

eliminates the tedious flipping among the different print volumes. Moreover, in our single point test, the web-staff responded quickly to our query. The authors note that this might be the last print edition of the manual as the on-line version replaces it, but we hope that future editions remain in print (albeit perhaps smaller). Nevertheless, with this new edition and its companion website, *MC* has once again established its primacy as the molecular laboratory manual and is likely to be found on lab benches, and book-marked on web browsers, around the world.

Stephanie Radner

Yong Li

Mary Manglapus

William J. Brunken*

Dept of Anatomy and Cellular Biology,
Tufts University School of Medicine, Boston,
MA, USA.

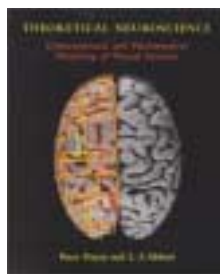
*bill.brunken@tufts.edu

Uniting the confederation

Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems

by Peter Dayan and L.F. Abbott, MIT Press,
2001. US\$50.00/£34.50 (576 pages)
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The natural function of the wing is to soar upwards and carry that which is heavy up to the place where dwells the race of gods. Plato, *Phaedrus*



As science continues to peel back layers of structure in the natural world and reduce it to collections of comprehensible pieces, we are often left wondering why

we didn't see the 'real' answer sooner. It seems that many parts of nature are arranged just to fool us – or more precisely, to fool our hard-won, but ingrained, habits of thought. For me, one of the more vexing examples is the flight of birds. Like me, my ancestors watched birds soar, swoop and land with unsurpassed grace, and the central players in such performances were

the wings. Flapping, tilting, adjusting and so forth...surely all this activity was the source of the magical capacity to fly? Now the trick – the birds fooled us. The wings played at least two crucial roles: thrust and lift; engine and wing. There is not a simple equation that reads 'wings = flight'; instead, the wings and their movement implemented thrust, lift, trim and innumerable reactive control functions. We were misled. The amazing feature, flight, is the result of multiple functions that are carried out by the wings and controlled by the nervous system. Movies have chronicled the erstwhile attempts of adventurous souls who try to flap their way heavenward; the strategies were different, but many of them seemed to have focused on the flapping. Now I really can't blame them, as flapping is the most conspicuous feature. But there is a lesson here – the obvious answer is not always the truth. Indeed, the obvious answer can hide the truth.

As we rush headlong into the 21st century, many fields in neuroscience offer their own analog to the flapping problem. In most of these areas, we generally don't know how to put the pieces together again. This need for synthesis is one of the grand challenges faced by the current generation of neuroscientists. To produce a truly synthetic view of brain function, it is not enough to possess only verbal descriptions of phenomena. We need detailed, quantitative descriptions and a population of scientists equipped to profit from them. This goal of quantification requires didactic syntheses of the current state of theoretical work and its connection to experimental findings. Such works play dual roles: education and inspiration. The need for education is obvious, but the need for inspiration should not be underestimated. It is crucial to motivate new students to reach farther than did the preceding generation. Earlier works such as *Ionic Channels in Excitable Membranes* [1] and *The Computational Brain* [2] were inspirational in their clear confidence that formerly complex problems of neural function could be broken down into their constituent parts and understood quantitatively. However, there has recently been a gap for a summary, didactic work that takes on the full scope of the computational problems facing neuroscience.

Theoretical Neuroscience fills an important gap in the didactic literature

for neuroscientists, both computational modelers and experimentalists. It takes its place beside its excellent first cousins *Biophysics of Computation* [3] and *Spikes* [4]. The book is divided into three major parts that can be paraphrased as (1) the problem of encoding and decoding (neural or otherwise), (2) the mechanics of computing with real-world neurons, and (3) the software problem. Before describing these sections, there is one interesting feature of the book that rides along quietly beside all the presentations and demands a comment. This feature is a kind of blurring of the normal distinction between mechanism and explanation. By mechanism, I mean mathematical phenomenology – that is, a mathematical description of neural phenomena. By explanation, I mean a set of causal descriptions that capture what a system is doing – that is, what a system is 'for'. Mathematical phenomenology is often the crucial first step toward a quantitative explanation. It provides a kind of compressed summary of a collection of observations. Causal explanations represent our current understanding of an issue. Whether by intent or happy accident, the authors move smoothly back and forth between mathematical phenomenology and explanation. One fruitful result of this blurring is that a reader is continuously made to contemplate exactly what a set of equations means. I found myself constantly asking: is this simply a description of the neural response or is there something more fundamental hiding in the formalism? In this respect, the book challenges readers at all levels.

