the photo-transduction cascade are especially useful. In addition, the author's love of morphology and of the retina can be savored through his fabulous original illustrations. The descriptions of these illustrations are woven into the text so that each drawing or diagram can be appreciated as the story is read. Finally, the topical chapters at the end of the text provide useful information on the biochemical cascades, as well as quantitative descriptions that involve radiometry and photometry.

Those readers, however, who are looking for a classroom textbook on vision will be disappointed. The book is idiosyncratic in its selection of topics, coverage, emphasis, and perspective. For example, although the dynamic nature of vision is emphasized and the importance of vestibular and other extra-retinal signals is discussed, no mention is made about the well-known brainstem circuitry or cortical brain areas (for example, the middle temporal visual area or frontal eye fields) that control saccadic eye movements. Instead, the book digresses to the tangentially related topic of directionally selective rabbit retinal ganglion cells. In fairness to the author, the former issues are really beyond the first steps in seeing. Although other central brain areas, such as the primary visual cortex, are mentioned, no details are provided about dynamic organization of this area or the existence of other important visual cortical areas to which the primary visual cortex connects. Overall, the rationale for selection of topics to be included in the book is unclear. Even at the level of the retina, coverage is uneven and many important topics are either not discussed or current views are not included. For example, important aspects of retinal adaptation are not considered, and the views of ganglion-cell physiology and receptive-field function are dated. Most issues are explained as if the ideas presented were established facts, rather than simply a favored perspective. The chapters 'Looking' and 'Seeing' are especially disappointing as one never learns much about how visual signals are processed. The serious reader will be frustrated by the lack of references; citations are mostly relegated to the very end of the book under 'Notes'. Side bars discuss the Latin or Greek origins of words used, but mention nothing about leading figures in the field or alternative hypotheses for the views discussed. Unorthodox exposition of familiar information also is confusing: for example, the use of frequency instead of wavelength to represent the visible spectrum. Topics such as ganglion-cell classes and organization of the lateral geniculate nucleus, among others, are presented in dogmatic frameworks, which miss the ongoing debates that characterize current understanding. The epilogue entitled 'Ignorance' is limited and inappropriate, given that some of the ideas mentioned are not covered adequately earlier in the book.

In summary, this is a beautifully illustrated work that provides a detailed overview of the photochemistry and morphology of the retina. Although the coverage is somewhat uneven and emphasizes structure over function, what is covered is presented in a readable, interesting and informative style. I would recommend this book to scientists and lay persons alike with an interest in the organization and the anatomy of the primate retina.

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Reference
1 **Walls, G.L.** (1967) *The Vertebrate Eye and Its Adaptive Radiation*, Hafner

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Biophysics of Computation: Information Processing in Single Neurons

by Christof Koch, Oxford University Press, 1998. £59.95 (xxiii + 562 pages) ISBN 0 19 510491 9

Marr and Poggio have proposed that for any computational machine there are three levels at which processing must be understood: computation, algorithm and implementation[1,2]. At the top level, computational theory formally characterizes the problem to be solved. At the bottom level is the question of implementation: for the brain this means the neuronal 'wetware' that perform the computation, including neuron biophysics and circuits, synapses, etc.

The link between these two levels is given by the algorithms used to compute the solution. As this level is only constrained by fundamental principles indirectly, the rules that focus the choice and determination of an algorithm are, in a sense, an emergent property from both top-down (for example, computational theory) and bottom-up (for example, element physics) considerations. As a result, finding the appropriate algorithms for information processing (useful, in the case of machine processing, correct, in the case of brain) requires an understanding of the formal nature of the computation, as well as the details of the hardware.

In neuroscience, the relationship between observation and interpretation is explicitly emphasized in what has come to be called 'computational' neuroscience[3]. For example, using this approach, the modeling of specific and defined biophysical mechanisms provides the conceptual basis for data interpretation.

