esis. 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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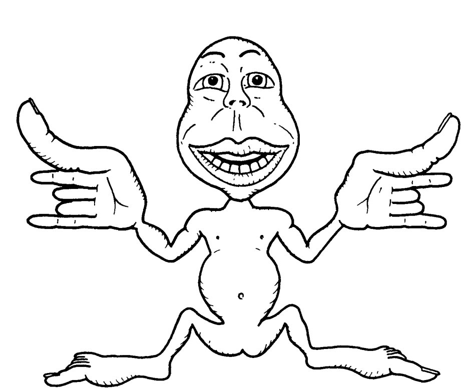
Visual Functions

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.

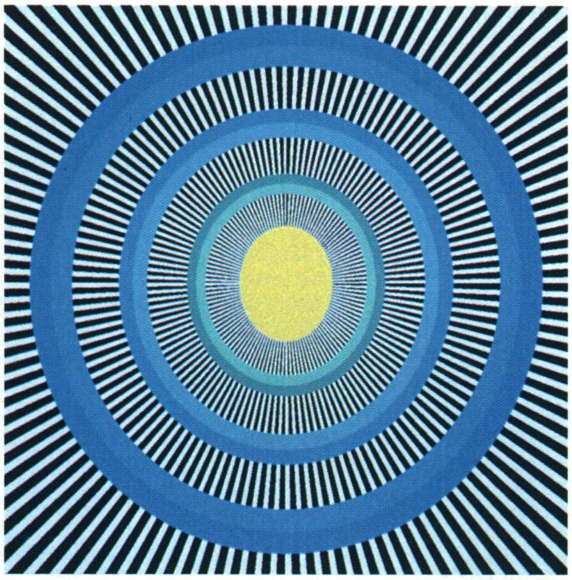
By the late 1960s, principally through the work of Hubel and Wiesel, we knew about the precise representation of the visual field on the primary visual cortex and about the remarkably specialized visual sensitivities of neurons within it. We also knew that there existed other representations of the visual 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-

