ACOUSTIC SYSTEMS IN BIOLOGY

NEVILLE H. FLETCHER

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Neville H. Fletcher

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PREFACE

I first became interested in the acoustics of biological systems when I had the opportunity of discussing with some biology colleagues the experiments they were performing on the auditory systems of insects. The neurobiological techniques, with which I was unfamiliar, were immensely impressive, but I found that they tended to discuss the external acoustics of the system only in terms of greatly simplified physical concepts such as the resonances of open or stopped pipes, or the behavior of a simple Helmholtz resonator. Such ideas can often, it is true, provide a useful qualitative guide, but rarely anything more. It seemed to me that physical acoustics should be able to do better for the subject than this, and to provide a description of the peripheral aspects of the auditory system at a level at least comparable with the sophistication of the neurophysiological investigation. A trial foray into the field showed me that, indeed, the physical input could be refined without too much effort, and some productive collaborations developed.

I do not mean to imply by this that all biologists are unsophisticated in the physical aspects of their studies, and indeed I came to admire the blend of careful physical analysis and expert biological experimentation that some workers are able to bring to their studies. In many cases, however, this stems in part from the fact that these individuals, or members of their teams, began life as physicists or engineers before turning to the more complex field of biology. What I have observed, however, is that biologists are singularly poorly served when they search in the library for acoustics texts that could aid them in their work. The selection is between rather elementary and descriptive books on sound that stop at the level of stretched strings and organ pipes, and the fully developed mathematical texts that have been written for graduate level courses in physics departments. The required results are certainly there somewhere, but it is very difficult to dissect out just what is needed and to apply it to understanding the biological problem.

It is with this situation as background that the present book has been written. I see a need among biologists studying auditory communication in animals at the physiological level for an exposition of acoustics directed explicitly towards their needs, covering the necessary ideas from acoustics and showing how these can be applied quantitatively to understand the acoustic periphery of auditory and sound-producing systems. It is only when this relatively simple mechanical part of the system is properly understood that attention can be focused on the underlying physiological processes.

The task immediately presents difficulties, since biologists are not traditionally well trained in mathematics, and a certain amount of mathematics is inevitable if the treatment is to be more than descriptive in a hand-waving sort of way. What I have tried to do, therefore, is to write the book simultaneously on three different levels. For those who want a brief general survey of the field, each chapter begins with a completely non-mathematical Synopsis which summarizes the content and refers to the figures, all of which are designed to be understood even apart from the main text. At the next level, the reader should follow the main text, but need not give close attention to anything but the general shape of the equations involved. This will give a fairly detailed understanding of all the concepts and techniques involved, and will probably suffice for most readers. At the third level, the mathematical arguments should be followed in detail, and the discussion questions at the end of each chapter attempted. Each question has a reasonably detailed solution provided, and serves not just as a formal exercise but also as further discussion of particular cases of biological relevance.

I hope the book will prove suitable for a one-semester course at beginning graduate level for biologists with a general interest in auditory and vocal systems, though the instructor will need to supplement the physical emphasis of the text with appropriately realistic biological examples. Turning its purpose in reverse, it should also be suitable for a similar course at advanced undergraduate level for physics or engineering students, if the instructor is seeking a new approach to a classical field of study.

Since the book is designed as a textbook rather than a research monograph, there is no detailed list of references, and I have not tried in any way to give a survey of the current literature. Instead I have simply given a short and rather general annotated bibliography that refers the reader to standard sources from which additional information or formal detail can be found on topics treated in the book. Acoustics of the sort used here is one of the classical branches of physics, and the treatments of 50 or even 100 years ago remain completely valid—Lord Rayleigh's classic treatise of 1894 is fortunately readily available in reprint—and can still provide guidance to the modern worker! This does not mean, however, that modern approaches have been ignored. Electric network analogs, nonlinearity, and information theory all have their appropriate place.

It is a pleasure to express my thanks to those colleagues here in Australia, in the United States, and in Europe, who have taken time and trouble to educate me in the facts and theories of sensory biology. The blame for any misconceptions expressed in the book must, however, be mine alone. I hope that this book, by making the techniques of physics applied to biological systems more accessible to their students, will help repay that debt. I am particularly grateful to Ken Hill and Jack Pettigrew for reading and commenting upon a draft of the manuscript, and to Suszanne Thwaites for her collaboration in the earlier stages of this work.

