of notation. For someone like me, reading (all right, *skimming*) the book from cover to cover, this deficiency is ameliorated by Brualdi's very patient repetition of main definitions (from Chapters 1–2) at the beginnings of sections where they are actually used. Someone like my straw mathematician, on the other hand, will scan the index in vain for such key search words and phrases as *conjugate partition*, *degree sequence*, *elementary* doubly stochastic matrix, *simplex*, and *total support*. And, while words like *contraction* and *symmetric interchange* appear (under matrix and interchange, respectively), they are not always to be found where one first looks.

A very minor quibble, having nothing to do with the straw mathematician, is that references are given by number according to a list at the chapter's end. As a practical matter, it is much easier to find, e.g., Brualdi and Ryser (1991) in the bibliography than references to the same book as [4] in Chapter 1, [5] in Chapter 2, [13] in Chapter 3, [19] in Chapter 4, and so on. For one thing, it is generally easier to find a bibliography at the end of a book than a list of references at the end of a chapter. For another, Brualdi and Ryser (1991) is identifiable wherever it may appear, whereas [4], [5], [13], [19], and so on, are less useful.

Nearing the end of its career, a swan, if ancient beliefs are credible, sings a song of exceptional grace and beauty. Moderns have adapted that image to refer to the final lasting achievement, e.g., of a composer, performer, civilization, or culture. Apart from his still youthful vigor, the most compelling reason not to think of this wonderful book as Richard Brualdi's swan song is the possibility, gleaned from a hopeful reading between the lines of its preface, that this may be, not the last, but the second volume in a to-be-continued series.

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Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting. *By Eugene M. Izhikevich*. MIT Press, Cambridge, MA, 2007. $60.00. xvi+441 pp., hardcover. ISBN 978-0-262-09043-8.

Neurons are the cells that form the basic structural unit of the nervous system. There are roughly 10^{11} neurons in the human brain, and these have a variety of shapes, sizes, and electrophysiological properties. Neurons receive inputs from other neurons via chemical and electrical synapses, and can respond by generating an action potential, or a spike, which is then communicated to other neurons. Ultimately, the interaction of neurons through such action potentials allows each of us to (1) receive sensory information from inside or outside our body, such as seeing the letters on this page; (2) interpret this information, such as recognizing visual stimuli as words, understanding the concepts the words convey, and relating these to concepts you have learned or remember; and (3) initiate motor responses if necessary, such as turning to the next page when you're done reading this page, or to the next book review if you lose interest in reading this one.

Neurons are also dynamical systems: there is a set of variables that describe the state of a neuron, and a rule that describes how these variables evolve. (Well, it may not always be clear what all of the relevant variables are, or what the precise rule is—more on this later.) The most influential model of the dynamics of a neuron is the Hodgkin–Huxley equations [1], which in space clamped form (i.e., without spatial dependence) are a set of four coupled, nonlinear ordinary differential equations which came from careful consideration of the dynamics of the squid giant axon. Models in the style of the Hodgkin–Huxley equations are referred to as conductance-based models, and they treat the neuronal membrane as an equivalent electrical circuit, with the membrane, protein molecules embedded in the membrane, and ionic pumps modeled as a capacitor, nonlinear resistors, and batteries, respectively. A conductance-based model consists of differential equations describing the time evolution of the voltage across the membrane and gating variables, the latter controlling the rate of flow of different ions across the membrane through the protein molecules. Different conductance-based models typically include different ionic currents, which can lead to different properties and dynamics for the neurons.

As the book under review persuasively illustrates, the theory of dynamical systems provides powerful tools for developing and analyzing conductance-based and other related models of neurons, including identifying mechanisms for their behavior and making experimental predictions. Such an approach is not new: as the author readily acknowledges, the book builds upon pioneering work found in [2, 3, 4] and elsewhere. But many of the results and insights *are* new. Indeed, the book is a tour de force on the use of dynamical systems concepts to understand the dynamics of single neurons.

The Dynamical Systems Approach to Understanding Neurons. Suppose that a neuron is resting, with the voltage difference across the membrane staying constant in time. In dynamical systems terms, this corresponds to the neuron being at a *stable equilibrium*. Furthermore, suppose that when a small perturbation is made (for example, a current input from an electrode or due to other neurons) the neuron undergoes a small excursion before returning to the resting state. However, if a larger perturbation is made, the neuron fires an action potential before returning to the the resting state. As the book argues, such *excitability* occurs when the system is near a *bifurcation*, that is, a qualitative change in the dynamics as a parameter is varied. Furthermore, the book describes how different details of the dynamics of excitable neurons can be classified according to the type of bifurcation that the system is close to, and how this affects the neuron's computational properties. This includes a careful treatment of the question of whether or not thresholds exist for perturbations leading to action potentials for excitable neurons.

