

In claiming (chapter 7, p. 300) to have devised something comparable in significance to Einsteinian relativity, the authors indulge in hubris and bombast. The latter word reminds me, by the false etymology from his middle name, Bombastus, of Paracelsus. Brooks and Wiley have in their joint enterprise fabricated a modern similitude of his extraordinary character. Does the mixed-up medieval, initiator in his day of a fusion of chemistry and biology that was later completed in more orderly fashion by van Helmont, have the fitness to survive in the more highly evolved ecosystem of 20th-century science? Possibly, but he must take heed of his Achilles' heel, that great weakness in basics of classical thermodynamics, and do something about it.

Read this book, then as Paracelsian: muddled philosophy, to be read quickly, requiring disregard of obvious errors but with a genuine fire burning in it for provocation and stimulation.

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## Muscle Contraction

**Energetic Aspects of Muscle Contraction.** ROGER C. WOLEDGE, NANCY A. CURTIN, and EARL HOMSHER. Academic Press, Orlando, FL, 1985. xiv, 360 pp., illus. \$79.50. Monographs of the Physiological Society, no. 41.

The use of energetics as a framework for developing and testing hypotheses about muscle contraction, which began in earnest with the work of Fenn in the 1920's and continued with the publication of Huxley's crossbridge theory in 1957, diminished in the early '70's as recognition of thermodynamic constraints introduced complexities into energetics studies, causing many outside the immediate field to lose interest. The considerable progress made since then, presented in *Energetic Aspects of Muscle Contraction*, shows that the time has come for renewed attention to what energetics is telling us about muscle contraction.

Most of the book, which treats the energetics of vertebrate skeletal muscle, is contained in three chapters describing relevant studies of the mechanics of intact contractile systems, the biochemical kinetics of isolated contractile proteins, and heat production and chemical change measured in whole muscles. A short introductory chapter describes general properties of muscle, summarizes the crossbridge hypothesis, and presents a list of unanswered questions. The

final chapter describes the 1957 theory and its recent variants and discusses them in the context of the experimental results presented in the book.

The organization of sections on biochemical kinetics and energy balance reflects the more rigorous hypothesis-testing characteristic of these relative newcomers among experimental approaches to muscle. The chapter on kinetics explains briefly how models of biochemical mechanisms are tested experimentally and summarizes some important issues concerning the mechanism of adenosine triphosphate hydrolysis by the isolated contractile proteins, all with commendable clarity. It is a palatable introduction to the subject and is especially recommended to those plagued by a high activation energy for learning about kinetics.

A section on energy balance contains the best lessons on energetics. The importance of studies on this subject and the progress made in recent years is readily appreciated by comparing the results of biochemical experiments by Kushmerick and Davies published in 1969 with those of very recent experiments by Homsher and colleagues in which both energy liberation and high-energy phosphate hydrolysis were measured. Kushmerick and Davies showed that although phosphate hydrolysis was adequate to account for the work done by active muscles it could not account for the heat production expected during rapid shortening, raising the possibility that heat is produced by a process unrelated to work production, which would call into question the relevance of Hill's heat measurements and thus compromise much of the predictive success of the 1957 theory. Homsher's experiments show that all the energy liberated by shortening muscles is explained by the quantity of phosphate hydrolyzed. The discrepancy appears because at high velocities phosphate hydrolysis lags behind energy liberation, and energy balance is achieved only after shortening ends. Although no existing model can accommodate this behavior, current crossbridge theories might be made to do so without drastic changes, and in the last chapter it is suggested that a branching physiological crossbridge pathway be explored.

The presence of so many facts and figures in one smallish volume makes it a handy reference. The book is also quite fun to read, for it provides the reader with many pieces of a large puzzle. One's sense of rediscovery in reading it is complemented by the style of presentation in sections on mechanics and on energy liberation. Sufficient information is included to make the uninitiated comfortable with concepts and methods, but the intellectual context of the experiments is not

so well developed that it discourages the reader from rearranging the facts into novel hypotheses. An additional advantage is that many sections can be read individually.

The book contains minor flaws. The figure legends are too brief, and some information, such as the magnifications of several micrographs in chapter 1, is omitted altogether. On p. 16 we read "what is the nature of the binding between actin and myosin, covalent, electrostatic, . . . ?" and on p. 147 "actin binds, noncovalently but very tightly, to myosin." Some calculations are more obscure than they need be; for example, the work done by a crossbridge (p. 24) and the lifetime of an isometric crossbridge (p. 117) could have been clarified by more specific references to appropriate sections of later chapters. But the flaws are not serious, and chasing the numbers is rewarded by enhancement of insight into how facts, theories, and guesses can be blended most productively to stimulate better questions and experiments.

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## Neuroanatomy

**The Thalamus.** EDWARD G. JONES. Plenum, New York, 1985. xx, 935 pp., illus. \$135.

Seduction by passionate interest in the thalamus must have its hazards. Jones relates with charm an anecdote about Sir Wilfrid Le Gros Clark, one of his mentors, facing his fellow Oxford dons proclaiming expertise on the thalamus—a word endowed with a nuptial or bedchamber connotation in classical Greek. For all that, Jones has succumbed to a scholarly and research interest that has resulted in the production of a truly monumental contribution. There are few books of such enormous scope in modern times—perhaps Grant's *Anatomy* and Boyd's *Pathology* may serve as exemplars—and in neuroanatomy nothing of such magnitude since the extraordinary contribution of Ramón y Cajal.

