NEURONAL MODELING: UNDERSTANDING THE MACHINERY OF THE BRAIN

Introduction to Theoretical Neurobiology

Henry C. Tuckwell

Vol. 1: Linear Cable Theory And Dendrite Structure
Cambridge U. P., New York, 1988. 291 pp. $49.50 hc ISBN 0-521-35096-4

Vol. 2: Nonlinear and Stochastic Theories
Cambridge U. P., New York, 1988. 265 pp. $49.50 hc ISBN 0-521-35217-7

Reviewed by Idan Segev

Brain science, an explosively growing discipline, is now a science on which a wide range of questions and approaches have successfully and fruitfully converged. It is enriched with meaningful input from biochemistry, genetics, anatomy, physiology, psychology, computer science, mathematics, physics and hardware design, all with the ultimate goal of understanding how the machinery of the nervous system performs its complex and diverse functions. However, one basic question is still open: How does the "hardware," or, more appropriately, the "lifeware," of the nervous system (the synapses, the membrane channels, the dendrites) implement the information processing tasks of the brain?

This question is the fundamental motive for the different theoretical approaches that are summarized in the comprehensive two-volume work of Henry C. Tuckwell, *Introduction to Theoretical Neurobiology*. These "bottom-up" theories were developed during the last 30 years with the underlying assumption that an understanding of elementary information processing at the level of single nerve cells leads to a better understanding of how information is encoded and processed by the nervous system as a whole. The aim of these approaches is therefore to develop *realistic* models of nerve cells to understand how neurons process inputs from the different sources to produce a meaningful output. Such models would have to take into account the detailed morphology and physiology of nerve cells and the properties of the (synaptic) inputs (for example, their location, time of activation, sign and strength).

Introduction to Theoretical Neurobiology is intended for graduate students and researchers with a basic knowledge of the theory of differential equations and statistics. Following an introduction that acquaints the reader with the typical morphology and electrical properties of nerve cells as well as with the basic terminology, the two volumes emphasize analytical solutions to problems in three main topics: the input–output properties of dendrites (the major receptive area of neurons), analyzed in the framework of Wilfrid Rall's linear cable theory; the theory of action potential initiation and propagation, starting with the full Hodgkin–Huxley model and followed by the reduced Fitzhugh–Nagumo equations and the corresponding analytical analysis; and stochastic models of nerve cell activity.

My main criticism of the two volumes is that they place too much emphasis on formal proofs and devote insufficient effort to developing an intuitive understanding of the problem at hand and to explaining the predictive power (and limitations) of the different models for the corresponding experimental systems. Also, some of the theoretical results are overstated, leading to oversimplified conclusions when applied to real neuronal systems. For example, Chapter 5, which deals with time-dependent cable theory, concludes with a section entitled "Role of Dendrites" which states that (for the class of dendritic trees that can be represented as an equivalent cylinder) "no input is discriminated by virtue of its position on the dendritic tree except with regard to electrotonic distance from the origin. Branching does not serve to attenuate, only to create, the possibility of a greater number of inputs (synapses) at a given distance from the soma." A major qualification should have been made immediately since this conclusion is valid only for the linear case (current input) and not for real synaptic inputs (conductance change).

The two volumes are clearly written and self-contained. They bring together for the first time several important approaches to the quantitative exploration of the dynamic behavior of nerve cells. One approach introduces stochastic differential equations and applies Poisson and renewal processes to the analysis of spike-train activity. It will undoubtedly prove to be very useful for experimentalists who commonly describe this activity only in qualitative terms. Another useful technique that is not found in related books is the phase–plane method for analyzing excitable phenomena (threshold and traveling waves as well as repetitive activity) in nerve cells. Its application will clearly help experimentalists and modelers to better understand the behavior of their research system.