There has been a huge increase in quantitative data in neuroscience and, increasingly, these data are gathered in the context of explicit mechanistic theories. The constraints imposed by complex system behavior underlie one axiom of computational neuroscience: explicit modeling to test these theories is not only important, it is necessary, despite the dubious reputation of computer models. As someone said, 'Give me four parameters, and I will build you a dog. Give me one more, and I can make its tail wag.' In other words, so what?

In his ambitious new text, Christof Koch demonstrates convincingly that 'so what?' can be countered by the fact that the constraints imposed by data mean that neuron models can (and should) demonstrate more than simply tail wagging by virtue of many parameters. While it is fair to say that the literature includes a surfeit of ill-posed computer simulations, fortunately the quality of this research is improving markedly. *Biophysics of Computation* will reinforce that welcome trend.

Koch combines two strategies: he covers a great deal of what is known about neuron biophysics (and anatomy, at least at the single-cell level), in all cases indicating potential computational relevance; and he also covers a wide variety of computational questions, always choosing those that are tightly coupled to experiments. Koch presents what can be now considered to be 'classical' computational neuroscience, for example, kinetic models of axon excitability and the work of Hodgkin and Huxley, or linear cable theory and the work of Rall. He also provides a comprehensive survey of current work, for example, the functional consequences of non-linear synaptic integration, stochastic properties of channels and spike trains, and intracellular diffusion of second messengers. Finally, he throws in a few tidbits of nascent research, for example, in the chapter 'Unconventional Computing', including the molecular basis for memory and the consequences of the very crowded extracellular space in the brain. It will be interesting to see which of the subjects presented here will make it into the conventional computing category.

Discussion of so-called 'neuromorphic' systems (integrated circuit technology that emulates certain biological neuronal properties) is spared, justifiably so in my mind, as the usefulness of this approach to brain theory is unclear. With respect to neural-network theory, which, conversely, might very well provide productive strategies for brain theory, the chapters 'Synaptic Plasticity' and 'Simplified Models of Individual Neurons' provide an appropriate liaison between the biophysical and connectionist worlds.

Several excellent neuroscience texts with a strong quantitative emphasis have been published recently (see, for example, Refs 4,5). Nevertheless, *Biophysics of Computation* is unique: it reflects the computation–algorithm–implementation trinity explicitly, thus illustrating the fundamental interdisciplinary nature of computational neuroscience, and is certainly written for the growing number of researchers who are trying to straddle both its theoretical and experimental domains. In general, the level is appropriate for senior-level undergraduates, as well as seasoned veterans. While the math could daunt pure experimentalists and the biology might daunt pure theoreticians, there is plenty of familiar territory in each to inspire one side to understand (and collaborate with) the other. At various points Koch draws a parallel between neuronal characteristics and silicon computing technology, which will especially appeal to the intuitions of readers who come from more of an engineering background.

There is an enormous difficulty in crafting a linear narrative for this subject: one cannot simply proceed, for example, from molecules to circuits without encountering numerous loops. As a result there is some repetition in the text, but overall Koch has organized the material in an excellent manner. In some places the presentation of technical concepts is not as tight as it could be, which could lead to some head scratching for the tyro. However, Koch is careful to add citations to more-primary sources throughout; the result is that he absolutely succeeds in first convincing the reader that the research questions are intriguing, worthwhile and have a reasonable chance of being ultimately important, and where more information may be found. The rich bibliography (I estimate on the order of 1200 citations!) attests to this strength.

Computational neuroscience has succeeded: it has earned a place under the neuroscience umbrella. *Biophysics of Computation* is this field's first bona fide textbook, at least with respect to the cellular components that underlie brain function. The quality of this contribution augurs well for the future of the field.

