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In search of computation

Reviewed by Eve Marder

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The Biophysics of Computation

by Christof Koch
Oxford University Press, New York, 1999.
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How does the brain work? Neuroscientists and laymen alike are fascinated, perhaps obsessed, by curiosity that leads to all kinds of inquiry into this question. Humans use introspection and psychoanalysis, clone genes, make electrical recordings and write theories replete with complex mathematical formulae, all in search of understanding the brain. Hidden beneath these varied endeavors is the assumption that we will recognize the answers to our question, and that these answers will be in the language that we use to formulate our particular and individual searches for the truth. Nonetheless, we are all cognizant of our ignorance of fields other than our own. In the face of this ignorance, some are wistful, some are arrogant,

and some search to synthesize conceptual frameworks of two or more fields, and in so doing become translators. Christof Koch's new book is, above all, an exercise in synthetic translation between the fields of experimental and computational neuroscience. It is Koch's attempt to place the myriad details of cellular and biophysical neuroscience in a framework that reinterprets them to theorists, and his attempt to define which findings of cellular physiology are of particular interest to those interested in how the brain computes.



The Biophysics of Computation includes full and mathematically rigorous treatments of many topics that are found conventionally in neuroscience texts, such as passive cable theory, synaptic physiology, mechanisms of synaptic plasticity, gating of ion channels and mechanisms of action potential initiation and propagation. These treatments will be of use to theorists wishing to familiarize themselves with how biological neurons and synapses work. They will also be useful to neuroscience students who are looking for a deeper understanding of basic biophysical properties. An attractive feature of the book for experimental neuroscientists is that it provides unusually fine intuitive descriptions of the results of cable theory for synaptic integration. But the book also contains material not found in conventional neuroscience texts, such as descriptions of the kinds of models used to model neurons and synapses, and why each of these models is particularly useful. For example, in passing, Koch explains why alpha functions are often used to describe synaptic potentials. He presents phase-space analysis of the simplified Fitzhugh-Nagumo and Morris-Lecar models often used to analyze action potentials and bursting neurons, and discusses the computational implications of resonant subthreshold membrane oscillations. A particularly nice chapter first presents the physiological bases of synaptic plasticity and then the formal learning rules that are used in a variety of modeling studies. This is an example of the kind of 'translation' between the computational and experimental sides of neuroscience that this book aims to achieve.

Other examples of translational synthesis are found in Koch's chapter on coding, integrate-and-fire and firing-

rate models. This chapter will go a long way toward demystifying these models for biophysicists, and Koch scrupulously discusses the extent to which these models are biologically faithful and when they are most useful. The next chapter, on stochastic models of single cells, provides a particularly cogent statement of the problems posed by the apparent noisiness visible in physiologically recorded spike trains. Moreover, it defines and explains a number of terms used for data analysis of stochastic processes that are not in the usual vocabulary of most neuroscientists.

In general, Koch has done a superb job of interleaving examples from mammalian, lower vertebrate and invertebrate nervous systems throughout the book. One notable exception is the relatively weak chapter on bursting, which neglects some salient and elegant studies that combine theoretical and experimental work to understand the mechanisms of bursting in molluscan, other invertebrate and cardiac systems.

Visually, this book is a pleasure to read. Despite its equation-rich text, it is liberally sprinkled with well chosen and well designed figures. Many of these are real biological images, and others are clear theory figures that illustrate simply the points the author wishes to make. Headings are pithy and frequent, and the chapters are relatively short. Consequently, it is relatively easy to flip around and find the sections relevant to one's interest. Moreover, each chapter has a 'recapitulation' of one or two pages that summarizes its salient points. Koch's style is captivatingly casual and extremely clear. The informality of the style communicates the excitement, mystery and challenge of the field. The last chapter ends with Koch's idiosyncratic suggestions for thesis topics, presented to illustrate some of the very many fundamental problems waiting to be tackled.

This book should be read by all aspiring computational neuroscientists. It will help physicists, computer scientists, engineers and mathematicians understand how nervous systems work. It should also be read by experimental neuroscientists who are somewhat befuddled by the kinds of problems that many computational neuroscientists find interesting. The perspective found here is just enough different from

that of conventional cellular neuroscience to make this book fascinating. For those biologists with less mathematical training, the book can be read around the equations, and will still provide intuition both into the nervous system and into why computational neuroscientists often fixate, somewhat seemingly inexplicably, on certain features of biological data.

In the 'bad old days' when neural networks dominated the field of computational and theoretical neuroscience, experimentalists were often accused by theorists of filling the literature with reams of boring biological details that obscured the 'big picture'. In contrast, in this book, Koch shows deep respect for the biological literature. This is seen eloquently in the chapter on unconventional computing, which introduces the kinds of computation made possible by macromolecular switches, gases, extracellular space and neuropeptides. This respect will ensure that the book will have credibility with its biological audience. Equally importantly, the respect and appreciation that Koch shows for the biological literature teaches young theorists that the aim is to understand the deep mysteries of how the brain computes, not deny them.



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