

lutionary biology as well. For researchers and students, the volume is invaluable as a reference book. There is surfeit of useful information. Have a look at this passage in chapter 8: 'The concentration of oxygen has remained within bounds of 15 to 35% for the past 500 million years'. Since the residence time of oxygen in the atmosphere is 4000 years, its concentration has held steady for 1,00,000 turnovers. In chapter 5, there is a model called TER (threshold elemental ratio), which is based on the Leibig's law of minimum. In plant physiology, it is known as Blackman's law of limiting factors. If one calls these concepts tautologies, they are the most welcomed ones, for they represent as much a conceptual advance as the much-needed repetition of ideas necessary to clarify our stand on many contentious issues. Explanatory and predictive power of science has been enhanced by such tautologies since the time of Aristotle. It makes sense to know that stoichiometry itself is a tautology, a refined statement of the law of definite proportions. Little did anyone realize that this tautology, like a paradigm shift, could produce an empirical formula of man! The book is full of such formulae for organisms spanning an entire evolutionary scale (chapters 3 and 4). The section on biological chemistry (chapter 1) has some interesting facts from Lotka (1925). Here, a comparison of the elemental composition of the earth's crust is given from which a disproportionate abundance of C, N and P in the human body is apparent.

The evolutionary and phylogenetic speculations are not only interesting, but also powerful enough to stimulate further research. In plants, there is a plasticity of C:N:P ratios. In fact, biodiversity of animals with strict CNP homeostasis is linked to this plasticity of autotrophs. But, how has evolution achieved this? Authors conclude chapter 3 by stating that physiologies of energy generation and nutrient acquisition are decoupled to a large degree in autotrophs (what a profound statement!). Physical properties of matter have constrained the ways in which animals and plants can develop. The ideas can be developed further to complement the theme of the book. In development, organisms do not allow a common factor that scales both time and space to alter their body shape. Shape-invariant transformations are possible by altering the Cartesian coordinates of

space alone, as seen in the isometric growth of some primitive organisms. A majority of vertebrates, including man show a disproportionate transformation of shape (no common scaling factor) and this type of growth is called allometric. In chapter 4, there is a reference to allometric N:P ratio in vertebrates. A common allometric pattern is the disproportionate increase in skeletal mass with body mass. The skeleton of a shrew is 5% of the total body mass compared to 27% of the total body mass in an elephant. Theoretical distribution of N:P in various organs for a mammal of 1 g and 1000 kg is given in chapter 4. This is the most interesting unpublished original data in the book. Central to the transformation of form is the mathematical concept of fractals. Each organ may represent a fractal and its own time-frame; for example, the life span of the kidney is 400 years compared to the life span of the entire human body (the calculation is done by the fractal theory). At a higher level than the organism, development may represent one trajectory and evolution, another. The rate of separation of these two trajectories is given by Lypanov exponents. These exponents put space and time coordinates on different footings, while the special theory of relativity puts them on equal footing – as a result, time scales independently from the space dimensions and thus each fractal will have its own time. This separation of space from time plays a key role in telescoping evolution into development – the basis of Haeckel's biogenetic law.

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Neuroscience: A Mathematical Primer.
Alwyn C. Scott. Springer Verlag, GmbH & Co. KG, Tiegartenstraße 17, D-69121, Heidelberg, Germany. 2002. 351 pp. Price: Euro 59.95/US\$ 49.95.

One would hesitate to suggest that the past decades have seen a decline in rigour in such a vibrant and exciting field as neuroscience. Nevertheless, it is somewhat star-

ting to revisit classical mathematical methods applied to neurobiological problems, and realize how old-fashioned and quaint they appear in this era of ridiculously powerful personal computers. Indeed, there is also the rather alarming possibility that computational neuroscience itself may soon be perceived as unnecessarily fussy and old-fashioned to students of the internet era. What is the point of understanding compartmental approximations, and should they not be hidden under a glossy user interface so that users can better focus on the biological issues? Well, here in Alwyn Scott's book, are the real nuts and bolts of mathematical neuroscience; and computational as well as internet neuroscientists would do well to appreciate how much of their work rests on this foundation.

