break down this symmetry and cause the optimal sex ratio to deviate from unity. The invariance of the product αM with respect to body size expresses the symmetrically opposing allometric relationships of α (0.25 power) and M (-0.25 power) to body mass, their product being related to the $0.25 - 0.25 = 0$ power of body mass, or 1 (constant).

One may ask whether the ideas of symmetry and invariance really add to understanding, especially of such an issue as sex ratio, of which evolutionary biologists including Charnov have developed a profound understanding without the benefit of the symmetry/invariance concept. Charnov would argue that his approach helps to reorient one's thinking about life histories and leads one to both recognize and inquire about patterns that have previously escaped notice. Compelling support for this rationale can be found in Charnov's own treatment of indeterminant growth. Charnov points out that life-history invariants described for fish more than 30 years ago by Beverton have not been pursued by theoreticians, who have been more preoccupied with the things about life histories that change. Beverton characterized three invariant, dimensionless numbers: the ratio of adult mortality to growth rate, the ratio of length at maturity to maximum length, and the negative exponential relating adult length to growth rate; Charnov adds to these another invariant related to the first two—the product αM. After characterizing these patterns empirically, Charnov proceeds to develop simple optimization models that predict the observed invariants, creating a plausible hypothesis for the causal relationships that control the evolutionary diversification of life-history patterns among fish.

Charnov's approach to understanding life-history evolution is distinctive and consistent. He consciously ignores (i) genetics, by confining his models to the fitness consequences of continuous phenotypic traits; (ii) historical effects, by assuming evolutionary equilibrium; (iii) phylogeny, by assuming that the traits of concern are responsive to selective forces; and (iv) internal physiological constraints, by assuming that optimization deals primarily with the allocation of time and resources among such competing demands as growth and reproduction.

The fundamental life-history relationships recognized by Charnov and his success in providing a theoretical rationale for them make *Life History Invariants* an important book. Charnov would, however, be the first to admit that much of what he has accomplished is only one hopeful step toward a goal still shrouded in the mists of ignorance. Even the impressive fit of Charnov's theory to data may, in some cases, be misleading or lack generality. For example, Charnov explains the 0.25 power relationship of age at maturity to adult body mass in mammals as a direct outcome of the 0.75 power scaling of net production to body mass, combined with optimizing the switch point between growth and reproduction. In this view, adult size is simply a consequence of the optimized age at maturity, after which net production is diverted from personal growth and allocated to offspring production. Thus, adult size is not targeted and has no particular ecological consequence. In contrast, birds grow to a targeted adult size long before achieving sexual maturity. Birds also exhibit an approximately 0.25 power relationship between age at sexual maturity and adult body mass. Thus Charnov's theoretical development either does not provide a generalizable explanation for a pattern common to several groups of organisms or has produced a fortuitous explanation for one of them.

In other cases, there is as yet no theory. Charnov himself suggests that "it would often be easier to find invariants than to explain them." Such a case is the ratio of annual fecundity to adult mortality rate in birds (about 5), further implying invariance in prereproductive survival (about 0.2), irrespective of the order-of-magnitude variation in mortality, fecundity, and age at maturity among species. In his final chapter, Charnov suggests directions for future inquiry into such questions, focusing on the insights of symmetry and invariance. After reading this book, it seemed to me that progress also will depend on developing a deeper understanding of the functional architecture of the organism and of its relationship to the environment. Only in this way will the empirical inspiration for theory adequately reflect the richness and complexity of life-history phenomena. And as Charnov rightly and thoughtfully points out, things that don't change are often as interesting as those that do.

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Vignettes: Genobiography

Sure, George Washington was tall, he did have long hands and feet, he had a prominent nasal bridge and bad teeth, and he was infertile, but that's not nearly enough to prove conclusively that the man had a 47,XYY chromosome complement.

—*Robert Marion, in Was George Washington Really the Father of Our Country? A Clinical Geneticist Looks at World History* (Addison-Wesley)

In writing the biography of great men and women, printing the DNA sequence of their genome would not be a good place to start.

—*Robert Cook-Degan, in The Gene Wars: Science, Politics, and the Human Genome* (Norton)

The Next Nets

The Neurobiology of Neural Networks. DANIEL GARDNER, Ed. MIT Press, Cambridge, MA, 1993. xiv, 227 pp., illus. $45 or £40.50. Computational Neuroscience.

