To the instructor

> The present generation has no right to complain of the great discoveries already made, as if they left no room for further enterprise. They have only given science a wider boundary.
> — *James Clerk Maxwell*

This book embodies a course that I have taught for several years at the University of Pennsylvania. The students who enroll are mainly second- through fourth-year science and engineering undergraduates who have had a year of introductory physics and calculus. Many have heard rumors about new imaging techniques, quantum phenomena, or something else, and want to know more. Their interest led me to present the radical notion that physics is interesting and important for its own sake, even to non-majors, because over and over we find discoveries being made by people who know in detail how their apparatus works, and so can extend its reach. We find discoveries made years before they "ought" to have been possible, by people who were able to carry out certain kinds of indirect reasoning. And so on.

Thus, I have attempted to "keep the physics in biophysics," not only to enrich students' understanding of the underpinnings of biophysical applications, but also to make basic physics ideas more vivid and concrete by reference to those applications. My goal is not to be comprehensive, but to tell one story that touches on a huge body of ongoing work, reaching all the way into the foothills of neuroscience, a topic of intense interest among my students. Students who know about light, imaging, and vision will find themselves well positioned to learn the many other topics not covered in this finite book.

I have also chosen topics for which I felt I could bring students to the point where they could do the key calculations for themselves (sometimes with a computer). Certainly bringing myself to that point has been a struggle! I hope that students can arrive at a working knowledge of the field more readily with some more guidance than is found in the primary literature.

I've also come to believe that

- Whenever possible, we should try to relate abstract concepts to familiar experience.
- It is possible, and even desirable, to tell students about the nature of light as we currently understand it. It is true that Maxwell's theory is an excellent approximation for some purposes—but unfortunately not for some of the most basic processes of Life. Instead, a single unified framework is now understood to cover all light phenomena. Remarkably, for some applications that framework is no more difficult than the old one.
- The study of basic science is fundamentally intertwined with the development of *instrumentation.* Understanding current instrumentation requires a more sophisticated model of light than what we present in first-year physics. This book positions the student to participate in the ongoing revolution in optical techniques.

- The traditional lead-in to quantum physics, via the energy levels of the hydrogen atom, has some drawbacks. For one thing, the student needs quite a lot of mathematical apparatus to arrive at a result that life-science students, at least, will not see as central to their concerns. Also, the nonrelativistic (Schrödinger equation) approach leaves us unable to say anything about photons, and their many applications to imaging technology. This book instead uses Feynman's viewpoint, which, besides handling photons, has some conceptual advantages.[2]

Another reason to study light has to do with a key skill that every scientist has to exercise, that of *abandoning long-held assumptions.* Of course, we all contend daily with our own mistakes, but not always in a mindful way. So this book pays some attention to the discovery that the wave theory of light could not explain most of how light interacts with individual molecules. Changing our model is not as simple as just walking away, however: Most entrenched, wrong models became entrenched because they succeeded brilliantly at *something.* Any successor must walk the tightrope of preserving those successes, while avoiding the failures. Chapters 1–4 tell the light story, with an eye to the more general situation of having to revise any partially successful physical model.

Rather than organize the material by organism type or by length scale, I have tried to arrange the plot line in a way that builds up the framework needed to understand one important system, the vertebrate visual system (Chapters 9–11). Mathematical ideas such as complex numbers are developed as needed. Sometimes concepts are introduced before they can be fully explained, for example, fluorescence microscopy. In those cases, I have given enough detail at the first appearance to support the point being made, with a forward reference to the chapter that gives more details.

This book is independent of my earlier ones (Nelson, 2014; Nelson, 2015); that is, they are not prerequisites for reading this one. Nor is there much overlap between the coverage of these three books. For example, both prior books intentionally omitted almost any mention of quantum physics, which gets star billing here.

The basic quantum ideas are central to some important biological phenomena (phototransduction, photosynthesis), as well as a host of experimental methods (fluorescence imaging, including superresolution, two-photon, and FRET). Extending that point, other cutting-edge laboratory techniques also rest on physical principles, which are often poorly understood by their users. Understanding some physics not only can improve lab practice, but also prepares students to invent new techniques (or adapt old ones).

Ways to use this book

Undergraduate course: Parts I–II of this book could serve as the basis of a course on the science underpinning contemporary biological physics. Alternatively, that core has enough overlap with the traditional "Modern Physics" course that it could be used for a version of that course, for students with particular interest in life science. Or it can be used as a supplement in more specialized courses on physics, biophysics, nanoscience, or several kinds of engineering or applied math.

Depending on how much you time you need to devote to background, you may find that even Parts I–II cover more than one semester's worth of material. In that case, you may want to consider skipping, or treading lightly on, any of Chapters 3 or

[2]One *dis*advantage is that it's hard to find the levels of the hydrogen atom! However, Chapter 12 makes a start via a simpler problem.

6–8, none of which are essential for Chapters 9–11. Conversely, if vision is not your goal, you may instead wish to drop some or all of Chapters 9–11.

This book assumes that, in addition to first-year physics, the student has had some introduction to the basics of probability. If that's not true for your students, you can cover the Prologue material very carefully, perhaps assigning extra problems from another source (such as Nelson, 2015). Otherwise, you can skip the Prologue, reminding students that it's there to set notational conventions. In later chapters, "Background" sections summarize other foundations in the same terse style.

Most chapters end with "Track 2" sections. Some of these contain material appropriate for students with more advanced backgrounds in physical or life science. Others discuss topics that, although at the undergraduate level, will not be needed later in the book. They can be discussed à la carte, based on your and the students' interests. The main, "Track 1," sections do not rely on any of this material. Also, the *Instructor's Guide* contains many additional bibliographic references, some of which could be helpful for starting projects based on primary literature.

Graduate course: Although Track 1 is meant as an undergraduate course, it contains plenty of material not generally included in undergraduate physics curricula. Thus, it could easily form the basis of a graduate course, if you add all or part of Track 2, Part III, and/or some reading from your own specialty (or work cited in the *Instructor's Guide*). The chapters in Part III assume that the reader has some more advanced background than the main text; see the introductions to each chapter.

Numerical work

To do research, students need skills including graphical presentation of data and model results, numerical math, and handling of datasets.[3] But few people enjoy studying a computer math package (nor math itself) in an antiseptic, context-free way. That's what makes computers and math so boring to some people.[4] My students get motivated when they have a concrete problem, perhaps one involved in obtaining a classic result, driving them to build up the skills to solve it. Specifically, many students find biological problems to be a compelling starting point.

In my own course, many students arrive with no programming experience. Two separate *Student's Guides* give them some computer laboratory exercises and other suggestions for how to get started using MATLAB® or Python (Nelson & Dodson, 2015; Kinder & Nelson, 2015). Several other general-purpose programming environments would also work for the exercises, depending on your own preference, for example, *Mathematica*®, Octave, R, or Sage. Some of them are free and open source.

The *Instructor's Guide* gives solutions to the Problems and Your Turn questions in this book, including code. You can request it by following the instructions at `http://press.princeton.edu/titles/11051.html`.

Classroom demonstrations

One of the most powerful teaching techniques involves bringing a piece of apparatus into the class and showing the students something weird and *real*—not a simulation, nor a metaphor. The optical part of the course provides many opportunities for such

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[3]The book's companion Web site features a collection of real experimental datasets to accompany the homework problems.

[4]It's also what makes them so exciting to other people!

experiences, partly justifying its prominent place in this book. The *Instructor's Guide* offers some suggestions.