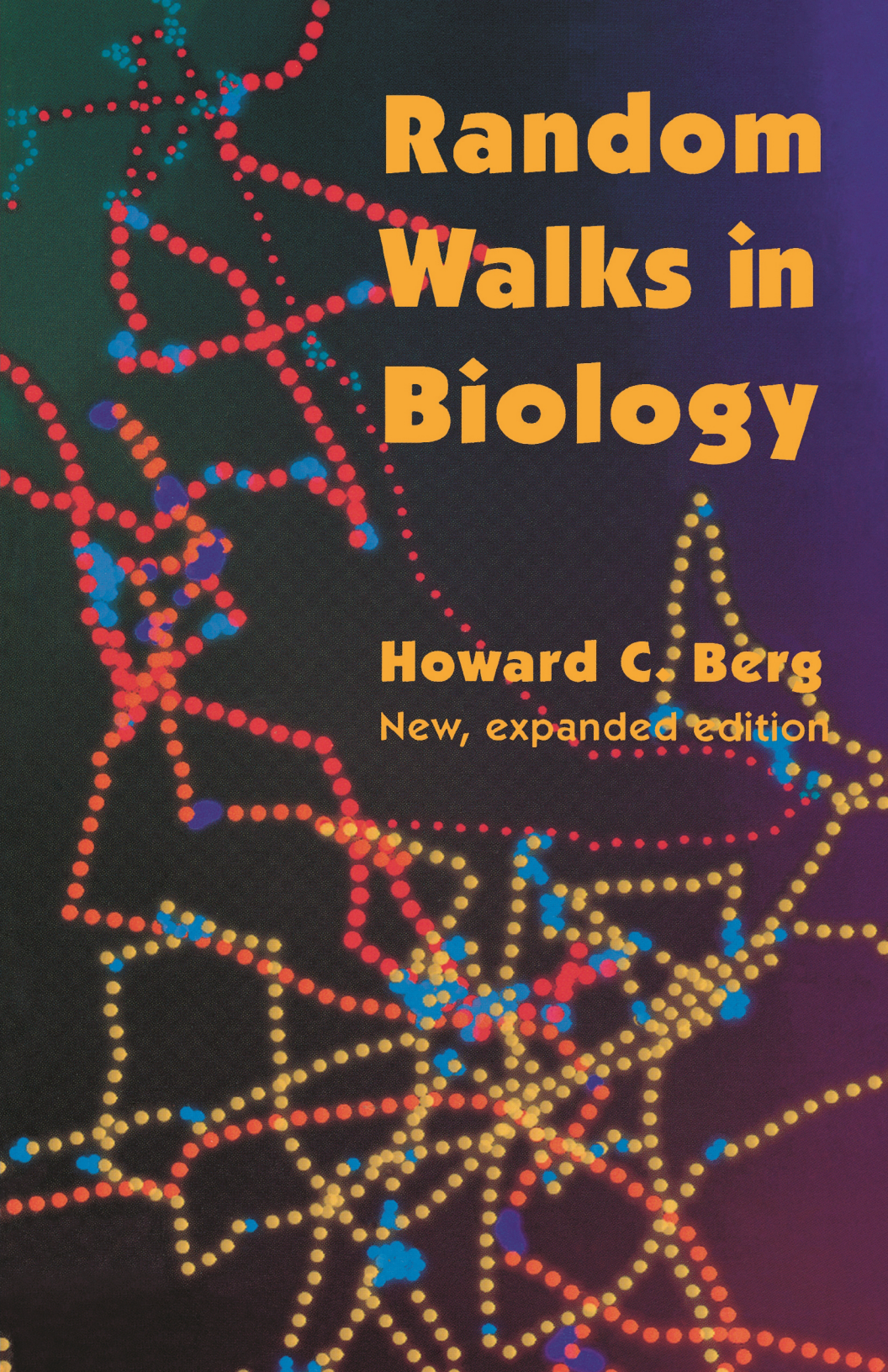
Random
Walks in
Biology
Howard C. Berg
New, expanded edition

Random Walks in Biology

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Expanded Edition

Howard C. Berg

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Preface to the Expanded Edition

I have added an appendix in which more is said about the behavior of self-propelled objects, the subject of Chapter 6. This includes the movement of ions across cell membranes. Ions are not self-propelled, but they drift in electric fields generated by their own displacement. Also, I have corrected the errata and updated the bibliography. Otherwise, this edition is identical to the first. I thank Joel E. Cohen, Nicholas J. Cox, Amal K. Das, Markus Meister, and Katsuhisa Tawada for spotting mistakes and offering suggestions. Finally, I wish to pay my respects to George Pólya, who coined the term random walks and initiated their study. He did this in 1921 in a paper in which he proved that a randomly moving point always returns to its initial position in one or two dimensions but not in three or more. He died 7 September 1985.

Howard C. Berg
Cambridge, Massachusetts
29 November 1992

Preface

This book grew out of lectures given in courses on biochemistry and biophysics at Harvard, at the University of Colorado in Boulder, and at Caltech. It is offered, in part, with the conviction that biologists and biochemists would enjoy their work more if they thought less in terms of thermodynamics and learned some of the rudiments of statistical physics. The intent is pedagogical, not seminal. Statistical phenomena of the sort treated here are met daily in the laboratory but are rarely appreciated as such.

Much of what I know about the physics of random walks has been learned through association with Edward M. Purcell. I have drawn on our conversations, correspondence, and joint publications. I am particularly grateful for his comments on the manuscript. I also wish to thank Steve Block, Rick Lapidus, Markus Meister, and Jeff Segall for help with the exposition and the physics and Connie Katz for masterful word processing. Work on the motile behavior of bacteria, described in Chapter 6, was supported by grants from the Research Corporation, the National Science Foundation, and the National Institutes of Health.

Without doubt, this book can be improved. If you have comments or suggestions, I would be pleased to have them.

Howard C. Berg
Pasadena, California
29 November 1982

Random Walks in Biology

Introduction

Biology is wet and dynamic. Molecules, subcellular organelles, and cells, immersed in an aqueous environment, are in continuous riotous motion. Alive or not, everything is subject to thermal fluctuations. What is this microscopic world like? How does one describe the motile behavior of such particles? How much do they move on the average? Questions of this kind can be answered only with an intuition about statistics that very few biologists have. This book is intended to sharpen that intuition. It is meant to illuminate both the dynamics of living systems and the methods used for their study. It is not a rigorous treatment intended for the expert but rather an introduction for students who have little experience with statistical concepts.

The emphasis is on physics, not mathematics, using the kinds of calculations that one can do on the back of an envelope. Whenever practical, results are derived from first principles. No reference is made to the equations of thermodynamics. The focus is on individual particles, not moles of particles. The units are centimeters (cm), grams (g), and seconds (sec).

Topics range from the one-dimensional random walk to the motile behavior of bacteria. There are discussions of Boltzmann's law, the importance of kT, diffusion to multiple receptors, sedimentation, electrophoresis, and chromatography. One appendix provides an introduction to the theory of probability. Another is a primer on differential equations. A third lists some constants and formulas worth committing to memory. Appendix A

should be consulted while reading Chapter 1 and Appendix B while reading Chapter 2. A detailed understanding of differential equations or the methods used for their solution is not required for an appreciation of the main theme of this book.