Book Reviews

Muscles and Movement

Muscles, Reflexes, and Locomotion. THOMAS A. MCMAHON. Princeton University Press, Princeton, N.J., 1984. xvi, 332 pp., illus. \$50; paper, \$15

This book is set to become a classic. In it McMahon uses relevant studies from anatomy, physiology, biophysics, biochemistry, bioengineering, and animal mechanics to construct a coherent conceptual scheme for understanding how animals and humans move. The coverage ranges from the kinetics of myosin cross bridges and force development to the production of coordinated walking movements and the development of "tuned" athletic tracks to reduce running injuries and improve race times.

The book is brilliantly successful. As might be expected of someone trained in mathematics and engineering, McMahon's conceptual scheme is, where possible, a mathematical model. This does not mean that students of biology or medicine will find it dry or hard going. On the contrary, the book is entertaining and lucidly written, with many fascinating asides and anecdotes.

The book is logically organized and has a strong historical perspective that gives the reader a feeling for the excitement and pace of development of new ideas. All the more mathematical sections, such as those on cross-bridge kinetics (chapters 4 and 5), are painstakingly worked through, giving all the intermediate steps in the argument.

An unusual feature in a book of this type is the inclusion of a series of worked examples and unsolved problems at the end of each chapter. The answers to the problems are given in a short section at the end of the book. McMahon carefully evaluates the usefulness of and explores the predictions inherent in the various theories and models he develops, and he gives a full account of the experiments that have been carried out to test them. In a few cases, some experiments and hypotheses are taken rather more to heart than they would be by those actively engaged in research on the subjects involved. For example, the idea (p. 79) that nonuniformity of sarcomere lengths "provides a unifying principle" for explaining both the extra tension following stretch of a muscle and tension "creep" in fixed-end tetani and other phenomena remains controversial.

The book starts with Hippocrates's early ideas about muscle contraction and proceeds rapidly to assess the experiments on isolated muscles carried out by A. V. Hill and his colleagues at University College London between 1910 and 1950, which laid the foundation for studies of muscle mechanics. There follows a concise and authoritative account of muscle energetics and heat measurement experiments. In a few cases, for example in the discussion of the hydraulic model of free energy flow in muscle involving floats, valves, and resistances, I found the analogies harder to follow than the facts.

Accounts are given of the organization of muscles, x-ray diffraction in active muscle, the sliding filament model of muscle contraction, and the biochemistry of the contractile proteins. The account of the contractile proteins is somewhat superficial and out of date. For example, it is now three or four years since alkali light chains were shown not to be essential, after all, for adenosine triphosphatase activity of myosin. However, it is unreasonable to expect the same depth of treatment as that in far longer and more specialized books. These accounts were worth including as background for the more "meaty" chapters that follow.

The second section of the book deals with more integrated studies on such subjects as the structure and physiology of proprioceptors, the operation of reflexes, the nervous control of coordinated locomotory movements, and the classifications of gaits. Lucid accounts are given of the various engineering principles involved. This section ends with an amusing account of attempts to build robots with legs.

Chapters on the mechanics of locomotion and the effects of scale are probably the best of all. Excellent accounts are given of the importance of elastic storage of energy and of positive and negative work done by muscles during running, walking, and hopping. Finally, the usefulness of dimensional analysis for studying the effects of scale is explored and models of geometric similarity, elastic similarity, and constant stress similarity are developed and evaluated for such diverse parameters as blood pressure and adenosine triphosphatase activity of myosin. As is the case throughout the book, these chapters are well illustrated and contain diagrams that are simple yet informative and often original.

In conclusion, the book is highly recommended to all those interested in muscle and animal movement. It is likely to be equally useful to students and to established research workers in biophysics, bioengineering, biology, and medicine.

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Comparative Neurobiology

Comparative Neurology of the Optic Tectum. HORACIO VANEGAS, Ed. Plenum, New York, 1984. xx, 850 pp., illus. \$125.

The optic tectum evolved into more than just a part of the midbrain roof. It became a model. To developmental neurobiologists, who used the regenerative capacity of fish and frogs to mimic ontogeny, the visual map in the tectum provided an opportunity to investigate how neural systems achieve a precise wiring. Following seminal work by Lettvin and his colleagues on prey catching in frogs, that group of sensory physiologists who would later be called "neuroethologists" explored the tectum for the type of feature detectors suggested by ethological models of behavioral control. The tectum's layered sensory and motor maps seemed an ideal substrate for extracting principles of sensorimotor integration. When comparative neuroanatomy became reenergized by the development of modern experimental techniques, vision, and especially the retinotectal system, became the focus of attention. Indeed, ten or 15 years ago, one might have thought comparative neuroanatomy was the comparative neuroanatomy of the optic tectum.

As comparative neurobiology has expanded, audition and electroreception have become the glamour sensory systems of the field. The volume of studies of the retinotectal systems in different vertebrates has gradually tapered off, with the exceptions of work on tectally mediated prey catching in frogs and on retinotectal plasticity. But investigations of the optic tectum have generated a tremendous amount of information on its anatomy and physiology in all vertebrate classes, so much information in fact that we have a far more detailed comparative picture of this structure than of any other in the nervous system. This information is presented in Comparative Neurology of the Optic Tectum, a compendium that begins with a chapter on tectal anatomy in lampreys by Kennedy and Rubinson and ends with three fine chapters on the mammalian superior colliculus by Huerta and Harting, Chalupa, and Stein.

