



## BOOKS: NEUROSCIENCE

## Simulating Nerves and Networks

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In 1951, Hodgkin and Huxley completed the equations that described the currents underlying neuronal action potentials, and plotted a numerical solution to their equations—using a hand-operated calculating machine. After performing calculations for 3 weeks they were halfway down the falling phase of the potential. They decided this was sufficient, and included a figure of the incomplete trace in their famous 1952 paper (1).

Today, undergraduates can watch simulation packages such as GENESIS or NEURON generate this trace in milliseconds.

Although further advances in computing power will continue to contribute to the rapid growth of computational neuroscience, increasing only the size and speed of simulations is not sufficient to sustain the field. Progress also requires understanding of the basic principles used in simulating the function of neurons and neural circuits. These principles are effectively presented in the second edition of Koch and Segev's *Methods in Neuronal Modeling*.

Seven new chapters reflect the considerable progress that has occurred in the 9 years since the first edition. In particular, the intrinsic cellular properties of neurons are now investigated in great detail. For example, De Schutter and Smolen's chapter describes sophisticated representations of neuronal calcium dynamics. (Calcium influences multiple neuronal processes, including spike timing and synaptic modification, but early models did not address the complex interaction of factors that ultimately determine calcium concentration.) Another topic that has seen much recent progress is the kinetics of individual synaptic currents, and the chapter by Destexhe, Mainen, and Sejnowski combines models developed by many researchers to simulate a small network of neurons exhibiting complex behavior. A separate contribution by Mainen and Sejnowski covers compartmental simulations for modeling active ion channels in dendrites. Other hot topics addressed in new chapters include the analysis of small network dynamics (Ab-

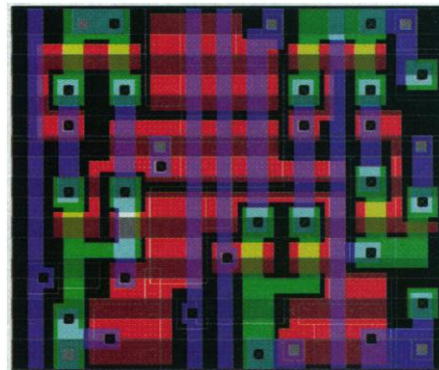
bott and Marder), spike time variability (Gabbiani and Koch), and the simulation of neurons on computer chips (Douglas and Mahowald).

Some of the seven chapters retained and revised from the earlier edition have already proved useful as references to a wide range of modelers. These include the contribution by Rall, a seminal figure in the field of cable theory (originally derived for calculation essential to trans-Atlantic telegraph cables, but highly relevant to computing electrical potentials in nerve cells), and Rinzel and Ermentrout's phase plane analysis of neuronal dynamics. The original chapter by Segev on compartmental models has been greatly extended to cover popular simulation software. It now provides the best starting point for a reader seeking a computational tutorial, although (overall) this volume is more useful as a reference for advanced research than an introductory text.

Those interested in becoming adept at computational modeling will find this book most helpful when it is read while carrying out simulations on software packages such as GENESIS or NEURON (2). Extensive experience with specific simulations provides a deeper understanding of how individual parameters influence overall dynamics. To this end, many chapters provide useful links to interactive tutorials, simulations, and programs on the World Wide Web.

Although many of the basic principles by which single neurons function are well known, many of the unifying principles at the network level remain undiscovered. For example, regularities in the anatomy and physiology of different subregions of the cortex suggest that similar cortical dynamics underlie a range of functions. A variety of computational models have addressed this problem, but they have not converged on a shared set of principles. This volume presents three different perspectives on models of cortical networks: Shamma examines unit activity in auditory cortex; Protopapas, Vanier, and Bower address local field potentials and neuronal properties in the olfactory cortex; and Hansel and Sompolinsky consider feature selectivity in the visual cortex. Given the vast scope of

the field of cortical information processing, these authors could not cover the wide range of theoretical work as comprehensively as do the authors of the other chapters; for example, they do not mention the many models of associative memory in hippocampus or self-organization of feature detectors in primary visual cortex. But they do retain the appropriate emphasis on accurate representation of biological parameters, particularly in the chapter by Protopapas *et al.* (who argue that realistic network models can provide more than just a demonstration of the plausibility of preexisting theories.) Ultimately the choice between cortical models will come down to biological constraints. Few, if any, existing models have simultaneously accounted for intrinsic properties of neurons, responses at the system level (such as unit recording and local field potentials), and behavioral function. But neglect of the biological level may miss essential information processing capabilities of the computational soup of membranes and modulators in the brain.



**Silicon cell structure.** The layout of a 86  $\mu\text{m}$  by 71  $\mu\text{m}$  delayed-rectifier potassium circuit for an analog (very large-scale integration) neuron.

As Shamma notes in his chapter, researchers choosing among the innumerable network topologies and algorithms must remember "It is relatively easy in general to come up with a network that can perform any desired task.... It is a different matter to come up with a biologically plausible network to perform the task." Research on brain function will only converge on a unified explanation when models are effectively constrained by biological detail at a cellular level. *Methods in Neuronal Modeling* provides an important step in that process.

### References

1. A. L. Hodgkin and A. F. Huxley, *J. Physiol.* 117, 500 (1952).
2. J. M. Bower and D. Beeman, *The Book of GENESIS: Exploring Realistic Neural Models with the GENeral NEural Simulation System* (Springer, New York, 1997); M. L. Hines and N. T. Carnevale, *Neural Comput.* 9, 1179 (1997).

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