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Book Reviews

Spikes: Exploring the Neural Code, by F. Rieke, D. Warland, R. de Ruyter van Steveninck and W. Bialek, MIT Press, Cambridge, 1997. $45.00 (cloth), xvi + 395 pp.

It is often said that you can tell much about a book by its title. Most neuroscientists know that a ‘spike’ is the sharp up and down electrical morphology of the most basic singular event of cognition—the action potential. If this book were about the singular spike, it would never have reached press, as there are many books that describe, dissect, analyse, and model this unitary event. However, the title is a plural—*Spikes*. The book is about a collection of action potentials, about a succession of action potentials. But what is between the individual events; nothingness—empty space separates individual neural events. So one could conclude that this book is about nothing. However, Rieke *et al.* show that much can be said about nothing.

The nothing that lies between action potentials has one crucial property—time. And the authors of this fine book clearly discuss how the timing of events between the spikes might serve as a neural code, much like the sequence of nucleotides serves as a genetic code in DNA. The book is well organized, both for an upper-year college student trying to get a handle on crucial issues underlying all the function of the brain and for the specialist who wishes to understand details of a complex and rapidly evolving field, that of the neural code. The initial chapters are a well-written exposition of some of the main issues now confronting electrophysiologists studying myriad neural systems. An historical overview is presented followed by a primer in the mathematical tools to be used throughout the book. It should be noted at the onset that the authors have a particular vocabulary to describe the world that is taken from the language of probability theory.

A minor quibble is that the entire possibility that there is a non-stochastic, deterministic approach to understanding neuronal coding is neither mentioned nor indexed. There *are* neural systems in which probabilistic components of spike trains are minimal (Glass and Mackey, 1988). Indeed, theory has been developed in physics that indicates a purely deterministic mechanism may provide data that appears probabilistic via the process of chaos (i.e. stochastic). The authors do cite some examples of deterministic behaviour, but the alternative discussion of a deterministic nonlinear description for neural function is never discussed.

Given the assumption of a probabilistic approach, two questions are developed (and answered) in parallel. First, how do experimentalists understand the processing performed by the particular neural system under study. It is proposed that a linear system approach is a good way to quantify these issues although allowance is made for more biological nonlinear effects (e.g. saturation). Second,

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how dies the organism understand its own neural signalling? This second question is most critical and the authors are to be commended for making it a central tenet. In each of the experiments used as examples the authors ask: What is biologically and behaviourally relevant? This focus on the organisms maintains a much-needed grounding, as esoteric concepts such as the Kolmogoroff–Wiener filter, entropy, and Shannon information are applied and integral signs proliferate.

A few thoughts are in order as to the reader who might understand *Spikes*. A mathematically illiterate neurological colleague of mine once said that to read Prigogine (1984), who makes liberal use of complicated analytical expressions, he would read the text as small islands and ignore the ocean depths of the equations. So it is with this book. Although there is considerable mathematical rigour, the authors continually recapitulate the main ideas in plain English making the ideas remarkably accessible. The text is further supplemented by nicely developed experimental examples that are carried across chapters. The response of a visual motion neuron in the blowfly is characterized first using Bayes rule, then with autocorrelograms. The data are used to reconstruct response-conditional ensembles, high-order Kolmogoroff–Wiener kernels, various power spectra, compute information capacity, and finally test theories about perceptual discrimination. One might wonder if the claims of temporal coding of invertebrate ‘perception’ are overblown by the authors. But we find no evidence that the authors are invertebrate chauvinists from their intercalculation of data from complex vertebrate central nervous systems. The reviews of various perceptual issues from human and non-human primate physiology are clear and essentially correct.