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References

1 **Marr, D.** (1982) *Vision*, W.H. Freeman
2 **Poggio, T.** (1983) in *Physical and Biological Processing of Images* (Braddick, O.J. and Sleigh, A.C., eds), pp. 128–153, Springer-Verlag
3 **Churchland, P.S. and Sejnowski, T.J.** (1992) *The Computational Brain*, MIT Press
4 **Johnston, D. and Wu, S.M-S.** (1995) *Foundations of Cellular Neurophysiology*, MIT Press
5 **Weiss, T.F.** (1996) *Cellular Biophysics* (Vols 1 and 2), MIT Press

Methods in Neuronal Modeling (2nd edn)

edited by Christof Koch and Idan Segev, The MIT Press, 1998. £47.95 (xiii + 671 pages)
ISBN 0 262 11231 0

Methods in Neuronal Modeling concentrates on the type of modeling approach formulated by Wilfred Rall in the 1960s to simulate a single neuron behavior on a computer by slicing the neuron's continuous membrane into compartments. The substantial difference between this edition and the first edition is reflected by the inclusion of seven completely new chapters, while five of the original chapters have been omitted. In comparison with the first edition, detailed circuit simulations using SPICE have been replaced with MATLAB, GENESIS and NEURON software, with an appendix by M. Hines. A particularly welcomed feature of this book is that the authors have been motivated to provide interactive tutorials and simulation programs to be found on the Internet.

The first chapter focuses on the kinetics of synaptic transmission; however, an introductory chapter that briefed the reader on the book's content and the rationale for each chapter might have been a more sensible starting point. The discussion of linear cable theory as a stepping stone to the compartmental approach includes a new section on boundary conditions, the morphoelectrotonic transform and the method of moments, which is appropriate for passive dendrites, although it is not clear how these methods can be extended to explore spatio–temporal integration properties in active dendrites. While this section does provide a reasonable introduction to related issues to be further developed in the rest of the book, it would have been interesting if some complementary approaches, such as tapered dendritic representations, and the equivalent cables, which are based on the Lanczos method, had been included.

One of the limitations of the compartmental model, the discussion of which forms the cornerstone of this book, is that it suffers from too many degrees of freedom and in most instances requires an 'educated guess' for the many unknown parameters required to model the neuron with sufficient accuracy. Another limitation that is not addressed but is clearly evident from Fig. 3.3, is structural realism or the lack of it. Without the angles between individual branch segments, compartmental models leave a one-dimensional caricature of the neurons, which, though suitable for the compartmental approaches covered in the book, is not enough for accurately investigating alternative effects, such as potential field interactions, spatial coverage and mapping of receptive fields.

The book also includes the membrane biophysics of a space-clamped neuron but this topic remains largely similar to that discussed in the first edition with some additional references. It would have been more useful to include this at the beginning of the book or to combine it with the chapter on Ca^{2+} dynamics in single neurons. As little is known about Ca^{2+} channels and their dynamic properties, these two subjects represent some of the most interesting and important contributions to the whole book.

The use of the compartmental model to simulate pyramidal neurons with active dendritic ion channels is dealt with in Chapter 5. This is a 'hot' topic in neuroscience but is covered relatively scantily using a meager four equations. Although the authors continue to argue that a method must be sought for constraining the parameters by matching simulations to experimental recordings, and then proceed to propose a trial-and-error approach, it would have been more interesting to use data on conduction velocities that are now available through optical recording and the application of a pharmacological agent to determine the optimum density of specific ion channels on the basis of Hodgkin's approach to Na^+ channels[1].

'Analysis of the Neural Excitability and Oscillations' is left relatively untouched from the first edition, although there is an expanded section on bursting, that focuses on a hybrid between the FitzHugh–Nagumo and Hodgkin–Huxley models known as the Morris–Lecar model. This chapter seems to set the pace for biologically realistic neural networks as 'point' neurons that reinforce the idea of computational neuroscience complementing the vast literature on artificial neural networks and, hence, biological cybernetics. Indeed, a completely new chapter is devoted to the possibility of using very large-scale integration (VLSI) technology for implementing more-realistic silicon neurons that incorporate various biophysical features, based on the Hodgkin–Huxley model and complementary metal oxide silicon VLSI technology.

The book also provides a reasonable survey on the modern and relevant issue of neural spike-train analysis. After motivating the subject in terms of the temporal coding