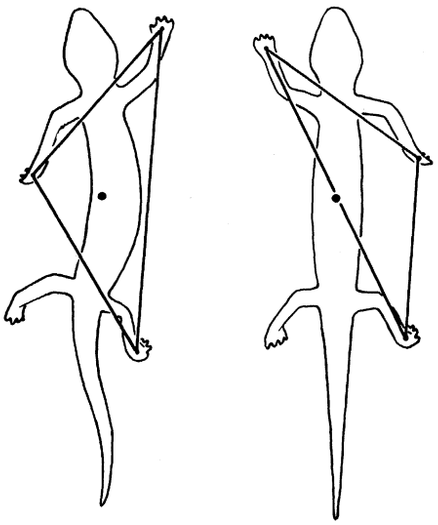

"Factors affecting stability for a sprawling salamander. . . . Using lateral sequence, the salamander benefits from a larger triangle of support that is better positioned under the center of mass (*dot*), as well as from undulation that increases excursion for both pairs of legs. If diagonal sequence were used, undulation could not simultaneously benefit excursion for both pairs of legs." [From M. Hildebrand's chapter in *Functional Vertebrate Morphology*]

little change in neuromuscular activity; the original pattern generators are retained. In a similar fashion, Lauder shows that suction feeding in primitive salamanders closely resembles that in fishes, despite important morphological changes. Suction feeding is ineffective in air, however, and terrestrial vertebrates have evolved a different feeding mechanism, in which head and tongue movements replace fluid movement in food transport. Bramble and Wake develop a model, incorporating stereotyped kinematic and motor events involving homologous muscle groups, that is common to a variety of tetrapods. They suggest that this is derived from a common ancestral system. Pattern generators in the brainstem may generate the stereotyped neuromuscular patterns of feeding, in a way similar to that described by Goslow for spinal cord generators in relation to locomotion. Hiiemae and Crompton show that many mammals use similar musculoskeletal mechansims to transport, process, and swallow food and speculate on the possibility of phylogenetically conservative neural control systems. If there is one idea that emerges repeatedly from the diversity of topics explored in this book, it is that the neural mechanisms controlling repetitive actions may evolve more slowly than the effector systems they drive.

The two chapters on neurosensory systems seem somewhat out of place in this book. Fay and Popper discuss the octavolateralis system and Levine the eye. Though individually excellent, these chapters do not provide a comprehensive review even of the special senses; why is there nothing on olfaction?

In the final chapter Liem and Wake conclude that functional morphology still lacks a coherent set of common principles or long-term goals. They propose that it should emphasize testable hypotheses in which the relationship between structure and function is explained in a phylogenetic framework studied through the developmental mechanisms whose modifications bring about evolutionary change. Thus cladistic analysis and evolutionary epigenetics, key elements of modern comparative biology, make a significant appearance only in the final chapter of this book. The methodological emphasis of most of the authors is on the machinery used to generate data. Liem and Wake suggest that the time has come for functional morphology to progress from the mere description of what animals do to the broader consideration of how they have come to do it.

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Cooperativity in Biochemistry

Cooperativity Theory in Biochemistry. Steady-State and Equilibrium Systems. TERRELL L. HILL. Springer-Verlag, New York, 1985. xvi, 459 pp., illus. $120.

Cooperativity Theory in Biochemistry is introduced as a book of methods for the physical biochemist or molecular biologist interested in the applications of fundamental molecular (for example, statistical mechanical) approaches to the analysis of cooperativity in equilibrium and steady-state biochemical systems. Though not intended primarily as a textbook, it follows naturally after Hill's 1960 classic *Introduction to Statistical Thermodynamics* and is suitable, with the reservations noted below, for use in graduate-level discussions of binding equilibria and kinetics.