Attempts to investigate the workings of the nervous system by computer simulation began with the pioneering work of Edwards and Minsky in the 1950s and now range from biologically detailed, conductance-based, *in silico* model neurons to abstract algorithmic approaches. Neural networks (distributed networks of simplified neuron-like elements) lie in the middle of this continuum. They have become popular owing to their remarkable ability, after training, to replicate many aspects of nervous system functioning.

The relevance of artificial neural networks to biology has nonetheless been questioned. This resistance may stem in part from the unfortunate naming of this modeling approach: co-opting a neurobiological term (and thus implying neurobiological verisimilitude) invites criticism. Three more substantive objections have been raised to the supposedly nonbiological properties of these networks. First, one widely used training method, back propagation, requires retrograde passing of an error signal from 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 sensory 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 Fetz 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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Books Received

An African Savanna. Synthesis of the Nylsvley Study. R. J. Scholes and B. H. Walker. Cambridge University Press, New York, 1993. xii, 306 pp., illus. $69.95. Cambridge Studies in Applied Ecology and Resource Management.

The AIDS Pandemic. Social Perspectives. Yole G. Sills. Greenwood, New York, 1993. xii, 247 pp. $55. Contributions in Medical Studies, no. 38.

Aircraft Emissions and the Environment. CO_x SO_x HO_x and NO_x. Leonie J. Archer. Oxford Institute for Energy Studies, Oxford, U.K., 1993. xiv, 163 pp., illus. Paper, £14. OIES Papers on Energy and the Environment.

Applied Micropalaeontology. David Graham Jenkins, Ed. Kluwer, Norwell, MA, 1993. xii, 269 pp., illus. $99 or £75 or Dfl. 170.

The Banach-Tarski Paradox. Stan Wagon. Cambridge University Press, New York, 1993. xviii, 253 pp., illus. Paper, $24.95. Reprint, 1986 ed.

Biocomputing. Informatics and Genome Projects. Douglas W. Smith, Ed. Academic Press, San Diego, CA, 1993. xii, 336 pp., illus. $49.95.

Biology of Fibrous Composites. Development Beyond the Cell Membrane. A. C. Neville. Cambridge University Press, New York, 1993. viii, 214 pp., illus. $64.95.

The Biology of Viruses. Bruce A. Voyles. Mosby-Year Book, St. Louis, MO, 1993. xiv, 386 pp., illus. $46.95.

The Correspondence of Sigmund Freud and Sandor Ferenczi. Vol. 1, 1908-1914. Eva Brabant, Ernst Falzeder, and Patrizia Giampieri-Deutsch, Eds. Harvard University Press, Cambridge, MA, 1994. xxxviii, 584 pp. $39.95. Translated from the German by Peter T. Hoffer.

Corticotropin-Releasing Factor and Cytokines. Role in the Stress Response. Yvette Taché and Catherine Rivier, Eds. New York Academy of Sciences, New York, 1993. x, 297 pp., illus. Paper, $95. Annals of the New York Academy of Sciences, vol. 697. From symposia, Montreal, Oct. 1992.

The Costimulatory Pathway for T Cell Responses. Yang Liu. Landes, Georgetown, TX, 1994 (distributor, CRC Press, Boca Raton, FL). vi, 122 pp., illus. $89.95.

Crystallography. Walter Borchardt-Ott. Springer-Verlag, New York, 1993. x, 303 pp., illus. Paper, $29.95. Translated from the German edition (Heidelberg, 1993).

Cyclic Voltammetry. Simulation and Analysis of Reaction Mechanisms. David K. Gosser, Jr. VCH, New York, 1993. xii, 154 pp., illus., + diskettes. $65.

Cyclophane Chemistry. Synthesis, Structures, and Reactions. Fritz Vögtle. Wiley, New York, 1994. viii, 501 pp., illus. $123.95. Translated from the German edition (Stuttgart, 1990) by P. R. Jones.

The Development of *Drosophila melanogaster*. Michael Bate and Alfonso Martinez Arias, Eds. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 1993. 2 vols. xxii, 1558 pp., illus., + atlas + poster. $350.

Dinosaurs. The Textbook. Spencer G. Lucas. Brown, Dubuque, IA, 1993. xx, 290 pp., illus. Paper, $45.67.

Doping in III-V Semiconductors. E. Fred Schubert. Cambridge University Press, New York, 1993.