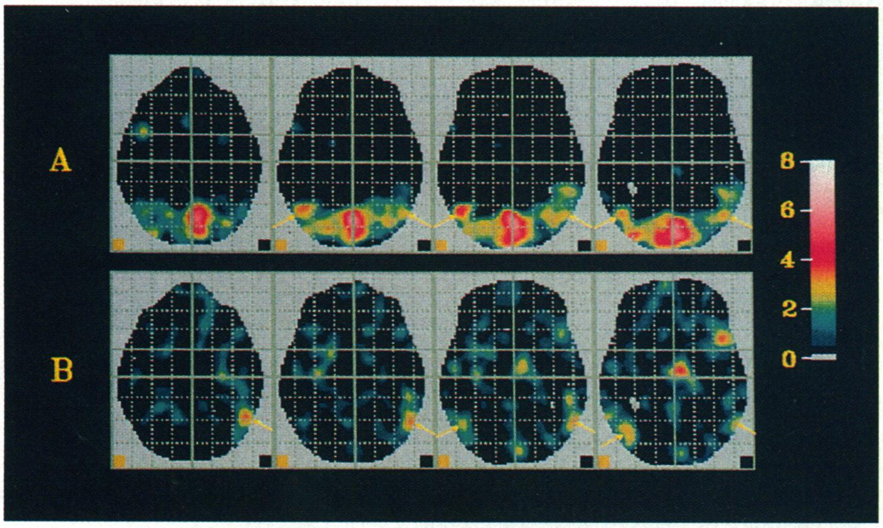


"The amount of cortex that the brain devotes to different parts of the body is in direct proportion to their relative importance. In the motor cortex, for example, relatively more space is devoted to the fingers and the lips than to the shoulder or the elbow, producing a sort of deformed map of the body. A map such as the one shown is often called an homunculus." [From *A Vision of the Brain*] archical (the analysis proceeds through distinct stages). The modularity is evident early in the visual pathway but has been most vigorously studied where it is expressed most obviously, in the multiple visual maps found in the cortex (in the macaque monkey more than 20 have now been identified, occupying an astonishing half of the cortical surface area). There is less agreement about the kinds of analyses undertaken in the different areas and about how the results of the analyses are brought together (if they are) to yield unified visual percepts. Part of the difficulty in understanding what is going on is that we are weak on theory—it is not at all obvious how a well-designed visual system *ought* to break up the task for analysis—but another problem is that the technique on which neurophysiologists most depend, recording the activity of single neurons while an animal is presented with a visual stimulus or makes some visual judgment, does not easily yield information about the larger-scale organization of the system. A book that promises a clear view of the workings of the visual system and introduces us to new ways of exploring its larger-scale functional organization is therefore doubly welcome.

Zeki has been a vigorous proponent of the view that the different visual areas have highly specialized functions; he is particularly associated with the position that one of these areas is the seat of color vision. It is therefore no surprise that much of the early part of *A Vision of the Brain* explores the rather checkered history of the idea that different perceptual and cognitive functions depend on different parts of the cortex. The history is exciting, yet in recounting the debate Zeki diminishes many of the figures involved by portraying the debates as propelled by animus, with little regard for experimental or clinical observation. But that is history, and we are assured that modern thinking about the organization of the cerebral cortex is more reliably founded on observation. The evidence has indeed convinced nearly everyone in the field that different visual cortical areas have specialized functions, but few are confident that they understand the nature of the specialization—for example, do different areas analyze different sorts of information available in the image, or do they provide different kinds of analysis of fundamentally the same information? Zeki has been a firm advocate of the position that different cortical areas analyze different sorts of information, so the reader might anticipate a persuasive account of evidence for specialized centers as well as an exploration of the attendant problem of how the results of different specialized analyses are brought together to yield unified percepts.



(a)



(b)

"When most human subjects view the figure shown in (a) (entitled *Enigma* and executed by Isia Leviant) and fixate the centre, they perceive movement in the circles. Positron emission tomographic studies (b) show that this perception is correlated with increased activity in a region of the prestriate visual cortex corresponding largely to area V5 and its immediate vicinity (regions of highest activity shown in white and red). In (b), (A) shows horizontal slices through the averaged brain, to indicate the active regions when human subjects looked at a pattern in motion (arrows point to area V5). (B) shows the regions of the most significant blood flow changes (arrows) when the same human subjects looked at *Enigma*." [From *A Vision of the Brain*]

Two cortical regions receive special attention, one a possible color center, the other a possible motion center. The idea of a color center has great appeal, not least because color is an attribute of objects that we can easily abstract and can imagine being analyzed in isolation (we are all familiar with black-and-white movies). Nevertheless, the evidence for a color center, either in the monkey brain or in the human brain, is at best equivocal. One would not guess this from reading *A Vision of the Brain*. An equally strong embrace of a "motion center" in the human brain compounds the serious reader's discomfort. On the most difficult question of how the results of these specialized analyses are brought together, Zeki draws attention to properties of neurons (and their interconnections) that might be important for integration but does not bring us much closer to understanding how the problem is solved.

If Zeki's account leaves the serious student of vision uncomfortable, what of its value for the interested nonspecialist, to whom the book is also directed? Here I think it succeeds. The major sensory systems share a remarkably similar organization, and the visual system, though not the vehicle for discovery of all the fundamental principles, is exemplary. Because of its size and accessibility we know more about it than we do about the other systems, and Zeki's account of its organization conveys, in characteristically vigorous prose, much of what makes systems neuroscience exciting.

A Vision of the Brain is a gorgeously produced book, with enviably lavish illustrations. For the nonspecialist it conveys the flavor of systems neuroscience admirably. The serious student of vision will enjoy it less, not because it simplifies complicated problems, or because it states an extreme view boldly, but because it offers a contumelious assessment of work in the field.

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