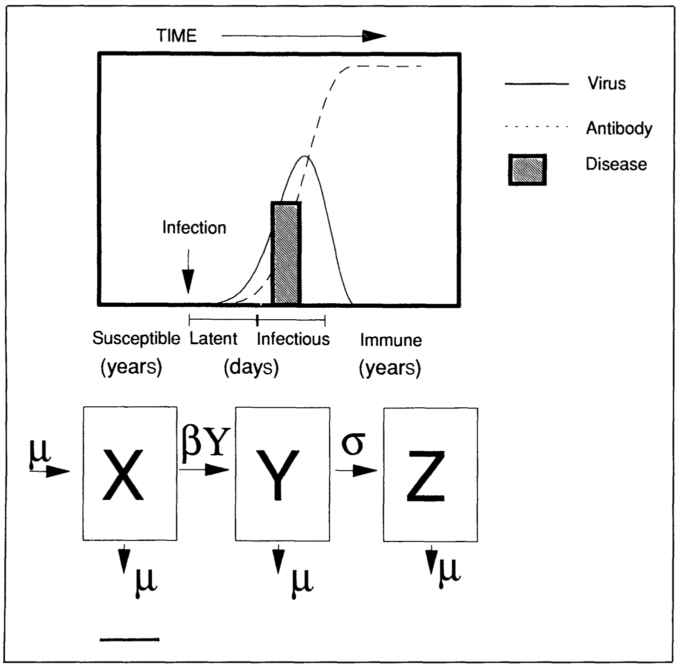
biologists who study viruses are increasingly unlikely to be colleagues in the same department. This perpetuates the training of evolutionary biologists who are ignorant of viral biology and of virologists and molecular biologists who are ignorant of evolutionary biology. *The Evolutionary Biology of Viruses* attempts to bridge the gap between these research groups by introducing virologists to basic evolutionary principles and methods as well as tweaking the interest of evolutionary biologists in viruses.

The quality of the individual contributions to the book varies from highly informative to superficial. The material on viruses is, on the whole, much better than that dealing with evolutionary biology. Several authors discuss mutation rates, generation times, and population sizes of various viruses—useful information that highlights the underlying reasons why evolution occurs so quickly among viruses (especially RNA viruses, which receive much more attention in this book than DNA viruses). Domingo and Holland document that many RNA viruses accumulate substitutions at a rate of 10^{-3} to 10^{-2} per site per year, or roughly six orders of magnitude faster than the rates typical of eukaryotic genes. Thus a gene in an RNA virus infecting a human host may accumulate as many changes in one year as a host gene would accumulate in a million years. Given the viral loads that may be present within a given host, the number of distinct genotypes present in an infected individual can be staggering. Wain-Hobson estimates that an HIV-infected individual harbors between 5×10^5 and 5×10^{10} genetically different variants of HIV, depending on the disease stage. Given that the entire genome of HIV comprises only 8×10^3 nucleotides, it is no surprise that drug-resistant strains of HIV are selected almost immediately after the onset of therapy, because most possible point mutations already exist in the population of viruses within an infected individual.



"The progress of a simple viral infection, such as measles, through a host. The growth of the virus population, the immune response to the virus, and the timing of acute disease are illustrated. *Below* these curves a flow diagram of the transmission between infection categories represented in a simple model is illustrated. In a constant population the birth and death rate per capita are equal (μ). People are born susceptible X, are infected at a rate βY and recover from the infectious category Y, at a rate σ." [From Garnett and Antia's paper in *The Evolutionary Biology of Viruses*]

In his excellent review of the evolutionary relationships of retroelements Eickbush discusses the origins of retroviruses, caulimoviruses, and hepadnaviruses and their complex relationships with retrotransposons. This chapter, along with others in the book, highlights the fact that viruses make up a class of organisms rather than a natural taxon: They have originated repeatedly from the cellular world, probably as escaped genetic elements. Neither viral taxonomists nor evolutionary biologists, however, seem to have grappled effectively with the obvious taxonomic implications of this fact. If the current hypotheses about viral origins are correct, retroviruses may all be more closely related to mammals than they are to most other viruses. It undoubtedly will upset traditionalists to think of retrovirologists as vertebrate biologists who study escaped portions of vertebrate genomes.

