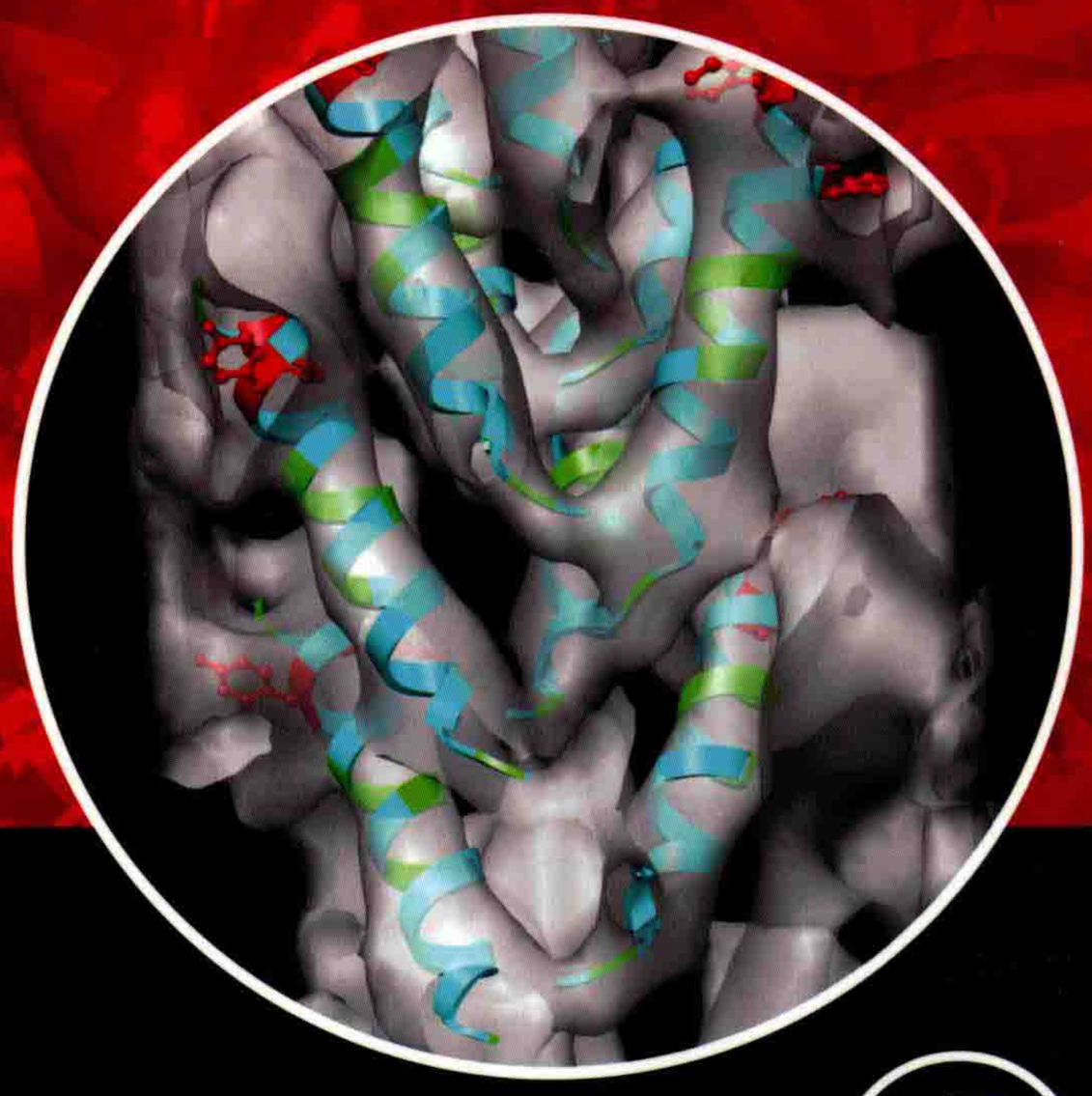
Volume 8

COMPREHENSIVE BIOPHYSICS

Bioenergetics



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COMPREHENSIVE BIOPHYSICS

EDITOR-IN-CHIEF

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VOLUME 8

BIOENERGETICS

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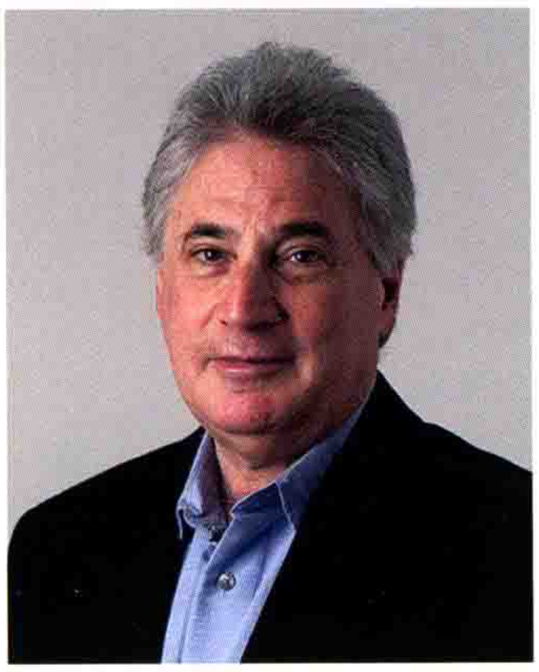

Edward Egelman received a BA in physics and a PhD in biophysics from Brandeis University. He was a postdoctoral fellow at the Medical Research Council Laboratory of Molecular Biology in Cambridge, UK, and then an assistant professor at Yale University. He was an associate and full professor at the University of Minnesota Medical School, and then moved to the University of Virginia in 1999 where he is a professor of biochemistry and molecular genetics. Professor Egelman is currently editor in chief of *Biophysical Journal*, and has been elected a fellow of the Biophysical Society and of the American Academy of Microbiology. His research focuses on the structure and function of macromolecular complexes, mainly using electron cryo-microscopy and computational image analysis. He has spent many years studying the structure of F-actin, as well as helical nucleoprotein complexes formed by recombination proteins (such as the bacterial RecA and the eukaryotic Rad51) on DNA.

