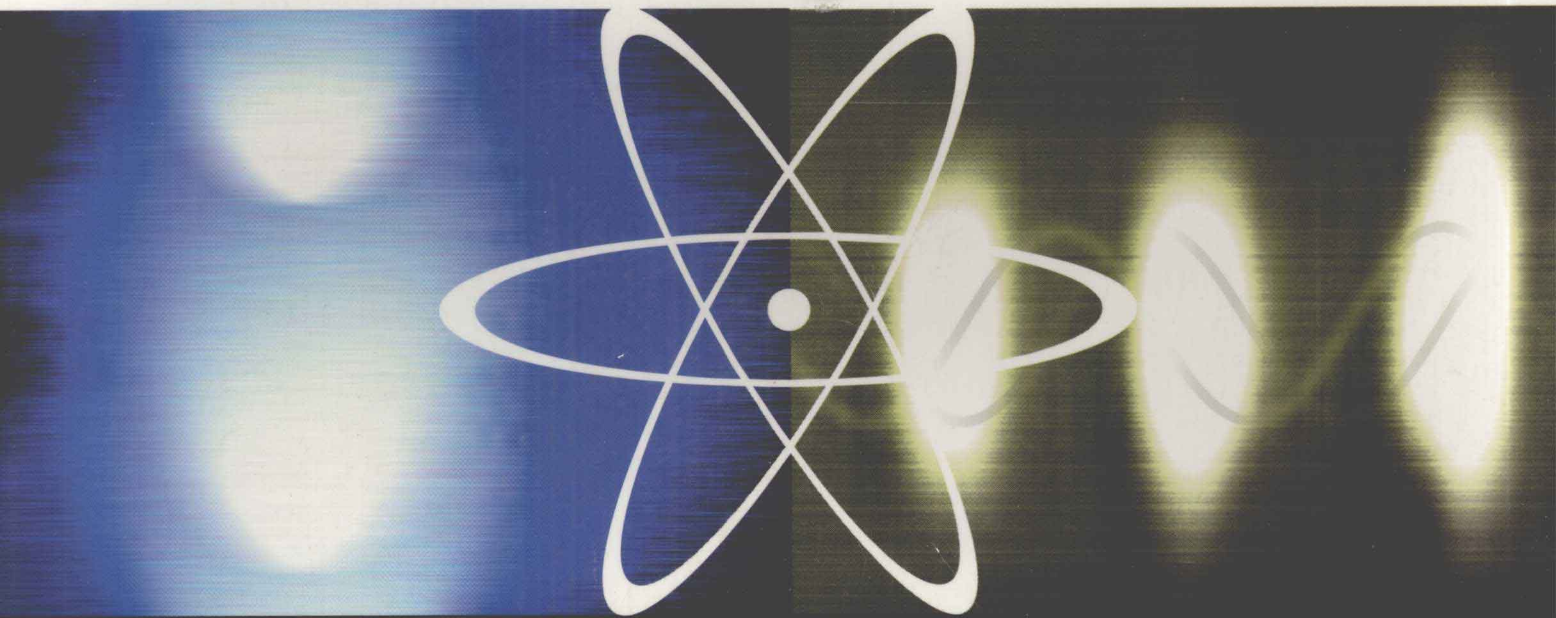
PHYSICS FOR THE BIOLOGICAL SCIENCES

A TOPICAL APPROACH TO BIOPHYSICAL CONCEPTS

Third Edition



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Preface

The last quarter of the 20^{th} century has witnessed a vast change in the life sciences. At the beginning of this period, although the role of DNA was understood and the basics of protein structures were being worked out, the bulk of biological understanding was at the level of taxonomy, genetics, population dynamics and microbiology. Although biologists have always been leaders in using the tools of the physical sciences, their discipline resisted the direct application of the theoretical foundations of physics and chemistry, and the rigour of mathematics.

Many developments have changed this situation, perhaps the most important being the ubiquity of powerful computing. With this tool it became possible to descend to the smallest entities of life-molecules and to understand them comprehensively in terms of fundamental physical and chemical processes. It is more important than ever that life scientists have a firm foundation in the physical sciences.