In section I (chapters 1–4), the problem of encoding and decoding is approached in the general terms of information theory. The chapters cover encoding, methods of data description, decoding and information theory. All four chapters are strong, but the chapter on decoding is particularly good and will challenge students. These chapters could easily support a self-contained one-semester course. Each chapter ends with a summary of the material just covered followed by mathematical supplements of the techniques used or referenced in the chapter. There is also a stand-alone and broader mathematical appendix at the end of the book. End-notes for each chapter are included in the main text (not in the index) and provide a kind of quick

commentary on the history of the problems addressed in the preceding chapter, along with references. This is a very effective device and we should praise the authors for their bravery – they are almost certain to leave out some important contribution, and even more certain to hear about it. Nevertheless, the effort makes the task of the reader much easier.

Section II (chapters 5–7) covers the issue of computing with real-world neurons. Because there are many kinds of real-world neuron and many systems in which they are employed, the three chapters in this section have a vast territory to describe. Standard topics are covered including membrane properties, ionic channel models, integrate-and-fire neurons, feedforward networks and recurrent networks. One strength of this section is the way that the authors demonstrate the features of the various models. For example, they give an excellent discussion of an old topic: action-potential generation. In particular, they contrast the Hodgkin–Huxley model with the Conner–Stevens model from the early 1970s, and provide a captivating discussion of how the A-current influences the neuronal response. This section also includes some technical discussion of phase-plane analysis as it has been applied to neuronal networks. This discussion is supplemented with links to helpful software.

Section III (chapters 8–10) covers adaptation and learning from a variety of perspectives. Chapter 8 addresses the types of learning and learning rules that have been used to model synaptic change in single synapses and across populations of synapses. The authors address the way that the synaptic adaptation rules achieve

stability and the limits on the way that they store information. Spike-timing-based synaptic modification rules are also discussed along with a collection of other topics including anti-Hebbian learning, contrastive Hebbian learning, and even an introduction to the perceptron-learning rule and its convergence. The annotated bibliography at the end of chapter 8 is among the most extensive in the entire book and could easily be used to direct the topics in a course on synaptic-learning rules. Chapter 9 addresses models of classical conditioning and moves into the more general area of reinforcement learning. This chapter provides one of the best, shortest syntheses on these topics. There is already an excellent book covering the now-large area of reinforcement learning (*Reinforcement Learning* [5]), but chapter 9 captures almost all of the important applications to neuroscience in a mere 24 pages. Chapter 10, on 'Representational learning', is the most challenging chapter because the content is less-well defined as a problem. It truly addresses central software issues for the brain: how is information represented? And why should it be represented one way and not another? These questions guide the presentation in this chapter and lay out the challenges ahead. This chapter presents an excellent introduction to density estimation, data-reduction techniques (e.g. factor analysis and principle component analysis) and hierarchical data structures (for the brain). Chapter 10 also illustrates the point made earlier, that the distinction between what the brain is actually doing and a mathematical description of data is blurred. Throughout, the reader will wonder what the equations presented represent. Accordingly, the chapter title

'Representational learning' is well chosen. This chapter was by far the most interesting and forward-looking.

Computational neuroscience is now a maturing confederation of models that describes channels, membranes, neurons, synapses, networks and abstract representations. *Theoretical Neuroscience* succeeds in summarizing the large central trend of this confederation while still looking ahead to more exciting discoveries of the future. The book is extensive and well annotated, and it provides an excellent set of problems for students. The authors pass both tests laid out earlier: they educate and inspire. However, keeping the birds in mind, one hopes that action potentials aren't like the flapping of their wings – multiple functions implemented in a seemingly singular neural event. Or worse yet, they might be some kind of unavoidable exhaust emitted while all the interesting computation takes place at vastly smaller scales in the dendrites of neurons and interior of glial cells. Whatever the future yields, the even-handed presentation by Dayan and Abbot has given the community a report from the front that is greatly appreciated.

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P. Read Montague

Division of Neuroscience, Baylor College of Medicine, Houston, TX 77030, USA.
e-mail: read@bcm.tmc.edu

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