

the piconewton range. Many of these motors use the actin and microtubule filaments of the cytoskeleton as dynamic "tracks," which the cell assembles where and when they are needed. In fact, the cytoskeletal polymers themselves can generate sufficient force as they polymerize or depolymerize to drive organelle movements. Some motors work alone or in small numbers (kinesin, myosin V), while others work in concert with many partners (myosin II). Despite this diversity, unifying principles have emerged according to which protein motors operate.

Traditionally, biologists characterize energy conversion using a free-energy diagram. But thermodynamics gives only a very limited picture and cannot address the issue of mechanism. Over the last 10 years, single-molecule techniques and structural-studies experiments, complemented by quantitative modeling, have provided a more mechanistic view of the functioning of motor proteins and cytoskeletal polymers and of the cell motility. Quantitative analysis of load-velocity curves and motion statistics for single molecules provide answers to the long-standing questions: How do these proteins move? How much "fuel" do they consume? How is this fuel converted into mechanical force?

Answering these questions requires knowledge of classical mechanics at a level covered in many physics textbooks. However, these books deal mainly with macroscopic systems, while mechanics on the molecular level is dominated by Brownian motion. Thermal fluctuations smear out deterministic trajectories and serve as a lubricant that allows molecules to surmount high energy barriers. All this leads to surprising and counterintuitive behaviors. What has been missing from the literature is an introductory treatment of this realm of classical physics that can be grasped by a biological audience.

Jonathon Howard's *Mechanics of Motor Proteins and the Cytoskeleton* fills this void, providing a physical foundation for cell mechanochemistry for students of biology, physics, mathematics, and engineering. Other books cover similar biological ground, but do not cover the physics of cell motility.

Howard is well suited to writing a textbook about cytoskeletal mechanics; he has done important work on the mechanochemistry of cytoskeletal molecules and is one of the foremost researchers on kinesin.

The first part of the book introduces the basic concepts of classical mechanics and statistical physics necessary to

treat a protein as a machine built from elastic rods, joints, levers, and latches. While these beginning chapters are likely to be quite familiar to physicists and engineers, they will surely be very useful for biology students. Even readers familiar with the physics will benefit from the plentiful examples, analysis of length and time scales, and back-of-the-envelope estimates for building intuition about a microscopic scale. Moreover, Howard treats carefully and clearly the difficult topic of the coupling between mechanical forces and chemical reactions.

The second and third parts of the book are devoted to the mechanics of the cytoskeletal filaments and motor proteins, respectively. This material will be challenging for students of all disciplines. Physicists and engineers will learn the importance of the voluminous structural and biochemical data about actin, microtubules, myosin, and kinesin. Biologists will be introduced to methods for applying the quantitative apparatus of the first part to modeling the cytoskeleton. Chapter two explains the phenomena of force generation by filament polymerization, treadmilling, and dynamic instability of biopolymers. The last part of the book introduces the concepts of motor-duty ratio, the mechanochemical cycle, force-velocity relations, and the role of thermal fluctuations in force generation. Comparisons between structures and mechanochemical cycles of kinesin and myosin give a glimpse of the diversity of molecular motors and illustrate some unifying principles of molecular mechanics.

The book is not without shortcomings. Howard discusses only the mechanical properties of individual filaments, ignoring the rheology of cross-linked actin gels and actin dynamics at the leading edge of migrating cells. Some well-studied (and extensively modeled) motors, such as ATP synthase and RNA polymerase, deserve detailed description in this book, but are all but ignored. The elementary hand-over-hand model for kinesin at the end of the book is too primitive and somewhat misleading. However, these minor faults can be overcome in subsequent editions. Moreover, the persistent and curious student can—and must—complement the book by reading recent reviews by Paul Janmey (*Results Probl. Cell Differ.* **32**, 181 [2001]), Gary Borisy (*Curr. Opin. Cell Biol.* **12**(1), 104 [2000]), Ron Vale (*Trends Cell Biol.* **9**(12), M38 [1999]), George Oster (*Biochem Biophys Acta* **1458**(2-3), 482 [2000]), and others. Altogether, this is an excellent multidisciplinary book that will help educate a

new generation of researchers in the field of quantitative biology.

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Elements of Modern X-ray Physics

▶ Jens Als-Nielsen
and Des McMorrow
Wiley, New York, 2001. \$99.95,
\$29.95 paper (318 pp.).
ISBN 0-471-49857-2,
ISBN 0-471-49858-0 paper

Over its 25-year life span, synchrotron radiation has left an indelible mark on physics. This "leftover" radiation, once the bane of particle accelerator designers, has been found to be far more versatile than that produced by conventional sources. The parasitic use by condensed matter physicists spurred great creativity with the development of totally new, x-ray-based analytic tools that could exploit the brightness, coherence, and broad-spectral and temporal structure of synchrotron radiation. Thus were born such techniques as EXAFS (extended x-ray absorption fine structure), magnetic scattering, surface diffraction, fluorescence holography, and magnetic circular dichroism. Existing traditional uses of x rays, such as small-angle scattering, atomic core-level spectroscopy, radiography, topography, powder diffraction, diffuse scattering, and protein crystallography, were similarly able to benefit from the millionfold flux gains, and the radiation could be thereby applied to totally new classes of problems.