In 1972 Hallett, Stinson, Graham and Speight produced a textbook for life-science students which was a radical change from the usual introductory physics text which has a presentation determined by the perceived needs of physical science and engineering students. The objective of their book was to educate the student in the fundamentals of physics (both classical and quantum) that were most appropriate for the life sciences. The topic of sound and acoustics was centred on human hearing and bat navigation; optics (ray, wave and quantum) was motivated by the human visual system; mechanics was centred around locomotion, material strength and scaling; and electricity led to an understanding of the neural spike. Gone was the emphasis on pulleys and machines, blocks sliding on ramps, and water flowing over weirs. In their place was the determination of forces acting at skeletal joints and quantitative analyses of the pulmonary system. Twenty-five years of use has justified the choice of topics and the engagement of life-science students with these examples.

With the passage of years, however, more has changed than just biology; physics and pedagogy have both advanced and there is a growing return to what is now called "student-centred learning." With less reliance on lectures and more on guided self-instruction it was felt that the time was ripe not only to update the content of the textbook but to try to make it even more self- contained and comprehensive. Hence the present new edition with some of the original, and some new, authors.

As is quickly noted from glancing through the chapters in this book, there is a considerable amount of mathematics. We make no apologies for this because we are convinced that one cannot hope to really understand the operation of a biological process such as, for example, vision without understanding in some detail pertinent physical phenomena in a quantitative manner. Further, it will be apparent that the book places a heavy emphasis on problem solving and there are numerous worked examples. This was done with the conviction that the process of working problems really does help the student to come to grips with important concepts. The level of the problems is such that they can be successfully tackled by first-year university students with a limited background in physics and mathematics. While the problems do not involve calculus, the calculus is used in some formula derivations. A great deal of emphasis is placed on simple wave functions (sine and cosine) and on functions of the form of an exponential because of their biological importance in population growth and decay, in light absorption, in radiation-biophysics, in bioenergetics and in neural spike propagation.

Our goal is to demonstrate that one can gain good insight into a biological process by approaching it from the physical point of view. Our experience is that a course of this type can be enjoyed by biology, agriculture and physical science students alike, especially if they have the opportunity to interact.

The entire book has been rewritten and new chapters have been added; for example, biomechanics that was confined to one chapter now is expanded into three. Remedial material (logarithms, graphing functions, etc.) have been removed since there is now a plethora of remedial tutorial material available on the World Wide Web. To this end we have included Appendix 2 with the Web address of a resource list of excellent remedial tutorials along with interactive applets that students are encouraged to use to augment their studies and, perhaps, spark their interest in biophysics.

This edition is a test version for the academic years 2000–2002 after which revisions and corrections will be implemented for the academic year starting in September 2002. We invite comments and suggestions from all users—students and teachers. The e-mail address is available on the Web page discussed in Appendix 2.

June 2000

FRH, JLH, ELM, GHR, RHS, and DES

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A Note from the Publisher

Thank you for selecting *Physics for the Biological Sciences: A Topical Approach to Biophysical Concepts*, Third Edition, by F.R. Hallett et al. The authors and the publisher have devoted considerable time and care to the continuing development of this book. We appreciate your recognition of this effort and accomplishment.

As this edition of *Physics for the Biological Sciences* represents a work in progress, please take a few minutes to fill in the stamped reader reply card at the back of the book. Your comments and suggestions will be valuable to us as we prepare new editions and other books.

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Figure 13-12 from *Random Walks in Biology* by Howard C. Berg (Princeton: Princeton University Press, 1983), p. 80, Figure 6.4.

Contents

1 Vibrations and Waves

1.1 Introduction

Vibrations and waves are among the most important types of motion found in nature. The movement of an insect's wing during flight and the oscillations of the tympanic membrane of the ear are examples of vibrational motions of interest in biology. Wave phenomena occur in studies of sound, light, and the energy and arrangement of electrons in atoms and molecules. In this chapter some of the terms and mathematics used to describe vibrational and wave motion are presented. Many applications to living systems will be discussed in later chapters.

1.2 Simple Harmonic Motion

Many objects in nature, ranging from atoms in molecules to fluttering leaves on tree branches, are subject, when displaced slightly from their equilibrium position, to a force that is proportional to the displacement from equilibrium. Such objects, if displaced slightly from equilibrium and then released, will undergo back-and-forth oscillatory motion, known as *simple harmonic motion* (SHM). A simple, although somewhat academic, model of such a system is shown in Fig. 1-1. A mass m rests on a horizontal surface on which friction is negligible. The mass is attached to a spring S that has a mass which is very small compared to m.