One of the extraordinary and valuable features of the book is that it contains a large number of high-quality photomicrographs, a large proportion of the best of them derived from the author's own preparations. There are several series of sections in different species, mostly transverse and Nissl-stained and all of high technical quality. They are not quite sufficient to serve as atlases, but they do provide a good guide for comparative anatomy. There are a few con-

sistent misfortunes such as the unintentional use of the same symbols for paratenial and pretectal nuclei, the latter receiving short shrift as well as confusing and inappropriate designation, but most of the illustrative material is well chosen and clearly explained.

There are a few other items of minor concern, such as failing to refer to some original contributions, but in general such failings can be forgiven because the author's own work has usually been superior to and better illustrated than that of others and the overall level of scholarship in the book is exceptionally high. Even a revisionist history of the posterior group (now a "complex") will serve as a stimulus to work on this subject, but some of the generalizations seem a bit broad. For example, Jones suggests that the spinothalamic tract terminations overlap the cerebellar and medial lemniscus projections and do not stray outside these borders, thereby dismissing the evidence of a more dense medial projection to nucleus submedius. But such oversimplifications, intended to establish general principles, are rare in this insightful and critical survey of the thalamic literature.

A comprehensive work on so expansive a subject cannot cover all bases with equal success. Discussion of the electrophysiological literature on such subjects as inhibition and joint efferent representation might evoke some serious debate, and there is obviously room for further scholarly accounts of the physiological literature or of the vast confusion concerning the nature of "thalamic pain." That said, I have no doubt that the book will stand as one of the great monographs on neuroanatomy of the 20th century. We are indebted to Jones for a superlative achievement in producing a huge reference work that is a joy to read for both its style and its provocative content. The illustrative material sets a standard of excellence that will be hard to match.

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## An Evolutionary Question

**Sexual Selection and Animal Genitalia.** WILLIAM G. EBERHARD. Harvard University Press, Cambridge, MA, 1985. xii, 244 pp., illus. \$25.

Why are animal genitalia, especially male intromittent organs, so extravagantly variable among species and why do they apparently evolve so rapidly? William Eberhard poses this conundrum and takes a major step

toward solving it in *Sexual Selection and Animal Genitalia*.

So inclusive were the original insights of Charles Darwin that it is unusual for modern students of organic evolution to discover genuinely novel applications of sexual selection theory. The relations of epigamic selection and sperm competition to the structure of animal genitalia represent rare exceptions and thus will be a topic of considerable fascination among evolutionary biologists.

Insect systematists, especially, have long recognized the incredible diversity of male genitalia. They have been delighted to find genitalic distinctions among closely related congeners that permit easy taxonomic diagnosis, often in the absence of other useful characters. Taxonomists have typically accepted this gift of morphological diversity with gratitude for its utility in their work but with little thought as to its ultimate cause.

None of the several theories previously put forth to explain the evolutionary lability of male genitalia has been rigorously tested, nor has any been received with such enthusiasm. Hence there is an obvious need for the present work.

Eberhard has meticulously researched and fully conceptualized the extent of the problem. Using the literature (primarily taxonomic) as a data base, he has designed keen tests of the old hypotheses and of his new one. Remarkably, he succeeds in communicating what clearly represents many years of work in less than 200 pages of highly readable, well-illustrated text. He has accomplished this by deft organization, uncluttered prose, and the extensive use of tables to present data summaries complete with all the relevant literature citations.

The book begins with a review of the problem and a survey of taxa in which fertilization is internal and genitalia have evolved rapidly and divergently. These are contrasted with groups with external fertilization, whose genitalia have remained unchanged through time and speciation events.

The illustrations of insect, mammalian, and reptilian genitalia in chapter 1 are truly amazing and should certainly capture the imagination of most readers. Eberhard's book later mentions, among other sexual oddities, hypodermic insemination of certain insects, disposable genitalia, amorous and exploding sperm packets, multipenised flatworms, and chondrichthian contraceptive douches.

Three chapters analyze existing hypotheses including, "lock and key," "genitalic recognition," pleiotropism, and intersexual mechanical "conflict of interest." The author

explores the logic of these theses and tests the predictions each would lead to. For example, island animals and parasites are categories presumably transparent to selection for mechanical isolating mechanisms, hence animals in these categories should have relatively uniform genitalia if elaborations are evolved by selection for species isolation. Using this and other, more sophisticated challenges, Eberhard ultimately and convincingly brings the reader to his conclusion that none of the previous hypotheses provides a general explanation.

Chapters 5 and 6 put forth a new hypothesis that sexual selection is the most likely explanation for male genitalic extravagance. Eberhard argues that in addition to transferring sperm, male genitalia function as "internal courtship" and intrasexual competitive devices to insure that the organ's owner's sperm will have a high probability of being used to fertilize the female's eggs.

Subsequent chapters expand the new hypothesis and provide further tests of its predictions. These include female discrimination after genital contact, frequency of remating by females, and the function of male genitalia in the stimulation of females. The penultimate chapter entitled "Specialized nongenitalic male structures," examines an important validation by analogy. If male genitalia have evolved primarily by female choice as a consequence of the stimulation they provide, then nongenitalic male structures that have an intersexual tactile function in courtship should be highly variable as well. The hypothesis is validated. The book concludes with a useful summary chapter.

Woven through the fabric of this treatise is a colorful historical thread that tracks the question, How could sexual selection have been so long ignored as an explanation for ornate genitalia? Eberhard observes that if Darwin had worked on beetles rather than barnacles he likely would have included genitalic elaboration in his listing of the products of sexual selection. Eberhard also notes that the historical pervasiveness of androcentricism in the biology of sex may well have obscured the truth.

The book is a study in academic honesty. Eberhard criticizes his own hypotheses in the course of developing them and presents and analyzes alternative hypotheses whenever appropriate. He also points out occasional deficiencies in the data sets that are used. It is a credit to his scholarship and writing skill that the book's integrity is achieved without tedium for the reader.

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