BIOLOGICAL AND MEDICAL PHYSICS
BIOMEDICAL ENGINEERING

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The fields of biological and medical physics and biomedical engineering are broad, multidisciplinary and dynamic. They lie at the crossroads of frontier research in physics, biology, chemistry, and medicine. The Biological & Medical Physics/Biomedical Engineering Series is intended to be comprehensive, covering a broad range of topics important to the study of the physical, chemical and biological sciences. Its goal is to provide scientists and engineers with textbooks, monographs, and reference works to address the growing need for information.



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Howard C. Berg

# *E. coli* in Motion

*With 42 Figures, 1 in Full Color*

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Springer

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# Series Preface

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Books in the series emphasize established and emergent areas of science including molecular, membrane, and mathematical biophysics; photosynthetic energy harvesting and conversion; information processing; physical principles of genetics; sensory communications; automata networks, neural networks, and cellular automata. Equally important will be coverage of applied aspects of biological and medical physics and biomedical engineering such as molecular electronic components and devices, biosensors, medicine, imaging, physical principles of renewable energy production, advanced prostheses, and environmental control and engineering.

Elias Greenbaum
Oak Ridge, TN

# Preface

Most bacteria are small, about one micrometer in diameter: ten thousand cells laid out side by side span the width of one's finger. Nevertheless, many species are motile. They swim using propellers (called flagella) that extend out into the external medium or, in the case of spirochetes, that rotate within the cell envelope. One marine bacterium appears to use submicroscopic external oars. Other common bacteria, equipped with large numbers of flagella, swarm rapidly over surfaces. Some bacteria glide over surfaces by extending and retracting thin filaments (called pili) that stick to the substratum at their distal ends, a kind of fly casting. Others move particles linked to the substratum along their outer membranes, by a mechanism as yet unknown. Bacteria of all kinds respond to changes in their environment, for example, to changes in temperature, light intensity, or chemical composition. In short, they move in a purposeful manner.

I have been interested in this world for more than 30 years. When I began, more was known about the genetics and biochemistry of the bacterium *Escherichia coli* than of any other free-living thing. So that has been the organism of choice. The emphasis has been on the responses of this organism to chemical stimuli: chemotaxis. Early work on the motile behavior of bacteria had been done with larger species, more easily seen in the light microscope, so these also are of interest.

How, exactly, does *E. coli* behave? What is the machinery that makes this behavior possible? How is the construction of this machinery programmed? How does this machinery work? And finally, what remains to be discovered?

Since *E. coli* is microscopic and lives in an aqueous environment, the physical constraints that it has had to master are very different from those that we encounter. For example, *E. coli* knows nothing about inertia, only about viscous drag: it cannot coast. It knows nothing about transport by bulk flow, only about diffusion;

as we will see, it can go where the grass is greener, but it has to wait for its dinner. So the methods that its cells use to move and sample their environment are strange to us. This is part of *E. coli's* charm.

This book is designed for the scientist or engineer, not trained in microbiology, who would like to learn more about living machines. However, it also should be accessible to the educated layman and of interest to the expert. I try to build on first principles. However, if you are overwhelmed by the facts that appear in a given chapter, please read on: the figures might suffice. References are given as entrée to the literature and a tribute to those who have done the work.

My own research has been supported by the Research Corporation, the U.S. National Science Foundation, the U.S. National Institutes of Health, and the Rowland Institute for Science. Much of the writing was done while a Fellow of the John Simon Guggenheim Foundation. Space for thought was provided by the Lorentz Institute, Leiden.

A large number of capable people have contributed to the body of knowledge to be described here: molecular geneticists, biochemists, microbial physiologists, physicists. Some, no doubt, will disagree with my emphasis. I can claim only a small part of this work as my own, built on the labor of students, postdocs, and other colleagues. The real hero is *E. coli*. If nothing else, I hope that this book will convince you that *E. coli* demands our admiration and respect.

Howard C. Berg

*Cambridge, Massachusetts*
August 2003

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