A facility sociology was thus thrust upon the once solitary x-ray branch of the condensed matter physics community, whose members learned to accept the demands for beamtime applications and user meetings. These physicists found that, by collaborating with their erstwhile rivals, they could build specialized endstation facilities that enabled all members to make progress far beyond the capabilities of their local institutions. With few exceptions, the appetite for more beamtime availability has been satisfied year after year by the skills of the accelerator physicists to design clever new insertion devices that amplify the usefulness of the x rays by concentrating them into brighter, narrower beams or narrower spectra. As each generation of sources reached its perceived limits, a breakthrough emerged that brought greater hope of future rewards. Until now, there has been a significant economy of scale in designing machines with so many

beam ports that it has not been necessary to form vast, high-energy-like collaborations to carry out the important experiments. Sadly, this may have to change with the latest generation of linear-accelerator free-electron-laser sources being planned.

When a new field of physics emerges, critical ideas and information about methodology will often travel informally by word-of-mouth. Only when the field matures will the textbooks get written. This is particularly true of the synchrotron radiation community, where the informal channels of communication are augmented by the strong user network; users meet each other, sometimes frequently, because they work at the same central facilities. The network is further encouraged by the frequent user meetings. There are well-established, formal training programs such as Hercules, which has been held annually in Grenoble for 12 years and whose lecture materials have served as a substitute for textbooks in the community at large.

The publication of Jens Als-Nielsen and Des McMorrow's *Elements of Modern X-ray Physics* is a defining moment in the field of synchrotron radiation, one that signals its maturity. The book combines in a single volume detailed descriptions of how the new sources work, how they are characterized, and how they affect the results of standard experiments. The reader is led through the topics of interactions with matter, sources, optical properties, diffraction (kinematical and dynamical), and absorption, all described from the synchrotron-radiation perspective. Examples and applications are kept to a minimum, introduced only to illustrate the principles. The physics is spread lavishly throughout the discussions, both as motivation and conclusion.

The level of Als-Nielsen and McMorrow's textbook is appropriate for senior undergraduate or graduate students. Quantum mechanics (at the level of second quantization) and electromagnetism (Maxwell's equations) are assumed, but the important radiation formulas are derived two ways: intuitively in the text and via Maxwell's equations in an appendix. No prior knowledge of solid-state physics is assumed, since the concepts of lattices and phonons are introduced from scratch.

The pedagogy is strong, with most of the mathematical derivations elaborated in detail. A few derivations or formulas are original, in that they are omitted from other texts, either because they are approximate-but-useful (the

form-factor expansion in exponentials, for example) or newly created. Some background concepts, such as the Dirac δ -function and Kramers-Kronig transform, are assigned to tinted text blocks so as not to interrupt the flow of arguments. Several of the derivations are intuitive, using either a commonsense or dimensional analysis approach.

Elements of Modern X-ray Physics will be a welcome addition to the bookshelves of synchrotron-radiation professionals and students alike. One of the book's goals is to reach nonphysicist users of synchrotron radiation. I agree with the authors' stated belief that "a greater knowledge of the underlying principles not only adds to the overall feeling of satisfaction, but also allows better experiments to be designed." The text is now my personal choice for teaching x-ray physics.

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Positron Physics

M. Charlton and J. W. Humberston
Cambridge U. Press, New York,
2001. \$120.00 (454 pp.).
ISBN 0-521-41550-0

Positron Physics by Michael Charlton and John W. Humberston is a clearly written compendium of theories and experiments on the elastic and inelastic scattering and annihilation of individual low-energy positrons and positronium atoms interacting with gas molecules. About three-quarters of the text is devoted to this material, to which the authors have made many original contributions. The book contains, as well, an introduction to positron experimental techniques and material covering the atomic properties of positronium and other small bound systems containing positrons. The book's completeness on its principal topics, including references to about 800 of the original works, is exhaustive enough that I shall finally be able to discard my extensive reprint collection.

While there are many review articles and countless edited volumes summarizing progress in positron solid-state physics, positron atomic physics and positron astrophysics, *Positron Physics* is a real textbook, though without exercises. Its unifying viewpoint and beautiful format as a Cambridge University Press monograph should be an inspiration for others similarly to summarize some other aspects of the last half-century of positron work in textbook format.

Such future writers will now have a high standard to meet, a standard that