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Book Review

Fiddling with the Neural Code

Spikes: Exploring the Neural Code
By Fred Rieke, David Warland,
Rob de Ruyter van Steveninck, and William Bialek
Cambridge: MIT Press. (1997). 395 pp. $ 45.00

On the cover jacket of *Spikes*, the authors' names, rotated sideways, appear as action potentials recorded from a neuron (Figure 1). These name-spikes have different heights corresponding to the different lengths of the authors' names. (Some have argued that only one of the authors represents a spike and the others are noise, but I will take a more charitable view.) How much simpler the neural code would be if real neurons had this option and could encode the characteristics of a stimulus through action potential amplitudes, while using the temporal pattern of spiking to reflect changes in stimulus properties over time. Although action potentials can vary in height and width, there is no indication that such variations encode information in any systematic way. From the point of view of coding, action potentials are stereotyped, all-or-none events; there are no "Rob de Ruyter van Steveninck" action potentials to provide amplitude signaling. Instead, information represented by sequences of action potentials must be carried solely by their timing.

The fact that action potential timing must encode the characteristics of a stimulus and, in addition, convey how the stimulus changes over time introduces a complexity into the neural code that is often avoided by using static or stationary stimuli. The authors of *Spikes* take the bull by the horns and deal directly with the problem of encoding time-varying stimuli. To understand the issues involved, a musical analogy might be helpful. When a violinist plays a single note, the pitch heard corresponds to the oscillation frequency of the violin string. During even the most rapid passages in a piece of music, we can still identify the pitches of individual notes because the strings vibrate much faster than the violinist's fingers. Thus, the understanding of pitch gained from listening to long, single notes is relevant for our understanding of melody. Imagine, however, a superhuman violinist able to play several hundred notes per second. The result would be a buzzing sound unlike anything we have ever heard from a violin. In this case, the temporal domains of pitch and melody would no longer be well separated, and listening to single, long notes would not prepare us for these novel sounds.

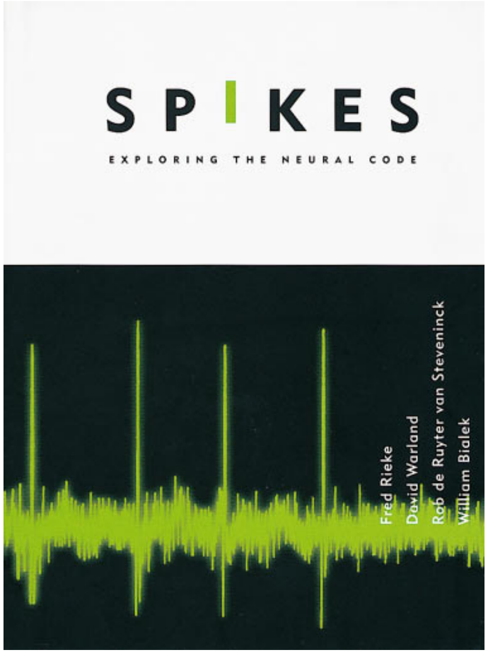

Figure 1. The Book Cover from *Spikes* Reprinted with Permission from MIT Press

A major point made in *Spikes* is that many neurons are indeed fast fiddlers. In other words, when these neurons respond to natural, time-dependent stimuli, they fire only about one action potential before the stimulus changes appreciably. This means that the results of experiments that measure the firing rates of neurons responding to static stimuli do not necessarily supply the information needed to understand responses to time-varying stimuli. Knowing that a particular stimulus causes a neuron to fire at 50 Hz when presented statically doesn't necessarily tell us what will happen when that stimulus is only around long enough for one spike to be fired.

The principal techniques presented and applied in *Spikes* to deal with this conundrum are spike train decoding and information theory. Decoding is an inversion of the usual procedure used to study the relationship between stimulus and response. Normally, we study neural encoding, the map from stimulus attributes to action potential sequences. Neural decoding refers to the inverse map and explores how properties of a stimulus can be extracted from knowledge of the neural response it evoked. Decoding is interesting because it is, in some sense, the problem an animal faces in continually trying to decipher and respond appropriately to the pattern of activity of its sensory neurons. The correspondence is particularly appropriate for the H1 motion-selective visual neuron of the blowfly, which is frequently the subject of experimental study and theoretical analysis in the book. Visually guided corrections during flight in the blowfly rely on a small number of neurons, including H1, and responses can occur within 30 ms, time for just a few spikes to be emitted.

Spikes presents an additional compelling reason to study decoding rather than encoding; the map from response to stimulus is, at least in some cases, approximately linear, even when the encoding map from stimulus to response is nonlinear. The decoded signal can, effectively, be linearly related to the firing rate of the neuron, even when the firing rate is nonlinearly related to the stimulus. The paradox in this statement is resolved by realizing that decoding depends not only on how the neuron generates spikes in response to a stimulus, but also on the probability distribution of stimuli. This fact emphasizes the importance of studying the statistics of the stimuli that a neuron responds to, as well as the mechanisms by which it generates its response. Mathematical methods for analyzing linear systems are so powerful that finding a linear map in neural coding is like finding a new pocket of gold in a long-explored mine. The authors have dug deeply into this new vein, both in their papers and in the results reported in this book.

Recording neurons from the brains of behaving animals has been surprisingly fruitful, considering that we are seeing only a minuscule fraction of the relevant activity in the brain. Individual neurons seem to convey a remarkable amount of information. *Spikes* reviews instances in which the ability of an observer to perform a discrimination task on the basis of spikes fired by a single neuron is close to, or matches, the ability of the animal to perform the task. In some of these cases, the single-neuron performance is close to fundamental limits imposed by physical laws. The book then extends the analysis of information content from single neurons down to the level of single action potentials.

Computing the information content of a spike train is a demanding task. Another major contribution of the book is to catalogue and explain the impressive techniques that the authors have developed to tackle this problem. Using spike decoding and information theory, they and others following their lead have now shown, in a number of systems, that not only each neuron but each spike conveys a considerable amount of information, as much as a binary number one to three bits long. This is a remarkably high figure representing a highly efficient use of the temporal sequences that comprise the spike train.

The methods of spike decoding and information computation discussed in *Spikes* have become standard and are now widely used. While the text of the book is more a discussion of the philosophy of this approach, a careful analysis of its rationale and its limitations, and a presentation of results, a long series of appendices (comprising a quarter of the book) provide the mathematical details. This division, presumably designed to make the book accessible to non-mathematically inclined readers, makes it somewhat difficult to integrate the mathematics with the results, but the reader who takes the time to shuttle back and forth between the main text and appendices will be rewarded. An advantage of this split is that the mathematics in the appendices is presented at a level of detail that would not have been possible within the main text.

Computational neuroscience requires a tight collaboration between theory and experiment, and *Spikes* illustrates what can be done when this works well. Major points in the text are illustrated by excellent figures, often made from data collected precisely for this purpose. The care with which the authors have integrated analysis with data, and text with figures, is admirable and sets an example for anyone applying mathematics to neuroscience.

L. F. Abbott
Volen Center and Department of Biology
Brandeis University
Waltham, Massachusetts 02254

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