Canberra, Australia December 1991 N. H. F.

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COMMON SYMBOLS

While the number of different situations discussed in the book requires that the same symbol must be used to represent different things in different places, an attempt has been made to unify the usage, and some symbols have unique meanings. This list specifies the usual meaning of symbols; exceptional usage is local and is explained in the appropriate section of the text.

- A, B, C unspecified constants, amplitudes, etc.
 - (A) (as superscript) acoustic, as of impedances
 - a radius of a pipe, horn, or diaphragm; with subscript, a mode amplitude
 - C compliance; electrical capacitance
 - c speed of sound, generally in air, subscripts for other materials
 - E Young's modulus
 - £ efficiency
 - e exponential function; e = 2.7182...
 - **F**, **F** force
 - f frequency in hertz; acceleration
 - g gravitational acceleration
 - $H_{ii} = Z_{ii}$ coefficients for a horn
 - I intensity
 - *i*, *i* electric current in a network
 - i, j, k (as subscripts) integers 1, 2, 3, ...
 - Im imaginary part of a complex quantity
 - J (with subscript) Bessel function
 - j imaginary number identifier, defined by $j^2 = -1$
 - K elastic bulk modulus
 - k (angular) wave number; $k = \omega / c$
 - *L* level in decibels, with argument *I* for intensity, p for sound pressure, v for velocity; inertance; electrical inductance
 - l length
 - (M) (as superscript) mechanical
 - m, n (as subscript) integers 1, 2, 3, ...
 - m mass; flare constant of an exponential horn
 - *N* (with subscript) Neumann function (Bessel function of the second kind);
 as subscript, neural transducer

- *n* integer $1, 2, 3, \ldots$
- P power
- $P_{ii} = Z_{ii}$ coefficients for a pipe
- p, p acoustic pressure; with subscript E analog source pressure
 - Q quality factor of a resonance
 - q acoustic source strength (volume flow)
 - *R* resistance; real part of impedance; as subscript, radiation
 - r distance to observing point
- Re real part of a complex quantity
- S area or cross-section area; as subscript, solid, generally biological solid
- T tension; as subscript, tympanum
- t time
- U, U acoustic volume flow
 - *u* vibration velocity of a surface; speed of an air jet
- V, V volume; electric potential difference in a network
- v, v velocity, usually acoustic particle velocity
- W width dimension; as subscript, water
- X reactance; imaginary part of impedance
- x, y, z coordinates or displacements
 - Y (acoustic) admittance; superscript (A) for acoustic or (M) for mechanical if necessary
 - Z (acoustic) impedance; superscript (A) for acoustic or (M) for mechanical if necessary; subscript R radiation; subscript N neural transducer; subscript T tympanum
 - Z_{ij} two-port impedance coefficients for levers, pipes, or horns
 - z wave impedance
 - α (alpha) attenuation coefficient
 - β (beta) spring constant; elastic coefficient
 - γ (gamma) resistive loss coefficient; Poisson's ratio; nonlinear coefficient; ratio of specific heats of air
 - Δ (capital delta) symbol for a small increment
 - δ (delta) boundary layer thickness; symbol for a small increment
 - ε (epsilon) nonlinear parameters
 - η (eta) coefficient of viscosity
 - θ (theta) angle

- κ (kappa) radius of gyration of the cross-section of a bar; transverse wave number in a pipe of horn
- λ (lambda) wavelength
- μ (mu) mechanical compliance of the root of a sensory hair; with subscript H, compliance of hair; with subscript B, compliance of bar; elastic shear modulus
- v (nu) kinematic viscosity, $v = \eta/\rho$
- ξ (xi) acoustic displacement
- π (pi) $\pi = 3.14159...$
- ρ (rho) density, generally density of air; ρ_s density of solid biological material
- Σ (capital sigma) summation
- σ (sigma) elastic stress; surface tension; with subscript, parameter ± 1
- τ (tau) time; time interval
- φ (phi) angle, generally phase angle
- ψ (psi) shape function for a normal mode, generally normalized
- ω (omega) angular frequency in radians per second, $\omega = 2\pi f$

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ACOUSTIC SYSTEMS IN BIOLOGY

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1 PHYSICS, BIOLOGY, AND MATHEMATICS

1.1 Physics and Biology

This book is about the application of physics to the understanding of biological systems, so that it is appropriate to think briefly about the difference between the approaches usually adopted in the physical and the biological sciences. This will serve to explain the background to the approach adopted, which shows physics not as an end in itself but as a tool to be used by biologists.