The apparent quaintness of mathematical methods in neuroscience arises from the fact that one trades human time and explicit mathematical assumptions for computer time and the hidden approximations in such programs. Nowadays, most scientists barely think about this trade-off – let the computer do the boring work, we say. This works for doing curve-fitting, but troublingly it also leads to more serious trade-offs in science. How many of us have reflected that we let the computer act as a censor when looking for interesting papers to read? In this book we see the power and also the limitations of the uncompromisingly rigorous approach, using mathematics to describe the functioning of neuronal systems. To a reader steeped in the more recent ambience of computational neuroscience, there is almost a subtext when reading the book: How would I do this computationally? What would be faster? What gives a deeper understanding?

The book leans heavily towards the mostly 'solved' problems of single-neuron function. Mathematically and computationally, neuronal biophysics is analysed by considering small cylindrical segments of the neuronal membrane, and examining the electrical properties of each segment. These properties include the 'passive' linear properties of resistance, capacitance and a battery formed from the build-up of ionic gradients across the membrane. This set of properties is equivalent to those of long insulated cables, and their analysis goes by the name of 'cable theory'.

The powerful computational functions of neurons arise from nonlinear effects due to voltage and ligand-gated ion chan-

nels. At this point, the mathematical and computational approaches part ways. Mathematics reduces these compartments to infinitesimals, and gets around the analytically intractable nonlinearities with approximations. Computational solutions use the approximation of large compartments, but there are no restrictions on the nonlinearities. Modern computers are fast enough to subdivide cells into hundreds of compartments, so the approximation keeps improving.

Alwyn Scott covers different aspects of cable theory and action potential formation and propagation in several chapters. The basics of these topics are admirably presented. The book is more concise in its treatment than the definitive book *Electrical Current Flow in Excitable Cells*¹, but it covers more topics. It is when the author begins to address some of the more difficult aspects of neuronal function that the lazy computer modeller feels vindicated. For example, the nonlinearities of ion channels introduce many complexities into action potential propagation. It is revealing to see the ingenious approximations and mathematical tools that have been brought to bear on these nasty nonlinear problems. However, a regular PC with any of several free neuronal modelling programs can tackle the same problems while actually making fewer

assumptions. Which gives better answers? At first sight, the computer does, especially if one subdivides the neuron finely enough to improve numerical accuracy. The mathematician has his rejoinder, though, in a list of outstanding research problems that are motivated by mathematical analysis and are sometimes difficult to simulate accurately.

The two chapters on networks of interacting neurons are the most interesting and open-ended part of the book. This is precisely the regime where mathematics is in its element – exploring the bounds of possibility, using analytical methods to make sweeping statements of what different kinds of networks can do. There are simply too many ‘free variables’ here for computational grinding to map out the terrain unaided. Instead, the author considers the happy combination of the analytical, computational and experimental approaches that are beginning to make sense of this level of brain function.

There are two undertones throughout the book that reflect some of the broader perspectives of the author. The first, which is particularly enjoyable, is the way the book is steeped in the history of the field. The second is the strong philosophical bent of the author. Philosophy is an occupational hazard for neuroscientists, especially those with theoretical leanings.

It surfaces in the brief final chapter, and has formed the basis of another of the author’s books².

The book is obviously written for the mathematically inclined, and this focus distinguishes it from the information processing viewpoint of the excellent textbook, *Theoretical Neuroscience*³. The book under review is more of an advanced work. It has its place on the shelf of all neuroscientists who believe in quantitative reasoning, and especially computational neuroscientists.

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1. Jack, J. J. B., Noble, D. and Tsien, R. W., *Electrical Current Flow in Excitable Cells*, Oxford University Press, 1975.
 2. Scott, A., *Stairway to the Mind: The Controversial New Science of Consciousness*, Copernicus Books, 1995.
 3. Dayan, P. and Abbott, L., *Theoretical Neuroscience*, MIT Press, 2002.
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