Action potentials can also occur periodically in time for a neuron, for example, when a sufficiently large constant current is injected. In dynamical systems terms, this corresponds to the neuron being in a *stable periodic orbit*. The frequency of spiking depends on the amount of current which is injected; for some neurons this can be arbitrarily small, while for others there is a nonzero minimum spiking frequency. Again, the book illustrates how these and other properties can be understood in terms of the type of bifurcation involved, in this case, the one leading to periodicity. It also shows how excitable and periodically spiking neurons can be understood by considering the *nullclines* for the model, which are the surfaces on which the derivative of one of the variables equals zero. (Equilibria exist at intersections of nullclines for all variables.) This is particularly true when the model is planar and the nullclines correspond to one-dimensional curves.

Neurons can also display *bursting* behavior, in which two or more spikes are followed by an interval without spikes, which might then repeat. In many cases, such bursting can be understood in terms of a dynamical system with fast-slow behavior, specifically,

$$\dot{x} = f(x, u), \tag{1}$$

$$\dot{u} = \mu g(x, u), \tag{2}$$

where $x \in \mathbb{R}^m$ describe fast variables responsible for spiking, $u \in \mathbb{R}^k$ describe slow variables which modulate the spiking, and $\mu \ll 1$ represents the time-scale separation between the fast and slow variables. For $\mu = 0$, the slow variables u can be viewed as parameters for the fast x subsystem, and bifurcations of the fast subsystem can be determined. When μ is small but finite, the u variables evolve slowly, and it may be possible to interpret the dynamics of the full system as "drifting" along the bifurcation diagram of the fast subsystem found for $\mu = 0$. Building on the work by the author of [3] and others, the author classifies the types of bursting behavior in terms of the bifurcations, in the above interpretation, which initiate and terminate spiking. Complementary treatments of bursting neurons are given in [5].

Models for Neurons. The book also promotes the use of several different classes of models for neurons. Before evaluating these, let me editorialize a bit on the question, "Is a given model of a neuron a good model?" Ideally one would like to accurately capture the entire electrophysiology of the neuron. Indeed, if this is all modeled correctly, presumably the behavior of the model will give the correct behavior of the real neuron. But this is not always possible. Despite their cleverness and hard work, experimentalists may not have worked out all of the currents that are relevant to the behavior of a particular type of neuron. Or, even if they have, the data may represent an "average" over different neurons or different operating conditions, rather than the dynamics of a "real" neuron. Furthermore, models for these currents are not derived from "first principles": they are really the result of fitting data, and should thus be viewed as empirical descriptions. This point was very nicely stated in Hodgkin and Huxley's paper (on page 541 of [1]):

> The agreement [of the model and the experiments] must not be taken as evidence that our equations are anything more than an empirical description of the time-course of the changes in permeability to sodium and potassium. An equally satisfactory description of the voltage clamp data could no doubt have been achieved with equations of very different form, which would probably have been equally successful in predicting the electrical behavior of the membrane.

So let's instead suggest that a good model should reproduce the "important" behavior of the neuron, say, the quantitative (or at least qualitative) features of the time series of the voltage across the membrane in response to different types of stimuli. It should also lead to the identification of mechanisms which explain the neuron's behavior, and it should make predictions that can be experimentally tested.

One class of models that the book discusses is that of *minimal models*. For example, a minimal model for periodic spiking could be obtained by starting with a model which has a stable periodic orbit and removing gating variables or currents until one obtains a model which also displays periodic spiking, but would not if any more gating variables or currents were removed. Minimal models are often planar, and can be understood from the geometry of the nullclines. Since different currents can lead to similar nullclines, it is not surprising that different electrophysiological models can have similar dynamics. But although such minimal models are useful for illustrating key mechanisms for neuronal behavior while retaining electrophysiologically relevant variables, the approach seems too cavalier to be ultimately satisfying. First of all, one might feel uneasy about removing currents that biologists know are present and believe to be important. More importantly, it is not clear if a minimal model will correctly capture the response properties of the neuron to different types of stimuli. So minimal models might be useful for pedagogy, but maybe not for serious modeling.

On the other hand, the following simple phenomenological model discussed in depth holds much greater promise:

$$\dot{v} = I + v^2 - u, \tag{3}$$

$$\dot{u} = a(bv - u), \tag{4}$$

with the additional rule that if $v \geq 1$, then the variables are reset as

$$v \leftarrow c, \qquad u \leftarrow u + d. \tag{5}$$

Here, $v \in \mathbb{R}$ is a voltage-like variable, $u \in \mathbb{R}$ is a phenomenological variable which models slow currents that modulate the spiking, and a, b, c, and d are dimensionless parameters. This model can be viewed as a generalization of integrate-and-fire models, but has the advantage that it dynamically captures the upstroke of an action potential, although not the downstroke. The book shows that, by tuning the parameters, it is possible to make this model display a huge variety of experimentally observed neuronal behaviors. Indeed, it is claimed that this model can quantitatively reproduce "subthreshold, spiking, and bursting activity of all known types of cortical and thalamic neurons in response to pulses of DC current." A bonus is that, as a planar model, it is possible to geometrically interpret the dynamical mechanisms for these behaviors. In my opinion, this model deserves further study and wider use.