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PREFACE

Writing a Preface to the nine volume *Comprehensive Biophysics,* which contains 141 chapters, is a daunting task. Assembling these chapters has been an even more Herculean endeavor, and most of the heavy lifting has been done by the volume editors. The first question that we needed to address when we embarked on this project was the scope, which gets to the question of what is biophysics? One might ask two biophysicists this question and receive three answers. On one level, biophysics can be thought of as the application of physical techniques, such as spectroscopy or diffraction, to biological macromolecules, cells or tissue. It can also be viewed as the attempt to reduce the complexity of biological systems to underlying mathematical models. However we care to define biophysics, it is clearly evolving. What might have been considered biophysics 50 years ago is certainly not viewed as biophysics today. The application of physical techniques has become so commonplace in most areas of biology that they are taken for granted. Many cell biologists routinely use tools such as confocal microscopes, but biophysicists are actively involved in developing new generations of microscopes for studying cells.

Realizing that we could never cover all of contemporary biophysics in nine volumes, we set out to provide chapters that could serve as definitive introductions to a broad array of topics. The planning for these nine volumes began at a meeting held in Washington, D.C. in January, 2009. We recognized at the time that not only were decisions about what to include arbitrary, but decisions about which volumes would contain what chapters were also open to much discussion. Fortunately, we think that links between and among the different volumes will allow the reader to surmount some of the problems of compartmentalization. We also hope that readers will recognize the difficulties of summarizing the impressive growth of biophysics in a finite number of chapters.

Most of the credit for the success of these volumes is due to the Editors of the individual volumes, who played the main role in developing the content of each volume and then soliciting the most appropriate authors. Volume One, which deals with physical techniques for studying macromolecular structure, has been edited by H. Jane Dyson of Scripps. Volume Two, which covers techniques for imaging cells, has been edited by Petra Schwille from the Technical University of Dresden. Volume Three, which is about the folding of proteins and nucleic acids, has been edited by Valerie Daggett from the University of Washington. Volume Four, covering muscle and molecular motors, has been jointly edited by Yale Goldman and E. Michael Ostap from the University of Pennsylvania. Volume Five, covering membranes, has been edited by Lukas Tamm of the University of Virginia. Volume Six, about channels, has been edited by Mauricio Montal of the University of California San Diego. Volume Seven, covering cell biophysics, has been edited by Denis Wirtz of the Johns Hopkins University. Volume Eight, on bioenergetics, has been edited by Stuart Ferguson from Oxford. Volume Nine, on simulations and *in silico* approaches, has been edited by Harel Weinstein of Cornell Medical College.

For the extensive content found in these volumes we are grateful to the wonderful contributions made by a large number of researchers who are at the forefront of their fields. It is hard to quantify knowledge, but many people reading these chapters will realize how so much of what we now know about biophysics has only emerged in the last ten years. Our greatest hope is that these chapters will serve as a guide and inspiration for the many people who will be greatly extending our current knowledge over the next ten years!

Edward H. Egelman
University of Virginia

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*Contributed equally

8.1 Ion Electrochemical Gradients, Roles and Measurements

SJ Ferguson, University of Oxford, Oxford, UK

Abbreviations

OSCP oligomycin sensitivity conferral protein

UCP uncoupling protein

8.1.1 Introduction to Electrochemical Gradients

Electrochemical gradients of ions play a large range of roles in cells. The aim of this chapter is to provide an overview of the nature of such gradients (often misunderstood), the diverse ways in which they are generated and utilized, along with some consideration as to how they are measured.

The gradient across a membrane of any charged species has to be defined in terms of both the concentration gradient and the membrane potential. The concentration and electrical terms can be combined to give the electrochemical gradient for a species X^+ ($\Delta\tilde{\mu}_{X^+}$) (or analogously for X^-) distributed at different concentrations [X^+] between two sides (1 and 2) of a membrane,

$$\Delta\tilde{\mu}_{X^+} = z.F.\Delta\Psi_{1\text{-}2} + RT\ln([X^+]_1/[X^+]_2) \qquad [1]$$

z is the charge (+ or −) on the ion, F is the Faraday constant, $\Delta\Psi_{1\text{-}2}$ is the membrane potential in units of volts or millivolts, depending upon the value taken for F, R is the gas constant and T the temperature in degrees Kelvin. The units of electrochemical gradient are thus kJ mol^{-1}. Sometimes, particularly in the treatment of mitochondrial and related energy transducing membranes, the gradient is expressed in terms of an ionmotive force which is obtained by dividing throughout by zF and thus will have units of volts or millivolts. This is often an area of confusion and it is not uncommon to see values of electrochemical gradient quoted in electrical units; this is always technically incorrect.

Thus, for example, if the concentration of sodium is higher outside (say side 1 of the membrane) a cell, and the membrane potential is relatively positive outside, then both terms will thermodynamically reinforce each other and favor movement of sodium into the cell. On the other hand, if for the same cell, the potassium concentration is greater inside than outside then the concentration gradient will favor the movement of potassium outward from the cell but the electrical term will oppose such movement. Depending on the relative magnitude of the two terms the thermodynamics may favor movement of potassium either into or out of the cell. An important condition is that of electrochemical equilibrium when the tendency to move down the concentration gradient