The focus of the book is on an explicit treatment of interactive cooperativity in equilibrium and steady-state systems. By this Hill means that the cooperative interaction free energies appear explicitly, rather than being buried in composite binding constants or rate constants used in more empirical analyses of these systems. The book is logically divided into three sections, the first of which reviews the statistical-molecular treatment of noncooperative systems and summarizes some of the statistical mechanics required for a full appreciation of the subsequent material. The second and third sections cover the molecular description of cooperativity in systems with small and large numbers of interactive sites, respectively. Within each section, an attempt is made to cover equilibrium and steady-state systems in parallel in pairs of chapters. The third section concludes with rather specialized chapters on Monte Carlo studies of equilibrium and steady-state cooperative processes on two-dimensional lattices and on the extension of the mean-field (Bragg-Williams) approximation to steady-state phase transitions. As Hill notes in the preface, these final chapters are likely to be of interest principally to theoretical physicists.

Most of the strengths and limitations of the book are discussed in the preface and the chapter introductions. The book seeks to integrate the author's recent analyses of cooperativity in steady-state enzyme systems into a broader context, as well as to review the uses of the grand partition function in the equilibrium treatment of cooperative noncovalent interactions, another subject to which the author has made important contributions. Since emphasis is placed on general methods rather than on particular applications, some of the best-known examples of cooperative biochemical processes, including both systems with small numbers of sites (for example, hemoglobin and aspartate transcarbamylase) and lattice systems (for example, conformational equilibria of the α-helix and nucleic acid helices) are omitted from the book, although some references to work on these topics are provided. These omissions would make it difficult to use the book as a primary textbook or as a primary source for someone entering the field. In the examples of cooperative systems chosen to illustrate the mathematical analysis (for example, Ca^{2+} and H^+ transport and ATP hydrolysis by the calcium ATPase of sarcoplasmic reticulum; interaction of Ca^{2+} and myosin S1 fragment with an actin-troponin-tropomyosin complex), little space is devoted to the physical description of the systems or to the physical significance of the results. Although the book is logically organized with regard to the extent and complexity of the systems analyzed and the range of the cooper-

ativity, the alternation of equilibrium and steady-state analyses, which utilize fundamentally different theoretical approaches (since no steady-state analog of a grand partition function exists), is not as didactically useful as it might first appear to be.

Hill repeatedly emphasizes the importance of an explicit introduction of free energies for cooperative interactions into equilibrium constants and rate constants and the superiority of analyses based on the grand partition function over more empirical thermodynamic analyses of cooperative equilibria. The criticism of previous work that is implied by this emphasis is not entirely warranted. The grand partition function is effectively equivalent to the so-called binding polynomial, which has frequently been used to analyze both noncooperative and cooperative binding interactions. Binding polynomials may be directly interpreted as ratios of the total concentration of a species (in all states of ligation) to the concentration of the fully dissociated species. This straightforward chemical interpretation is intuitively appealing and may confer additional insight. Hill demonstrates that the grand partition function provides a direct and elegant route to the analysis of cooperativity and site exclusion in the binding of large ligands to a linear lattice. This derivation is characterized as "much simpler" than the equivalent approach of McGhee and von Hippel, which is based on conditional probabilities and which has been widely utilized for the analysis of ligand-binding to nucleic acids and ligand effects on nucleic acid equilibria. However, each step in the McGhee-von Hippel analysis is intuitively clear, and one gains an understanding of the molecular basis of the contributions to positive and negative cooperativity from an understanding of the derivation.

Hill acknowledges that conventional methods of treating cooperativity in biochemistry have been effective but considers that a more fundamental molecular approach is now warranted. However, many biochemical systems are sufficiently complex that rigorous statistical mechanical treatments, based on detailed molecular models, may not generally be feasible at present. In particular, biochemical systems are characterized by extreme thermodynamic nonideality, as a result of excluded volume effects and preferential (for example, electrostatic) interactions, which cause concentrations to differ significantly from activities and therefore introduce large dependences of apparent equilibrium constants and rate constants (defined on the basis of total reactant concentrations) on the composition of the solution. Whereas substantial progress is being made with some systems in the analysis of these effects, it remains in general difficult to determine intrinsic equilibrium and kinetic constants for biochemical processes. The use of apparent equilibrium and kinetic constants, and the conventional methods of analysis based on these quantities, will of necessity continue in most cases. The availability of more detailed statistical-molecular approaches such as are presented here should inspire more comprehensive experimental investigations of these systems.

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