

postsynaptic to presynaptic elements, which until recently has not been considered a property of most neurobiological networks. Second, these networks generally have exhibited an exclusively feed-forward connectivity pattern rather than the recurrent patterns that characterize most biological neural networks. Third, the neuron-like elements that make up artificial neural networks lack the voltage- and time-dependent conductances that endow real neurons with active and long duration responses (for example, post-inhibitory rebound) to input. This volume, written by neurobiologists who employ neural-network models, attempts to demonstrate the usefulness of neural-network approaches to understanding real neural networks and to encourage biologists to participate in the design of the next generation—the third generation—of artificial neural networks.

In two introductory chapters Gardner and Stevens discuss the limitations of earlier generations of neural networks and define the changes in individual element design and network architecture that must be made if the third generation is to be more biologically verisimilar. Gardner then addresses the issue of retrograde determination of synaptic strength by summarizing his studies of synaptic strength in a small biological neural network in the sea slug *Aplysia*. An advantage of this system is that it contains both multiple presynaptic neurons that each contact the same postsynaptic neuron and multiple postsynaptic neurons that each are contacted by the same presynaptic neuron. He finds that synaptic inputs received by a single postsynaptic neuron have similar synaptic strengths, quantal release parameters, and time constants, whereas synaptic outputs from a single presynaptic neuron to different postsynaptic neurons do not. These data, particularly those regarding quantal release, strongly suggest that the postsynaptic neuron helps determine synaptic strength and that retrograde information flow occurs in this system.

Modification of synaptic efficacy is examined by Baxter and Byrne in a concise summary of the mathematical and biological processes that underlie learning. This chapter is particularly useful because it matches mathematical learning rules to specific types of learning (for example, nonassociative, associative, Hebbian), thus providing a bridge between modeling and biology. Taken together, the chapters by Gardner and by Baxter and Byrne strongly support the idea that retrograde transfer, and hence possibly some type of back-propagation mechanism, occurs not only in artificial neural networks but also in many forms of biological learning.

The second objection (regarding feed-forward connectivity) is motivated both by the recurrent anatomy of biological networks and by the time-varying nature of biological sen-

sory inputs and motor outputs. Simple feed-forward networks are generally incapable of such dynamic activity. A particular strength of recurrent networks, however, is their ability to interpret and generate dynamic patterns, and Fetzi reports on recent investigations into recurrent artificial neural networks. Included are descriptions of recurrent networks capable of generating oscillations, performing step-tracking tasks, retaining short-term memory, and integration and differentiation. This wide-ranging chapter demonstrates both the development of training algorithms appropriate for this class of neural networks, and the additional power that recurrent architecture adds to networks.

A chapter by Lockery and Sejnowski on reflex bending in the leech and another by Chiel and Beer on hexapod locomotion address the third objection (regarding oversimplified neurons). Lockery and Sejnowski used experimental data to set their neuronal and synaptic time constants; back propagation was then used to train the network. Their work shows that more realistic neurons can be successfully integrated into neural networks and strongly suggests that the biological neural network underlying leech reflexive bending is distributed—that is, that all or most of this network's neurons are active during bends in any direction. Chiel and Beer used endogenously active pacemaker model neurons to build a central-pattern-generator network for their hexapod organism and then added to this network biologically based motor neurons and sensory input. In this system the relative importance of the central pacemaker and sensory input in controlling locomotion was found to depend on walking speed, an observation that may be relevant to the ongoing controversy concerning the relative importance of the center and the periphery in the biological generation of rhythmic motor pattern. These two contributions are compelling examples of how integration of biological data and neuronal-network modeling can generate insights applicable to both fields.

Nonetheless, it is on this third objection that artificial neural networks still fail, because in these two cases the more biologically realistic elements were constructed by hand, not trained into the network. Until training rules are developed that allow minimization of network error by adjustment of active neuronal properties as well as of synaptic weights, the full usefulness of neural networks, both as illuminators of biological processes and as information processors in their own right, will remain unrealized. Far from constituting a criticism of this volume, however, this observation highlights its central theme—that by recognizing and incorporating biological processes that are not captured by the current generation of neural networks, biologists and modelers together can ultimately produce a generation of networks as rich and powerful as

their biological counterparts. I recommend this well-written and well-illustrated book to biologists interested in neural networks, neural networkers interested in biology, and anyone curious about the offspring of this disparate union.

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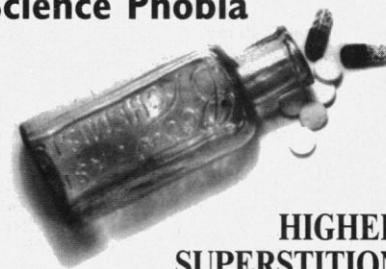
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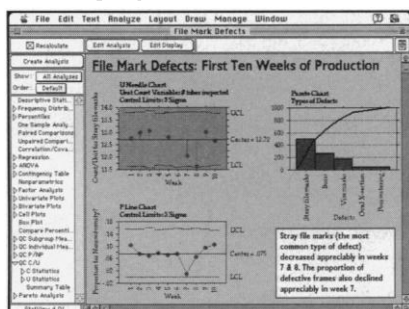
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