For this reviewer the most interesting text is in the final chapter called ‘Directions’. Many of the most crucial issues in brain function are addressed. For example, few believe that single neurons initiate a behaviour or encapsulate perception in the vertebrate central nervous systems, yet in most instances we are limited to studying one cell at a time. Neurons are spatially distributed and recurrently connected to each other in vast numbers. The spatial distances involved range from tens of microns to centimeters. The spatially distributed neurons work together in ensembles. Population codes should be as important as purely temporal codes and might be profitably explored with the same tools the authors espouse throughout the text. The authors select a few of the recent exciting experimental studies on these issues, but do little more. There is no vision as to how the heavily developed statistical approaches so admirably applied to single cells could be applied to the neuronal collective. Ideas as to probabilistic origins for oscillation and for synchronicity are not developed at all. This development is crucial, as it has been suggested that these two properties underlie many cognitive processes in both the sensory and motor domain (Edelman, 1990; Singer *et al.*, 1990; Crick and Koch, 1990).

The historical import of a theory strongly depends on the domain of facts that it may explain. It remains to be seen whether the well-developed and useful temporal neural-code theory expounded in *Spikes* will have an impact beyond the domain of the single neuron. I look forward to their next book called *Neurons*.

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Nonlinear Dynamics, Mathematical Biology, and Social Science, by Joshua M. Epstein. Addison-Wesley, Reading, MA, 1997. $34.38 (paperback), xi + 164 pp.

There is a genre of books that looks to simple mathematical models as tools for obtaining insight into complex social and biological interactions. It is easy to discredit such efforts as too naive and indeed a certain fraction of the literature can charitably be dismissed as well meaning but irrelevant. In spite of this hazard, I am attracted in principle to the idea that tractable and transparent models based on a few plausible assumptions can offer some understanding of how complex processes work, especially if this is accompanied by cogent and persuasive arguments, as is the case in this book.

Epstein provides a concise and engaging account of the implications of ecological models for problems of conflict resolution in society by showing that the well-known Lanchester and Richardson models of arms races and warfare are special cases of Lotka-Volterra when suitably interpreted. This much may not be news to students of population dynamics, but Epstein makes significant and novel extensions of the basic models allowing for such things as the effect of territorial give and take during combat and the impact of assisting threatened nations to defuse a potential conflict. Similarly, conventional epidemic models, closely linked to those of Lotka-Volterra, are forged into tools for understanding political upheavals, the suppression of ideas, and the spread of drugs. It is amazing what a wealth of striking analogies this short book manages to present, all speculative but always provocative and entertaining. It is like a repertory theater with just a few actors who reappear in different guises to play multiple and often unexpected roles.

Of course, one must be careful to admit that such models are at best suggestive metaphors and at worst dubious fairy tales. The author is at pains to remind us of this in virtually every chapter as if to preclude premature dismissal by the cynical reader. Words like ‘crude caricatures’ and ‘tentative’ pepper the text and we are reminded that these are not predictive models.

All the models considered have quadratic right-hand sides. Surprisingly, the author makes no mention of equations with cubic terms since these can reveal bistable behavior with sudden changes that occur as certain thresholds are exceeded. This is precisely the kind of situation that takes place in explosive upheavals and in cycles of revolution, the situations treated in this book. Feedback models of activation and inhibition in which sporadic outbursts are damped (repressed) back to endemic levels are commonly handled in biology by cubic models (see Murray, 1989, for a number of illuminating examples) and could be suitably reinterpreted in terms of the problems considered by Epstein. Indeed, Zeeman (1977) did just that a couple of decades ago when he presented a collection of speculative models (but I believe no more speculative than those in Epstein’s book) that dealt with conflict resolution, uprisings, and censorship, all under the banner of catastrophe theory. Since much of this work later fell into disrepute, Epstein may have wished to remove himself from any taint that his own work would acquire by even mentioning these earlier efforts. Nevertheless, to not comment on Zeeman’s oeuvre, however briefly, is a sorry omission. Also not mentioned is a related model dealing with three-species competition considered by May and Leonard (1975), a negative version of the more uplifting collective security model treated in Epstein’s lectures. Here too oscillations damp down to equilibria which are maintained for extended periods of time. Gilpin’s model (1979) for preventing extinction between competing species by having a third species moderate the growth of the more abundant competitor can also be seen as a more far-fetched variant having the same (moral) implication.

A final chapter in this brief and somewhat ambitiously titled book provides an efficient if incomplete survey of the mathematical tools needed in the study of dynamical systems. This includes a summary of index theory on closed manifolds that is sure to elude anyone not already conversant with this topic. However, since this material is largely irrelevant for the purposes of the text, it may safely be disregarded. There is a good list of references.