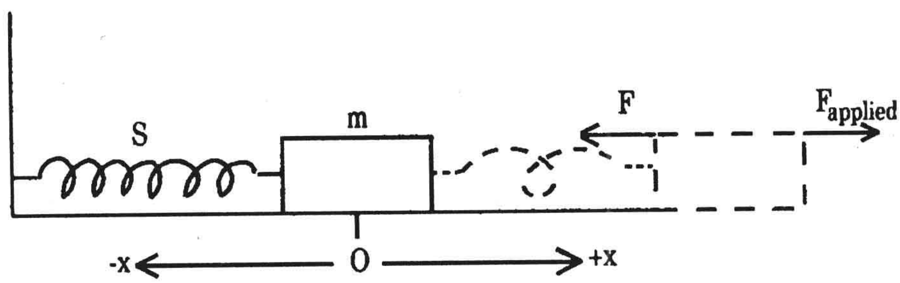


Figure 1-1

Mass-spring system undergoing simple harmonic motion.

When the mass is at the equilibrium position ($x = 0$), the spring exerts no force on it, and if the mass is released from rest at equilibrium, it remains there. If the mass is displaced to the right ($+x$-direction) or to the left ($-x$-direction), the spring is stretched or compressed and exerts a force $\mathbf{F}$ (see Box 1-1) on the mass in the direction opposite to the direction of the displacement, i.e., the force is directed back towards $x = 0$. This force is referred to as a *restoring force* since it tends to push the mass back towards equilibrium. For small displacements, it is found that the magnitude of $\mathbf{F}$ is proportional to the displacement x.[1] Because of this proportionality, a graph of F vs. x is linear, and the force is called a "linear" restoring force.

Box 1-1 Vector and Scalar Notation

Vectors are quantities that have both magnitude and direction. Examples include force, velocity, acceleration, and electric field. *Scalar* quantities have only magnitude; time, temperature, and speed are examples. In this book, vectors are shown in boldface type, such as $\mathbf{F}$ for force. Scalars appear in non-boldface type—for example, t for time.

The *magnitude of a vector*, which is always a positive quantity (or zero), is also displayed in non-boldface type. Hence, the magnitude of the force vector $\mathbf{F}$ is F.

Vectors are often expressed in terms of their *components* in x- and y- (and possibly z-) directions. These components, which can be positive, negative (or zero), are shown in non-boldface type with subscripts. Thus, the x- and y-components of force $\mathbf{F}$ are F_x and F_y.

The proportionality between F and x can be expressed as an equation by introducing a positive constant of proportionality, k, giving $F = kx$. The constant k is known as the *force constant* of the system and represents the force per unit displacement of the spring. A stiff spring has a large force constant, and a soft spring has a small force constant. In the equation $F = kx$, the SI units of F and x are newton

1. The proportionality between F and x is often called "Hooke's law," although it is really an experimental observation rather than a law of nature. This "law" was first stated by the English scientist Robert Hooke (1635–1703).

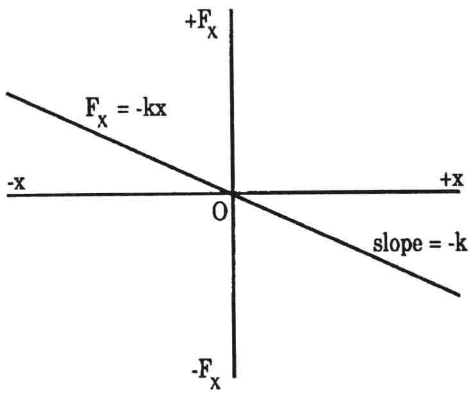
(N) and metre (m), respectively, and hence the SI unit of k is newton per metre (N/m).

The equation $F = kx$ presents a difficulty with signs,[2] and is more correctly written as $F_x = -kx$.

$$F_x = -kx \qquad [1\text{-}1]$$

Figure 1-2

The linear restoring force for simple harmonic motion.



