

The dynamics inside the box



Spikes, Decisions, and Actions: Dynamical Foundations of Neuroscience

by Hugh R. Wilson

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The brain shows complex dynamics, due to its time-varying sensory inputs as well as its intrinsic processes at every level from ion channels to behavior. Although neural processing can be studied effectively with black-box approaches like spike decoding and information theory, to fully understand the brain we must also concern ourselves with the contents of the black box. Hugh Wilson's book *Spikes, Decisions and Actions* looks inside the box and outlines theoretical techniques for studying the dynamics of the neurons and neuronal networks within. Although many books describe nonlinear dynamics at a similar level, this one is unique in its exclusive reliance on examples from neuroscience.

Nonlinear dynamical systems such as the brain are hard to deal with experimentally. We try to control as many variables as possible, we assess the effects of manipulating a handful of parameters and we average over many trials to decrease the influence of noise. It is, however, difficult or impossible to predict how multiple nonlinear processes interact unless we have a theoretical model. Models can provide experimentally testable predictions and a level of insight not otherwise achievable. A classic example is the Hodgkin-Huxley model for the generation of axon potentials in the squid axon. This model was based on four variables: membrane potential, activation and inactivation of the sodium current, and activation of the potassium current. Using a set of four differential equations (one for each state variable), Hodgkin and Huxley described how these state variables interact and vary over time. The model was very successful at reproducing the experimental data and generating further predictions. For example, Rinzel and colleagues used it to predict, correctly, that a precise and brief current pulse

could in certain cases annihilate repetitive spiking. More generally, the Hodgkin-Huxley formalism has led to enormous progress toward the understanding of neuronal spike generation and information processing.

As anyone who works with such models knows, educated guesses can go a long way toward finding the set of parameter values that best fits the data. The mathematical techniques of nonlinear dynamics, reviewed in Wilson's book, can help to provide such guesses. More importantly, they provide a systematic strategy for understanding complex systems.

Although the title may seem ambitious, the book provides a basic introduction to nonlinear dynamics, drawing on examples ranging from spike generation and propagation to perceptual phenomena and central pattern generation. And so, in this context, the title is not off the mark. Although the examples are diverse, the underlying theme is that to understand a particular neural phenomenon, we should develop models at various levels of complexity, and that we should use intuition gained from the simplest models to formulate more complex ones. With multi-disciplinary graduate programs in neuroscience and computational neuroscience becoming more common, this book, which focuses on teaching methods of analyzing simpler models, could form a nice basis for a semester-long course. The pedagogic slant in no way hinders the readability of the text, so the book would be equally suitable for self-study or for the reader interested in learning something about how nonlinear dynamics can be applied to neuroscience.

The experimentalist (or non-mathematician) should not be intimidated by the anticipation of high-powered mathematics. The first few chapters carry the reader gradually through the necessary mathematical concepts, and the supplementary software (written in Matlab™) is particularly useful. To take advantage of these files, a familiarity with Matlab at an introductory level is required—a level that can be achieved by going through the program tutorials or ask-

ing a knowledgeable colleague. The Matlab files are not required, but they are a nice supplement because they illustrate model dynamics visually, and they can be modified by the curious reader and used as a vehicle for additional study.

The author's examples are drawn both from his own work and from the literature. One area where modeling at different levels of detail has been especially successful is network oscillators and central pattern generators. For example, a central pattern generator in the lamprey spinal cord generates the necessary rhythmic pattern for the muscles that enables the animal to swim backward and forward. A neuronal oscillator generates the rhythm in each segment along the cord, and these oscillators are connected in a long chain. During swimming, a single sinusoidal wave of movement propagates along the length of the animal's body. Wilson shows how a phase oscillator model (where each segment is described by a generic sinusoidal oscillator) provides a simple solution to the problem that the phase difference between adjacent pairs of segmental oscillators must remain constant (a constraint which is dictated by the behavior of the animal). Namely, forward or backward swimming result when the rostral or caudal segment, respectively, receives the greatest external drive. Although the results of the phase oscillator models were controversial, they served to focus the field of central pattern generation.

If there is one general aspect of the book that may rub some readers the wrong way, it relates to what it means to 'understand' a particular phenomenon. Some may consider a neural system understood when they discover its qualitative behavior, whereas others will not be satisfied until they have a detailed description of the neural mechanisms underlying that behavior. The author states, "My bias is to choose the simplest possible description consistent with the data one wishes to explain." The notion of consistency and the choice of what data to consider, however, can be very subjective. For example, you could model the process of deciding whether to read this book by a two-neuron network: one neuron says "read the book", the other says "don't bother", and the neuron getting the most votes determines the outcome (a winner-take-all network). This seems like a reasonable description of a decision process at some level, but in no way does it explain the multiple brain processes that occur during such a decision. Although the author doesn't always state so explicitly, such simplified models are not an end in themselves but, rather, are steps toward an increased understanding of how real neuronal networks function.

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