explains how development paints on a canvas that is expanding. At first glance, these cases may appear to stretch the painting metaphor too far to where it no longer fits properly, but Coen turns the apparent misfit into an effective didactic tool because it shows just how different developmental processes are from our day-to-day experience. The simile of the expanding canvas, while it initially may seem fanciful, makes it intuitively clear how the same processes that always operate over a distance of one or at most a few cells can first lay down what will end up as the largescale features of the body plan and then elaborate on this pattern by sequentially adding the finer details.

hroughout the book, numerous reproductions of works by Leonardo da Vinci, M. C. Escher, René Magritte, Albrecht Dürer, and Vincent van Gogh, and even cartoons by Heath Robinson, make yet more connections to art. These are by no means mere ornaments, but Coen puts them to work to convey difficult ideas in a manner that make them appear intuitive and almost self-evident. For instance, he compares the original Las Meninas by Diego Velázquez with the paintings Pablo Picasso created in response and uses these relationships to illustrate how the various types of plant leaves or the segments of an insect are variations on a common theme. The reader thus gets a grasp of the concept of serial homology without even reading the technical term!



As the story of development unfolds, the reader is also presented with the more conventional explanations of interactions among biological macromolecules based on geometry. However, even here Coen takes a fresh approach and goes beyond the classics such as the lock-and-key principle. For example, he explains that a protein molecule can "perform" a particular task in the cell, just as a bucket "holds" water: both are suitable for those specific tasks because they have the right shapes. There are also descriptions of the mechanisms of signaling and the control gene expression, which link these molecular-level explanations to the larger-scale metaphors of scents and hidden colors.

Along the way, Coen introduces examples from the classical model systems in developmental biology, much from the fruit fly Drosophila melanogaster, but also including a healthy dose of Coen's own research on flower development in the snapdragon (Anthirrinum majus). He explains how developmental geneticists use the effects of mutations to infer the normal role of genes and presents a few selected episodes from the history of recent discoveries in this field. These additional materials are included to introduce and illustrate steps in the central account of the principles of development.

The book concludes with a discussion of evolutionary aspects of development, giving a more coherent perspective on comparative information provided in earlier chapters and bringing up some additional questions, such as the origin of signaling and multicellularity and the creation of novelty by "tinkering" of evolution with existing developmental processes. Altogether, the book covers the field of developmental biology remarkably well.

n sum, the metaphor of human creativity proves remarkably helpful. It gives the book coherence and makes easily accessible even those concepts that are the most remote from our everyday life, at least for the reader who will not hesitate to plunge into a world where multiplying artists collectively paint an expanding canvas with rainbows of hidden colors. Also, because the metaphors are so obviously not what goes on in developing organisms, they do not seduce the reader into thinking that this is how development *really is*, unlike some metaphors of control by genetic programs [2].

But what sort of explanation for development do these mental images convey? The reader of the book will probably be skeptical of a perspective dominated entirely by "master control genes" [4] or of statements such as, "A defining property of metazoans is the regulatory program for development hardwired in their genomic DNA sequence" [5]. Rather, the metaphor of creativity facilitates a view in which genes have a more modest role [2] within a system of other cellular components and the context of the whole organism [6, 7]. Exploring the many interactions among the participating entities, spanning across the levels from molecules to the whole embryo, will be a challenge to the science of complexity because research will go "beyond the genomic analysis of protein and RNA components of the cell (which will soon become a thing of the past)" [7].

t the end of the book, Coen turns his central argument around and uses the parallel between human creativity and development to give an account for creativity. I believe this attempt is not nearly as successful as the core argument of the book. The reasoning from development does not seem to yield any more specific insight about the nature of human creativity than the conclusion that it is an iterative process in which an object emerges gradually through interaction with the creator's mind, rather than as the realization of a preexisting plan. However, this is the starting point upon which Coen built his central metaphor to account for development by comparison with human creativity. What makes the difference is the rich body of evidence presented to flesh out the metaphor that organisms create themselves. In contrast, there is little specific information on just how a work of art develops. That would be a different project.

The Art of Genes is an excellent introduction to developmental biology, which makes fascinating reading whether or not one is already familiar with the field. It is written in a style that makes it accessible to a wide readership, even to those without background in biology. While to the novice the book will open up a strange new world (from which we all originate), it will also give a fresh perspective to readers already familiar with the material. And definitely, I think it is required reading for all who teach introductory classes in developmental biology.

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