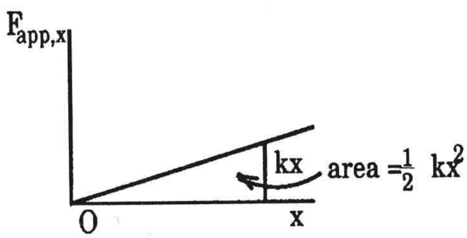
The correctness of Eq. [1-1] can be confirmed as follows. When the mass in Fig. 1-1 is displaced to the right of equilibrium, x is positive and, from Eq. [1-1], F_x is negative, indicating that the restoring force $\boldsymbol{F}$ is (correctly) to the left. When the mass is displaced to the left, x is negative and F_x is then positive, indicating a force to the right. Equation [1-1] is expressed graphically in Fig. 1-2; notice the linearity of the graph.

Elastic Potential Energy

The system of Fig. 1-1 may be described in terms of its potential energy, expressed in SI units as joules (J). Suppose a force is applied such that the mass m is displaced from equilibrium at constant velocity. Since the velocity is constant, the acceleration $\boldsymbol{a}$ of the mass is zero, and from Newton's second law of motion ($\boldsymbol{F}_{net} = m\boldsymbol{a}$), the net force must be zero. This means that the applied force $\boldsymbol{F}_{app}$ must be equal in magnitude to the force exerted by the spring, but in the opposite direction, i.e., $F_{app,x} = +kx$ (Fig. 1-3).

Figure 1-3

As the spring is stretched a distance x from equilibrium, the elastic potential energy stored is $\frac{1}{2}kx^2$.



2. The symbol F represents the magnitude of the force vector, which cannot be negative (see Box 1-1); however, the displacement x can be either positive or negative, and k is positive. Hence, if x is negative, the equation $F = kx$ has a positive left-hand side and a negative right-hand side. This difficulty is overcome by replacing F with the x-component of $\boldsymbol{F}$ (i.e., F_x), and introducing a negative sign on the right-hand side of the equation.

As the mass moves, work is done by the applied force. If the force were constant, then the work W done could be calculated from $W = F_{app,x}\,\Delta x$. However, since the applied force is proportional to x, which is variable, the work done is $W = \int F_{app,x} dx$, which is equal to the area under the graph of $F_{app,x}$ vs. x. Hence, the work done in stretching the spring from 0 to x is simply the area of the triangle in Fig. 1-3, which is $\frac{1}{2}(x)(kx) = \frac{1}{2}kx^2$. This work is positive for elongation of the spring ($x > 0$) and for compression ($x < 0$), and may be considered as *elastic potential energy* E_p stored in the spring. Thus, for a linear restoring force, the elastic potential energy of the system is given by

$$E_p = \tfrac{1}{2} kx^2 \qquad \textbf{[1-2]}$$

More generally, elastic potential energy refers to energy that is stored in any object as a result of twisting, stretching, or compressing. It may be converted to other forms of energy, such as kinetic energy, if the spring in Fig. 1-1 is released when away from equilibrium.

Angular Frequency, Period, and Frequency of SHM

If the mass of Fig. 1-1 is pulled aside from equilibrium to a position $x = A$ and released, how will its position x vary with time t? In a truly frictionless system, the mass will oscillate indefinitely between the positions $x = A$ and $x = -A$. The position x is a sinusoidal function of t, and can be expressed as

$$x = A \sin(\omega t) \qquad \textbf{[1-3]}$$

where ω (the lowercase Greek letter *omega*) is a constant related to the force constant k and the mass m. The quantity A is the *amplitude* of the oscillation, which is the maximum distance that the mass moves away from the equilibrium position.

In the next few paragraphs the sinusoidal nature of the motion is justified, and ω is determined in terms of k and m. The starting point is $F_x = -kx$ (Eq. [1-1]). Newton's second law of motion can be used to replace F_x with ma_x, where a_x is the x-component of the acceleration. Hence, $ma_x = -kx$, or

$$a_x = -\frac{k}{m}x \qquad \textbf{[1-4]}$$

Equation [1-4] indicates that, for a linear restoring force ($F_x = -kx$), the acceleration is equal to a negative constant ($-k/m$) times the position x. Acceleration is the time derivative of velocity, which in turn is the time derivative of position. Hence, acceleration is the second derivative of position, and Eq. [1-4] can be written as