The 20 contributions to the volume are arranged so that a chapter on tectal anatomy is followed by one or more chapters on tectal function (physiology and behavioral correlates) for each vertebrate class. In deference to the tectum's central role in many regeneration studies, two chapters on retinotectal plasticity in fish (by Sharma and Romeskie) and frogs (by Levine) are added.

With a few exceptions, the contributing authors have elected to present detailed, and fairly exhaustive, expositions of data amassed from previous tectal studies without much synthesis or speculation. Because of this, and because nearly all the contributions focus on a single vertebrate group, a truly comparative overview is missing from the book. (One notable exception is a chapter by Freeman and Norden on neurotransmitters in nonmammals.) It is a shame that one or more additional chapters were not added to summarize and compare the principles of tectal organization presented for the various vertebrates, because each section reveals common patterns of tectal organization, such as the greater response of the tectum to moving visual stimuli, and common unresolved issues, such as the nature of the interaction of the tectum with forebrain visual centers.

Early in the book, Bullock raises one such issue during his discussion of elasmobranchs: is the optic tectum part of the visual system or a center for multimodal integration? At one level, the answer is that it is both. Certainly any structure with a massive input from the retina and widespread visual activity is part of the visual system. But as the chapters in the volume progress it becomes clear that the tectum also receives highly ordered, multiple nonvisual sensory inputs in every vertebrate so far examined. The problem is more complex than this, however. At the root of Bullock's query is the question of what if 14 DECEMBER 1984

anything these other sensory inputs contribute to the visual function of the tectum. Most investigations of the nonmammalian tectum implicitly assume that there is an interaction, or that at the least both visual and nonvisual maps laver onto a common "motor map" that provides the output of this structure. But Bullock states explicitly that there really is little evidence for this in sharks. And, in an excellent chapter, Huerta and Harting detail the vast morphological and physiological differences between the superficial and deep zones of the mammalian superior colliculus, differences that suggest strongly that in mammals the colliculus consists of two functionally independent systems, a purely visual area above and a multimodal (including visual) area below. Does such an organization exist in any nonmammals? Or is the segregated condition a mammalian specialization with a still unknown purpose?

There is no answer to this question, and it is worth exploring. For when investigating how the functional organization of different tectal zones varies across vertebrates and how the tectal functional organization may have evolved, one is also addressing a far more fundamental problem in comparative neuroanatomy: whether homologies can be established between subregions, and even between types of neurons, within homologous regions of the brain. Underlying many of the anatomical contributions to this volume is a feeling that the identification of such microhomologies is not only a desirable goal but a real possibility. One can detect the feeling most strongly in a chapter by Freeman and Norden on neurotransmitters in the tectum, in a chapter by Hunt and Brecha correlating morphological, biochemical, and physiological properties of avian tectal neurons, and in a chapter by Northcutt on reptilian tectal anatomy that compares the variation in lamination and cell type among reptiles and briefly discusses the problems of extending the comparison to other vertebrates. If neuronal homologies can be explored anywhere in a complex vertebrate brain region it will be in the tectum. A great deal of groundwork has already been laid in describing neuronal morphology, transmitter biochemistry, laminar arrangements, and the details of afferent terminations in a wide spectrum of vertebrates.

The contribution of Vanegas and his authors is that they present this groundwork in detail. This is a book one buys for raw information, rather than for a new synthesis. It is a book to have for reference rather than a book to read for the latest ideas. But its expansive treatment does present the type of information that might cause a reader to wonder if the optic tectum could be pressed into service as yet another model system: a model to explore neuronal homologies and the evolution of intranuclear organization.

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The Geology of Africa

The Geochronology and Evolution of Africa. L. CAHEN, N. J. SNELLING, J. DELHAL, and J. R. VAIL with the collaboration of M. Bonhomme and D. Ledent. Clarendon (Oxford University Press), New York, 1984. xiv, 512 pp., illus. \$110.

In 1902, just six years after radioactivity was discovered, the New Zealand physicist Ernest Rutherford and his student Frederick Soddy, armed with their concept of the half-life, dated Canadian pitchblende at 700 million years old. In 1948 the visionary British geologist Arthur Holmes, working in Africa, first demonstrated the power of geochronology for systematic correlation of Precambrian crust.

Africa is a good place to decipher earth history. The Precambrian covers 87 percent of earth history, and more Precambrian crust is exposed in Africa than on any other continent. The authors of this book undertook an ambitious geochronologic survey encompassing the African continent, Madagascar, and the western Arabian shield. Their task was daunting. Mainland Africa has 47 recognized countries, ranging from Gambia (10,403 square kilometers) to Sudan (2,505,813 square kilometers). Below or next to little-deformed cratonic strata lie about 60 juxtaposed or crosscutting Precambrian tectonic provinces whose interiors and boundaries are thoroughly mangled by pervasive strain and regional metamorphism.

The book assumes familiarity with or provides references to techniques of age dating but begins with a chapter summarizing recent developments in methodology and interpretation. The authors illustrate the uses and pitfalls of discordant ages and discuss the scale of open and closed systems and many causes of daughter nuclide leakage. They go back