To conclude, this book is an up-to-date, comprehensive effort that encompasses the major analytical approaches to neuronal modeling at the cellular level. Two related books have by now become classics in the field: *Membranes, Ions and Impulses* (University of Califorinia Press, Berkeley, 1968) by Kenneth S. Cole and *Electric Current Flow in Excit-*

Idan Segev is Lecturer in Neurobiology at the Institute of Life Science, Hebrew University of Jerusalem. In his chosen research area, computational neuroscience, he combines theoretical and experimental tools to study the processing of synaptic information in nerve cell.

able Cells (Clarendon Press, Oxford, 1975) by Julian Jack, Denis Noble and Richard Tsien. Along with these two books *Introduction to Theoretical Neurobiology* should be on the bookshelf (or beside the bed) of every student and researcher interested in neuronal modeling.

Elements of Differentiable Dynamics and Bifurcation Theory

David Ruelle
Academic, San Diego, Calif., 1989. 187 pp. $27.50 hc ISBN 0-12-601710-7

David Ruelle's book is a gem. For the last few weeks my desk has been covered with books on chaos, bifurcation, dynamical systems—and a request from PHYSICS TODAY to review several of them. Ruelle's book is so far superior to the others that any of them, reviewed alongside, would by contrast appear unsatisfactory.

Several colleagues perusing these books put down Ruelle's book after a cursory look, saying "Too sophisticated for me." Yes, one may need to read it slowly; yes, one may find in another book an example that explains an abstract statement. But as one savors each paragraph of Ruelle's book, one acquires the tools for studying differentiable dynamical systems, which then enables one to extract the highlights from the other books. As the author says, "The serious reader . . . should . . . be better equipped to enter the treacherous jungle of the literature on chaos."

This monograph is all that it intends to be: "An introduction to differentiable dynamics with emphasis on bifurcation theory and hyperbolicity, as needed for the understanding of complicated time evolutions occurring in nature (turbulence and 'chaos')." This is one of the rare books that does what its preface promises.

▷ *Coverage.* The first part of the book contains definitions of manifolds and differentiable dynamical systems; fixed points, periodic orbits and their invariant manifolds; attractors, bifurcations and generic properties. The second part is centered on bifurcations: elementary bifurcations for a fixed point or for a periodic orbit of a map, and related bifurcations for semiflows. It includes a study of hyperbolic invariant sets with applications to homoclinic intersections. Appendices and references constitute the third part.

▷ *Readership.* The author says the book is intended for "mathematicians or mathematically inclined students of the natural sciences." I recommend it also to any theoretical physicist interested in dynamical systems. If one is not familiar with the mathematical language in Ruelle's book, one can refer to a more elementary book. His presentation, which may have seemed too abstract at first, will then reveal its perfection—and will clarify the confusion of discussions in other references that may have seemed more attractive at first sight.

▷ *Style.* Ruelle does not take one for an easy ride or a passive admiration of the scenery. He guides one on a mountain climb. And when the going gets rough, when one wonders at the need for so much intellectual discipline, or when the material seems dry, he offers "Notes" that relieve the thirst of the tired reader ("Note that the spirit of the above proof is the following . . . "). In his words, "In order to get to the heart of the matter quickly I emphasize ideas rather than proofs."

▷ *Price.* The price of $27.50 for 187 pages is high. I am unhappy with publishers who price their books high when they expect a small market. This strategy is a self-fulfilling prophecy. Betting on a large market for Ruelle's book would be a negligible gamble. However, even at the present price, if one rates this book not in dollars per page but in dollars per unit of substance, Ruelle's book is a bargain.

CÉCILE DEWITT-MORETTE
University of Texas at Austin

Proteins: A Theoretical Perspective of Dynamics, Structure and Thermodynamics

C. L. Brooks III, M. Karplus and B. Montgomery Pettitt
Wiley, New York, 1988. 259 pp. $55.00 hc ISBN 0-471-62801-8

Many of us went into physics because it advertises itself as a discipline that unifies and codifies a large body of seemingly incoherent data into a highly predictive, satisfying and consistent set of rules. What then are we to make of a field such as biophysics with its enormous and low-resolution set of seemingly incoherent data? Many physicists, both theoretical and experimental, are quite proud of their total ignorance of biological systems; after all, how can anything that is good to eat be worthy of serious study? I suspect that most experimentalists understand their personal computers better than the fundamentals of the