Biology is immensely complex, and it is in that systematic complexity that much of the interest of the subject lies. Leaving aside ecologists, most biologists work with individual animals (or, of course, plants) or with the subsystems that make up those individuals. A good understanding of the biochemical and biophysical systems that make up a functioning individual has been achieved, and the same is true of many of the features of the neurophysiological system. The biologist makes free use of many physical concepts down to the molecular level, but beyond that the subject ceases to be biology and becomes biochemistry or even physics.

Physics, on the other hand, deals essentially with simple laws and theories that describe the behavior of the building blocks (from the interactions of elementary particles to the structure of space-time) from which the universe is made. The fact that the universe is complicated reflects the complicated pattern in which the blocks are arranged. Philosophically, physics does not claim that it will ever truly understand the nature of the universe, but only that it may succeed in constructing a mathematical model, or hierarchy of models, that predict adequately the behavior of the systems to which they apply. Ultimately we might hope that the phenomenon of life-leaving aside consciousness-might also be predictable from physical principles within this philosophical context, but the time when that prediction will be possible is not yet near. Even if physics were to be successful in this attempt, it would still not usurp the role of biology, nor, on a more philosophical plane, would it necessarily imply a "clockwork" universe. Modern developments in the mathematics of nonlinearity and chaotic behavior preserve us from that unpalatable possibility!

The theories of physics have been developed as a hierarchy, and the choice of one level or another depends upon the degree of sophistication and accuracy that we want in our model. To model the interaction of elementary particles, quantum chromodynamics is essential, but it merges into ordinary quantum mechanics at the atomic and molecular level. This, in turn, gives results that are essentially identical with those of Newtonian mechanics for all ordinary macroscopic phenomena but, if we increase scale and speed, we must use the theories of special and then general relativity. The seams between these domains are not yet entirely smooth, but in principle we could put together a grand theory unifying them all. To use a model in that form, however, particularly for ordinary laboratory-scale applications, would not make sense, for many of the large-scale and small-scale features of the theory would simply turn out to have no effect. The whole art of investigation in physics is to use an appropriately complex theoretical model. If the complexity is too small, we may miss out on modeling important features of the real system, while if it is too great we may find the mathematics too difficult or too tedious to complete.

With these ideas as background, it makes sense to look at the areas of biology, particularly the areas of biological acoustics, to which physical theories and models can make a useful contribution. In doing so, we should again be guided by the hope of finding an appropriately complex model. In fact there are two areas to which physical ideas can immediately contribute. The first is at the behavioral level, where acoustic and vibratory signals often serve as a means of communication among individuals of the same or even of different species. Physical theories can tell us a great deal about the propagation of such signals in the environment, about the information content they can convey, and about appropriate coding schemes to optimize performance. The second area is at the mechanical level in an individual. The way in which sound signals are captured and led to an appropriate neural transducer is simply physical, and we might hope for a physical understanding of the important anatomical and physiological features that have developed under evolutionary pressures. The same is true of the sound-production mechanism, though the analysis here may be more complicated since the system is active, rather than simply passive. All this can be done within the domain of ordinary classical Newtonian mechanics. The next level in the biological organism involves the transduction of mechanical signals to neural form, and is much less straightforward. The physics involved is at the level of quantum mechanics, which is no great difficulty, but the biological mechanisms and membrane processes are so complex that only parts of the system have yet been elucidated in detail.

Our discussion will therefore stop after brief consideration of the mechanical behavior of the transducer organ. An understanding of the mechanical behavior of the auditory system to this level is a good guide to many features of total system behavior, and it does provide for the neurobiologist a specification of the mechanical input to the neural transducer cells. At a more preliminary level, even a partial understanding of the behavior of the external part of the system allows the design of crucial experiments to extend the model. Similar remarks can be made in relation to vocal systems.