This book also briefly discusses *canonical models* for families of neurons that share common properties. Here, "a model is canonical for a family if there is a piecewise continuous change of variables that transforms from the family into this one." This might not be an invertible change of variables, but the canonical model retains many important features of the family, and thus allows one to study universal properties of families of neurons. The canonical model framework is developed in more detail in [6].

Pedagogy. This book covers both neuroscience and dynamical systems theory starting from the basics, and the typical *SIAM Review* reader will only rarely be overwhelmed by the biological descriptions. (For example, I found the explanations of the behavior of the minimal models in terms of electrophysiology to be a bit tedious.) Of course, it would be helpful if the reader had some background in neuroscience and dynamical systems, but it is not necessary. The text has an informal style that makes it quite readable. Also, there are summaries and exercises at the end of the chapters, including some graded as being M.S. or Ph.D. level. Notably, detailed solutions are given at the end of the book for nearly all of the non-M.S. or non-Ph.D. exercises! This provides a great way to check if you understand the material.

As might be expected for a book about the "geometry of excitability and bursting," there are many figures. Actually, this is an understatement: there are over 400 figures, which are all of high quality. Many of the figures illustrate the phase space geometry of a certain model, or give comparisons of experimental and computed time series of a neuron's voltage. There are also some "fun" figures, such as pictures of pioneers of the dynamical systems approach to neuroscience, including John Rinzel on a motorcycle and Bard Ermentrout with a parrot on his head. There are also cartoons of the author in different situations, for example, in the following actual conversation with his boss. Author: "I am a mathematician. All I need is paper, a pencil, and a trash basket!" Boss: "Too bad you're not a philosopher, you wouldn't need the trash basket!"

It is also worth noting that key papers and books from the Soviet literature are cited, a great service to those of us who would find it difficult to navigate through this body of work.

Final Thoughts. The book under review claims that it is "more ambitious, focused, and thorough in dealing with neurons as dynamical systems" than other books on mathematical and computational neuroscience, such as [7, 8, 9]. This is certainly true, and it succeeds in showing that the concepts of dynamical systems theory (such as equilibria, periodic orbits, nullclines, stability, and bifurcations) provide a powerful framework for understanding the behavior of neurons geometrically.

A "weakness" of the book is that it focuses too exclusively on the dynamics of single neurons. (It should be noted that although the book seems exhaustive—and to some it might seem exhausting—in this regard, it is not complete in its treatment of single neurons. Most notably, neurons typically have a complex branched spatial structure which affects their dynamics, a point mentioned in the book but not developed in detail.) Yes, single neurons are interesting and important, but all of the amazing things that our brains do are the result of the interactions of networks of neurons. As has been amply demonstrated in research by many people, dynamical systems techniques can also be used to help to understand such networks. Having said this, a very good chapter on "Synchronization" is available from the author's website—apparently some of the reviewers and the publisher felt that it was "off-topic" for a book about single neurons, and that its inclusion with the rest of the book would make it too long. This online chapter primarily covers phase models for neurons, including isochrons, phase response curves, and phase-difference models for weakly coupled neurons. This is important material presented in a very readable way, but after such a thorough treatment of single neurons, one naturally wants more.

Overall, the focus on single neurons limits the book's usefulness as a textbook for a general course on mathematical or computational neuroscience.

A final point: the author of the book under review is the Editor-in-Chief of Scholarpedia [10], an online encyclopedia focused primarily on neuroscience and dynamical systems, and which could be viewed as an "unofficial supplement" to the book. (Disclosure: I have coauthored several articles for Scholarpedia.) Each Scholarpedia article is initially authored by an expert on the topic and refereed, but then can be edited by anyone, with the edits incorporated into the article upon approval of the curator of the article (typically the original author). This setup allows the articles to continually evolve and improve. A quick surf around this site shows that there are many topics that should be of interest to mathematical neuroscientists but that are not covered by the book under review. Fair enough. What the book does cover, it covers very well. It and Scholarpedia deserve a wide audience!

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The Nonlinear Universe: Chaos, Emergence, Life. *By Alwyn C. Scott.* Springer, Berlin, 2007. $69.95. xiv+364 pp., hardcover. ISBN 978-3-540-34152-9.

Alwyn Scott (1931–2007) completed this summary of his life's study in December 2006 and, sadly, he died shortly thereafter. This history book wonderfully summarizes ideas that were so important to him in a way that is largely accessible to "general readers who would understand science and for university undergraduates who would become researchers in or teachers of science." It also displays his humanity, charm, and broad-reaching interests and knowledge. The 1087 references he lists will give those seeking more information much opportunity to do so, in addition to consulting his more technical monographs *Nonlinear Science: Emergence and Dynamics of Coherent Structures* (Oxford University Press, 2003) and *Neuroscience: A Mathematical Primer* (Springer, 2002) and *The Encyclopedia of Nonlinear Science* (Routledge, 2005) that he edited. His 1961 MIT thesis on the dynamics of Esaki (tunnel) junctions required a nonlinear model and his subsequent engineering work on active solid-state devices led him to study the sine-Gordon equation. By the 1980s, Al was highly active at Los Alamos and elsewhere in the vigorously developing, highly interdisciplinary, and