One other very minor complaint: in at least three places the author states the origin is the sole equilibrium of a linear system of differential equations. The hidden assumption of matrix invertibility is not mentioned.

Overall, this is a clear and well-paced account of some fascinating topics and a recommended text, if suitably supplemented by some additional materials, for any modeling course that deals with social and biological systems. It is accessible to anyone with a modest preparation in differential equations and matrix algebra, and could be profitably taught to prepared undergraduates.

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Evolutionary Games and Equilibrium Selection, by Larry Samuelson, MIT Press, Cambridge, MA, 1997. $40.00 (cloth), ix + 309 pp.

Evolutionary game theory originated in the 1970s to model the behavioural evolution of biological species (Maynard Smith, 1982). Its acceptance can be seen by the widespread use in the biological literature of ‘strategic reasoning’ to describe how different strategies (whether observable behaviours or genotypic characteristics) interact and evolve. Of particular interest is the prediction of the long-run equilibrium of the model which is often taken to be an evolutionary stable strategy (ESS) of Maynard Smith. To an economist (hereafter, I take this to mean, more accurately, to a practitioner of classical game theory that has had its main practical applications to economic theory) an ESS is a Nash equilibrium (NE) that has a secondary stability condition. Thus, if there are many NE (as is often the case), evolutionary games can be used to select an ESS among them. If no such ESS exists, other NE may be selected using evolutionary dynamics and this is reflected in the book’s title.

The book is the first in the *Series on Economic Learning and Social Evolution* edited by Ken Binmore of University College, London. The series is intended to bridge traditional interdisciplinary boundaries among scientists interested in the dynamics of human interactions. Other tentative books in the series include *Theory of Learning in Games* by Drew Fudenberg and David Levine and *Game Theory and the Social Contract: Just Playing* by Ken Binmore.

The book is written primarily for economists as shown by the direct quotation: 'There is no biology in this book.' While this is true in the literal sense, since no biological system (other than human behavior) is modelled, there is much that is relevant to biologists. For instance, Chapter 3 develops a model based on imitative behaviour, Chapter 6 considers dynamics with drift (i.e., a deterministic perturbation of the underlying evolutionary dynamic), and Chapter 7 introduces stochastic mutation effects (i.e., noise) into the system. One of the most difficult aspects of the presentation for readers more familiar with the biological perspective of evolutionary game theory will be its reliance on and comparison to rationality arguments. On the other hand, Samuelson chooses his examples to illustrate the theory carefully from a limited number of basic games where players have only a few possible strategies. This makes the presentation easier to follow. The first time through, I would recommend a careful reading of the extended Introduction (that places the biological perspective of evolutionary game theory in context while developing the economic one) and Chapter 2 (on ESSs and other stability notions of evolutionary dynamical systems) before examining those parts of the next seven chapters that are of interest. Although these chapters are based on separate articles by Samuelson, he has done a commendable job of giving a clear and connected focus.

Samuelson argues strongly that equilibrium selection through evolutionary games is qualitatively different than the other static NE refinement methods developed by economists over the last 20 years. Throughout the book, he makes the case that the implicit dynamic aspect of evolutionary game theory more accurately reflects how rational individuals learn to behave in a game situation and feels that 'the best chance for game theory as a whole to retain its central position in economics . . . is through evolutionary arguments'. However, ESS theory, as developed for biological applications (Hofbauer and Sigmund, 1988; Cressman, 1992), is often inadequate for games of interest to economists (specifically, ESSs usually fail to exist for extensive form games that model sequential interactions between pairs of individuals). In such cases (e.g. the Ultimatum Game, the Chain-Store Game, the Dalek Game, repeated Prisoners' Dilemma), Samuelson demonstrates how dynamics select a long-run equilibrium and also explain discrepancies between this prediction and short-run experimental results on human behavior observed by economists.

For the past 10 years, much more research has been done on the theory of evolutionary games from an economic perspective (Weibull, 1995) than from a biological one. Samuelson's book gives biologists a valuable resource that discusses the important issues in this research and also its future direction.

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