1.2 Building Blocks and Models

Physics proceeds by studying the simplest possible building blocks, because for these the mathematical analysis is simplest and the physical behavior is most easily defined. When the behavior of the simplest cases has been understood, then we can go on to more complex cases until we have enough building blocks to build a conceptual approximation to the system we wish to study. The physical behavior of this conceptual model can then be evaluated quantitatively by solving the equations describing its components and their interactions.

That is the plan we shall follow in this book. The very simplest component is a massive particle, constrained to move only along a straight line and bound to a fixed point on that line by a force that is proportional to the displacement of the particle from that point—the so-called simple-harmonic oscillator. The analysis, we shall find, is very simple, and indeed it is probably familiar to all readers. Nevertheless the behavior of this oscillator when acted upon by external forces shows many of the features that turn out to be important in more complex systems. Even the mathematics has a strong family resemblance, so that the more complex formulae met later have an element of familiarity.

This one-dimensional point oscillator is a reasonable model for only one biological component—the mass-loaded hair cell; in all other cases the biological system has a significant extension in space. The first move towards this is to discuss the behavior of a stretched string. Once again, this is the simplest such system to analyze, and it shows up many of the features that are important in more complex and realistic system elements. A string stiffened to the extent that it becomes a rod is closer to a biological system component, so this is considered next. From here we move on to the behavior of taut membranes—certainly important biological components—and stiffened membranes, which behave more like plates or elastic shells. This provides an adequate stock of mechanical components from which to construct our model system.

We then focus attention on the medium with which the vibrating element interacts and through which the sound or vibration is transmitted. The media of greatest biological importance are air and water, and we consider waves in both these fluids, as well as waves that travel along the surface of water. The other major components of biological acoustic systems are air-filled tubes, horns or cavities, generally connecting in some way with the outside environment. Understanding and modeling the way in which sound propagates through these components is an important part of understanding the whole system.

This list provides an adequate stock of components to model most of the systems in which we are interested. Our understanding of each component must, of course, be quantitative, since we now wish to assemble a selection of the components into a simplified model representing the real biological system, and to calculate its acoustic behavior. The rules for this model building are mostly intuitive, but a few precautions must be observed and, of course, we need to have available some simple way of carrying out the necessary final calculations to determine important elements of the acoustic behavior such as sensitivity, frequency response, and directionality. We consider this for a variety of model systems, closely related to those found in the peripheral auditory apparatus of

insects and vertebrates. We also give a brief discussion of the neural transducer organ from a mechanical point of view, but stop short of considering transduction at the cellular level.

In the case of active sound-producing systems, the model building proceeds in much the same way, but we supply a source of steady energy, often in the form of a supply of air under a small excess pressure. An important extra feature, the necessity for nonlinearity in at least one of the system components, enters when we begin to analyze such an active system to determine its acoustic output. We will have met nonlinearity in the earlier discussion, but now we will put our knowledge to use.

Finally, we examine the external environment in which acoustic communication takes place: the propagation of sound in the atmosphere and the ocean, the competing sources of interfering noise, and the coding strategies that animals use to transmit information. This is a large subject—the whole basis of modern communications theory—and a rather brief survey must necessarily suffice.

1.3 Appropriately Complex Models

The whole art of applying physical ideas to the analysis of biological systems rests on constructing an appropriately complex model for the system under study. Experience acts as a guide here, but the general philosophy should be to construct first the simplest model that appears to be a possible representation of the system. This will generally have a relatively small number of components connected together quite simply, the physical dimensions, densities and elastic properties of all these elements being reasonably well known. The behavior of such a simple model will be easy to calculate and to compare with such experimental data as are available. When this has been done, refinements can be added to improve the agreement, again constrained by anatomical and physical information, and their effect evaluated. Any refinements that make negligible difference to the system behavior can be discarded.

In the course of the book we shall try to give some guidance, by example, on the way this should be done. A model must often be based, however, on some sort of physical or biological intuition, and the process of analysis allows this intuition to be critically tested through additional measurements. In this way, we hope that the procedures outlined will be of value to active researchers in the field, as well as to those simply seeking a general understanding.