The book gives relatively little attention to the potential for experimental studies of evolution using viruses, although Chao does discuss experiments on the evolutionary effects of sex and the lack of sex in different viruses, and a few other natural or planned experiments are described and discussed elsewhere. Biologists are so accustomed to inferring evolutionary history and processes across millennia that many rarely consider the possibilities of directly observing large-scale evolutionary changes over months or years.

The appearance of *The Evolutionary Biology of Viruses* is especially timely, as virologists and evolutionary biologists are beginning to realize the importance and benefits of interdisciplinary interactions. The book succeeds in providing a forum for some of the work occurring at this interface, but it would have been even more successful had the chapters been planned and coordinated for better coverage of both disciplines. I suspect that some specialists will be frustrated by the relative superficiality of discussions of their own field but will find the material on other topics enlightening. The book should find a broad audience, particularly among evolutionary biologists, most of whom have much to gain from it.

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Getting into Shape

Kinetic Theory of Living Pattern. LIONEL G. HARRISON. Cambridge University Press, New York, 1993. xx, 354 pp., illus. $69.95 or £40. Developmental and Cell Biology Series, 28.

Like to a chaos, or an unlick'd bear-whelp
That carries no impression like the dam.
[Shakespeare, *Henry VI, Part 3*, 3.2.161–62]

The origin of biological form has intrigued and puzzled us for a long time. One of the earliest written speculations appears in *Historia Animalium*, in which Aristotle writes, "After parturition [the vixen] warms her young and gets them into shape by licking them." By Shakespeare's time, the view that the shapeless newborn is given its proper shape by the mother's clever tongue had taken on the power of metaphor.

How indeed do the "formless young" get their proper shape? We owe the most influential modern speculation to Alan Turing, who published a remarkable analysis of the problem in 1952. In his paper we find the first detailed and explicit model of how reacting and diffusing chemicals might interact to form standing and traveling waves of chemical activity, the peaks of which could then be used to specify the location of body parts in the young embryo. He called these chemicals morphogens. Remarkably, the mechanism envisaged by Turing can break symmetries as well, so that periodic patterns can grow from what at first glance look like uniform morphogen concentrations.

During the past decade there has been an explosion of new experimental results that go a long way toward explaining the molecular and cellular basis of morphogenesis. An extraordinary feature of this era has been the realization that all animals share a few basic mechanisms responsible for setting up the body axes. Moreover, comparative studies make it crystal clear that shape-determining gene products are highly conserved—the recent excitement over the spatial expression of the *Drosophila* gene *hedgehog*, fundamental to spatial patterning in flies, chickens, and mice, is but one stunning example. And yet, with few exceptions, this large body of work has yet to be incorporated into a dynamic model that reflects the ever-changing properties of a developing embryo; thus the dynamical aspects of Turing's insights are still largely absent from modern descriptions.

There are many reasons for this. One is the enormous complexity of any developing organism. It is still not possible, even in *Drosophila*, to list all of the molecular and cellular parts. Another is our limited knowledge of biochemical and physical detail, which has resulted in current models' being insufficiently constrained. Models we do have are also frustrating to the experimentalist because, while powerful and satisfying at a quite abstract level, they do not point the way to the next experiment, except in the most general sense. Lionel Harrison believes that there is also a "two cultures" problem, with few biologists thinking as physical scientists, who cut their teeth on kinetic theory. Biologists thus ignore the dynamical aspects of morphogenesis altogether; in Harrison's words, they confuse equilibrium and kinetic thinking. *Kinetic Theory of Living Pattern* is his attempt to introduce biologists with no background in the physical sciences to the modeling of spatial patterns in developing systems, taking full account of the kinetic aspects of the process. He takes great care, using many examples, to distinguish between equilibrium and kinetic systems and to argue that, on the whole, the evolution of structure in space and time requires kinetic models. He also adopts the reasonable view that realistic models of morphogenesis will be nonlinear, and thus an understanding of how the subunits of a developing system interact will usually be counterintuitive, with complex interactions among the many parts leading to outcomes that can only be grasped analytically.

