

BOOK REVIEWS

Action Potentials Reconsidered

Spikes. Exploring the Neural Code. FRED RIEKE, DAVID WARLAND, ROB DE RUYTER VAN STEVENINCK, and WILLIAM BIALEK. MIT Press, Cambridge, MA, 1996. xviii, 395 pp., illus. \$45 or £38.50. ISBN 0-262-18174-6. Computational Neuroscience. A Bradford Book.

About 70 years ago, the physiologist E. D. Adrian reported his observations on the response of single muscle stretch receptors to a fixed load. He found that the number of action potentials (spikes) recorded during 10 seconds increased as the load on the receptor increased. Subsequent observations confirmed that in a very wide variety of sensory systems the spike rate increased with stimulus intensity. These now-classic observations laid the foundations for what has become the standard model of the neural code in modern neuroscience. Rate coding, as it is sometimes called, is the notion that the average rate encodes the "message" in a neuronal spike train and that this message can be "decoded" by simply counting the number of spikes in some long time window.

Spikes: Exploring the Neural Code challenges the standard model. The epilogue, "Homage to the single spike," neatly summarizes the book's theme: "Individual spikes are important." It continues, "The individual spike, so often averaged in with its neighbors, deserves more respect." As we arrive at this epilogue after almost 300 pages of thoughtful arguments, we are compelled to agree.

One of the main arguments is that neuroscientists have emphasized neuronal responses to stimuli devoid of interesting temporal structure. Adrian, for example, studied the responses to prolonged (seconds long) muscle stretch; yet the stretch imposed by a frog's jump is orders of magnitude briefer. Behaviorally relevant decisions must often be made very quickly, leaving time for just one or two spikes. Thus though it makes sense to speak of an "average" spike rate during a one-second response, we need to think carefully about what "average" rate means when the average is over so few spikes.

The authors muster a wealth of experimental data to support their challenge and develop the theoretical and mathe-

matical tools required to appreciate it. The book is a joy to read, as both the theoretical and the experimental results are presented with respect, precision, and clarity. The first chapter briefly summarizes the history of neural coding, through the seminal work of Adrian through the present. The second chapter lays out the mathematical foundations for characterizing neuronal responses. Chapters 3 and 4 form the core of the book. Chapter 3 shows how information-theoretic techniques can be used to quantify rigorously how much information a spike train from a sensory neuron conveys about the stimulus. Chapter 4 argues that the nervous system operates near the physical limits imposed by noise in the sensory input. The fifth and final chapter proposes future directions in which work on the neural code will (or should) proceed and is followed by a nearly-100-page mathematical appendix.

The authors of the book are all physicists by training, so it is no surprise that the text is very mathematical, written in the dialect of mathematics favored by physicists (rather than, for example, by signal processing engineers). All the arguments are carefully developed, and the book should be completely accessible (albeit with a bit of work) to anyone who has had an undergraduate-level training in physics, engineering, or mathematics. The approach and the conclusions are of such importance, however, that it will be read by a much wider audience of motivated neuroscientists—anyone interested in issues of neural coding—even some readers will be unable to follow some of the arguments in detail.

The only criticism to be made of this book is that we are left wanting more. The book provides such a compelling framework for understanding sensory processing in single neurons that one would like to see how far it can be extended. We would ask for more about the techniques required to analyze data from simultaneous recordings of dozens or hundreds of neurons (there is only a brief section devoted to this); about the computations that occur beyond the earliest stages of sensory processing; and about the output (motor) end of the brain. Let us hope for an encore.

This book will undoubtedly become a classic. The ideas presented in it have al-

ready begun (in no small part through the work of the authors) to reshape our views of the neural code. This book will make them accessible to a much wider audience.

Anthony Zador
Salk Institute for Biological Sciences,
La Jolla, CA 92037, USA

Development and Diversity

Cells, Embryos, and Evolution. Toward a Cellular and Developmental Understanding of Phenotypic Variation and Evolutionary Adaptability. JOHN GERHART and MARC KIRSCHNER. Blackwell Science, Cambridge, MA, 1997. xiv, 642 pp., illus., + plates. Paper, \$69.95 or £29.50. ISBN 0-86542-574-4.

New paradigms in science set the stage for major advances in research and understanding. Such a change occurred when homeoboxes were discovered in the middle of the 1980s and similar sequences, and genes, were rapidly identified in many animal species. Developmental biologists gradually came to realize that molecular mechanisms for fundamental biological events must have predated the major burst of multicellular diversity in the Cambrian era. Although the implications of this paradigm shift have been building for the last 15 years and a few books have already appeared that make it the central theme, Gerhart and Kirschner's *Cells, Embryos, and Evolution* is remarkable for breaking new ground. More than 10 years ago, as the authors were attempting to write a modern book on developmental biology, new discoveries were continually pointing to the amazing conservation



"A marine flatworm, *Pseudoceros ferrugineus*, Coral Bay, Australia. Phylum Platyhelminthes. Triploblastic, bilateral symmetry, a blind gut, light sensitive eye spots, a ladder-like nervous system, and no coelomic cavity. Development involves spiral cleavage and a 4d blastomere as the source of mesoderm. Length, 2–8 cm." [From *Cells, Embryos, and Evolution*; A. Flowers and L. Newman]