1.4 Mathematics

The object of this book is to show how we can construct simplified models that will help us to understand the behavior of biological systems. It would be possible to build these models in physical reality and then to measure them. Though this would be easier than making measurements on biological systems, it would tell us little more and, every time we wished to vary a physical parameter to see its effect on the behavior of the system, we would have to build a new model. For this reason all our models are mathematical—they are quick to build, trivially simple to change, and calculation provides predicted behavior over very wide ranges of frequency or other parameters.

This means, however, that we must be prepared to use mathematics at every stage of the development, and this may not come naturally to many people trained in the biological sciences. In writing the book, therefore, I have assumed very little in the way of prior mathematical knowledge or technique apart from elementary algebra and the ability to differentiate and integrate, and I have introduced only those mathematical ideas that are essential for analyzing the acoustic models. When a mathematical technique is needed, it is developed at that point, so that its use is clear, and a few practice examples are given at the end of the chapter. For convenience of reference, some relevant mathematical results are collected in Appendix A.

The same comments apply to computers. In the present context they are simply machines for quickly doing arithmetic, and we should recognize that there are powerful numerical procedures that can help us in the calculation. The final stage of evaluating a model will almost always be the calculation and graphical display of its performance, giving, for example, membrane vibration amplitude as a function of frequency or of the direction of sound incidence. Most of these calculations are quite straightforward for anyone with a modest background in computer programming in a language such as Basic, and require only a small desk-top microcomputer.

Finally, a word of caution. With modern computers, and even hand-held calculators, it is very easy to arrive at results to many decimal places, and it is tempting to believe that this precision is significant. For the simple entities of physics-electrons, atoms, electromagnetic waves, and so on-this is often true, for our mathematical models take proper account of all the features of the system. For the complex systems of biology, however, the models with which we are working are only first approximations to the real world, and many subtle factors have been omitted in the interests of simplicity. Even anatomical shapes, and basic physical quantities such as density and elastic moduli for many biological materials, are not well defined in many cases. While, therefore, we hope that our models are able to mimic and explain the behavior of the real system, we should not expect very close numerical agreement. In general, agreement to within 10% would be extremely good, while agreement to within a factor 3 in either direction (or $\pm 5 \text{ dB}$) might be completely acceptable, provided the qualitative behavior of the system is predicted over a wide frequency range. With these limitations in mind, it is rarely useful to give numerical results to more than two significant figures, and often one figure will suffice. This convention has been adhered to in the text.

2 SIMPLE VIBRATORS

SYNOPSIS. The simple vibrator, or simple harmonic oscillator, is perhaps the most important system in all of physics. In particular, it is vital for the understanding of acoustic phenomena, and for this reason we treat it in some detail. Essentially it consists of a small mass, able to move only along a line and bound to a fixed point on that line by a spring that exerts a restoring force proportional to the displacement. Such a system vibrates about the fixed point with a natural frequency ω_0 which is determined by the mass of the particle and the strength of the spring. This behavior is illustrated in Fig. 2.1.

In all real oscillators there is dissipation of energy, the most usual mechanism in simple systems being losses caused by the viscosity of the medium in which the mass moves. Even air has appreciable viscosity. The viscous force is proportional to the speed of the motion, and we can define the constant of proportionality, divided by twice the mass, to be the damping constant α of the oscillator. The oscillations of a damped vibrator decay with time as shown in Fig. 2.2. We define the quality factor, or Q value, of an oscillator to be $\omega_0/2\alpha$.

The response of an oscillator to an external force of frequency ω depends on its natural frequency and Q value as shown in Fig. 2.3 for displacement and in Fig. 2.4 for velocity. The response is a maximum when $\omega = \omega_0$, a phenomenon called resonance. The resonance is sharply defined in frequency if the Q value is high, but becomes very broad for Q values near 1 or less. Indeed the full-width of the resonance at points where the amplitude has dropped to $1/2^{1/2} = 0.707$ of its peak value is just ω_0 / Q . The Q values for biological oscillators typically range from about 1 to 10. The phase angle for the response is also shown in these two figures. If the phase angle for displacement is zero, then the displacement lags behind the force. Similar remarks apply to the phase of the velocity. The velocity is always 90° ahead of the displacement in phase. It is often useful to plot the displacement or velocity response on logarithmic scales, as shown in Fig. 2.5.