Is there a "two cultures" problem? If we compare Harrison's book to others that discuss similar topics—those by Edelstein-Keshet, Segel, Meinhardt, and Murray come to mind—we find that the assumption has already been made by these authors that an understanding of dynamical behavior is crucial to understanding morphogenesis. This fundamental assumption is hidden from many biologists, and so in this respect I think that Harrison is right and that by discussing these central issues at length and with little recourse to mathematical reasoning in the first third of his book, he performs a real service for beginners.

In the second part, Harrison introduces the novice to reaction-diffusion (Turing) theory, which is a major, but far from the only, concern of this book. He begins with an intuitive discussion of symmetry breaking, proceeds with some simple examples of reaction-diffusion, again viewed intuitively, and then gives the minimal mathematical apparatus, showing why nonlinearity is important. He then works hard to develop some mathematical and physical intuition in the reader.

Finally, Harrison turns to real biological systems—his own favorites, *Acetabularia* and *Microstarius*, and mine, *Polysphondylium pallidum* and *Dictyostelium discoideum*, as well as *Drosophila* and vertebrates. This part of the book is excellent, both because he chooses from a broad and diverse group of single- and multi-celled organisms and because of the care with which he has read and thought about the literature. In this section, and elsewhere, there is an admirable degree of precision, and an almost compulsive desire not to sweep problems under the rug.

Kinetic Theory of Living Pattern has a very distinctive feel to it. It is the work of a teacher and scholar who does not mind revealing his (and others') prejudices, successes, and failures. Harrison writes in a discursive yet engaging manner. Those who would like a qualitative introduction to the subject should read the first third of the book; the second third is a good introduction to quantitative reasoning; the last third shows how accurately morphogenesis has been modeled, albeit at a still abstract level.

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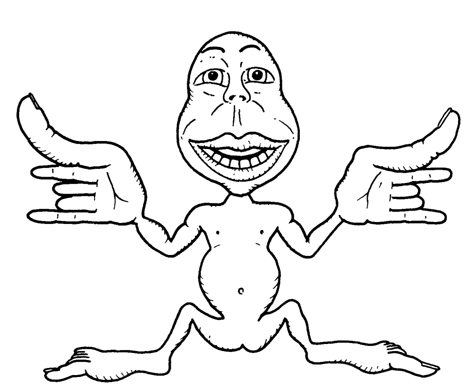
Visual Functions

A Vision of the Brain. SEMIR ZEKI. Blackwell Scientific, Cambridge, MA, 1993. xii, 366 pp., illus., + plates. Paper, $36.95.

One of the impediments to understanding vision has been that our percepts are so reliable that we underestimate the problems the brain has solved. Two modern developments ought to have humbled us. One is the limited success that computer scientists have had in designing seeing machines; the other is the recent explosion of anatomical and physiological discoveries about the organization of the visual cortex.

By the late 1960s, principally through the work of Hubel and Wiesel, we knew about the precise representation of the visual field on the primary visual cortex and about the remarkably specialized visual sensitivities of neurons within it. We also knew that there existed other representations of the visual field in regions near the primary cortex, but we understood little about what these regions did and how they were organized. The work of Semir Zeki, first by identifying multiple distinct projections of the visual field in secondary visual cortex, and then by demonstrating that the individual neurons within these areas have characteristic properties (for example, in one region that Zeki was the first to study, the neurons are especially sensitive to the movement of visual stimuli), has profoundly influenced our thinking about the scale and complexity of the task undertaken by the visual system. Indeed, no one during the last 25 years has done more to shape the research agenda of visual neuroscience.

There is now broad consensus among visual scientists on two major organizing principles in the visual system: the analysis it undertakes is modular (different aspects of an image are analyzed separately) and hier-



"The amount of cortex that the brain devotes to different parts of the body is in direct proportion to their relative importance. In the motor cortex, for example, relatively more space is devoted to the fingers and the lips than to the shoulder or the elbow, producing a sort of deformed map of the body. A map such as the one shown is often called an homunculus." [From *A Vision of the Brain*]