In discussing vibrating systems it is very helpful to introduce complex numbers, written here in **bold italic** type. The imaginary part of a complex number is labeled with the symbol *j*, which is defined to have the property $j^2 = -1$. A complex quantity has real and imaginary parts, or equivalently a phase and an amplitude, so that its connection with vibrations is formally very close. In interpreting complex quantities representing physical variables such as velocity or position, we always take the real part of the quantity.

We define the admittance $Y^{(M)}$ of a mechanical system to be the ratio of the velocity response to the exciting force. The admittance of a simple oscillator thus has the form shown in Fig. 2.4, with a sharp maximum at the resonance frequency. Because the velocity differs in phase from the exciting force, except at the resonance frequency, the admittance is a complex quantity with both a magnitude and a phase angle. Another way to express this is to split the admittance into the sum of two parts, one exactly in phase with the force and one 90° ahead of the force in phase. We refer to these as the real and imaginary parts of the admittance. Fig. 2.6 shows how they behave. The real part is always positive, but the imaginary part may change sign. The mechanical impedance $Z^{(M)}$ is defined to be the ratio of the force to the velocity, and is thus the reciprocal of the magnitude of the admittance, the same is not true individually for the real and imaginary parts, because of complications caused by phase changes. The real and imaginary parts of both admittance and impedance, for a simple oscillator, are shown in Fig. 2.6. Often in biological systems we are concerned not with steady signals but rather with transients. The response of an oscillator to a transient force can be calculated. The simple case of the behavior of an oscillator with natural frequency ω_0 and quality factor Q = 10 in response to an abruptly applied sinusoidal force of frequency ω is shown in Fig. 2.7. It takes a time equal to about 10 cycles of the natural oscillation before a steady-state response is reached. In general the duration of the transient is about Q cycles of the natural frequency. A similar transient occurs when the force is switched off.

In quite a general way we conclude that oscillators with low damping and therefore high Q values give a large response at resonance but have a narrow frequency bandwidth for that response. They also have transients of long duration. In contrast, oscillators with low Q values have good transient response and relatively wide bandwidth, but are handicapped by low sensitivity.

2.1 The One-Dimensional Simple Oscillator

Much of the theory of acoustics, and indeed of many other branches of physics, is based upon the behavior of a mass connected by a simple linear spring to a fixed point and constrained to move only along a line. This is often called a onedimensional simple-harmonic oscillator. Most of this chapter will be devoted to examining the behavior of this simple system, not because anything exactly like it occurs in biological systems, but because it is often a good first approximation, and the mathematics of more complex models is usually quite similar.

In the simplest case, let us suppose that the mass of the oscillating particle is m and that its displacement from the fixed point x = 0 along a straight line is measured by the coordinate x. Let the elastic force in the x direction when the particle is at position x be $F_E = -\beta x$, where β is a constant identified with the stiffness of the spring, so that the force is always directed back towards the origin x = 0. Then the motion of the particle is described by the law that the force is equal to the mass times the acceleration or, in calculus notation,

$$m\frac{d^2x}{dt^2} = -\beta x. \tag{2.1}$$

This differential equation tells us all about the behavior of the system if we know the position and velocity of the particle at some initial time, usually taken as t = 0. Let us see how this comes about.

We can guess a formal solution to (2.1) based on our knowledge of the properties of elementary functions. If we try

$$x = a\cos(\omega_0 t + \theta) \tag{2.2}$$

then this satisfies the equation provided that

$$\omega_0 = (\beta/m)^{1/2}.$$
 (2.3)

No condition is placed upon the other parameters a and θ . This gives us a formal solution for the motion, but we must look to see what it means. (An equally good



Figure 2.1 The sinusoidal displacement of a simple oscillator as a function of time. Because we have chosen a cosine representation, the phase angle θ is defined to be such that the displacement is $a \cos \theta$ at t = 0.

solution could have been obtained with a sine rather than a cosine function, as we discuss at the end of this section.)

Figure 2.1 shows a plot of the behavior of the particle displacement x with time t. It undergoes a regular repetitive oscillatory motion with period $2\pi/\omega_0$ and amplitude a. The number of periods executed in each unit time is

$$f = \omega_0 / 2\pi \tag{2.4}$$

and *f* is called the frequency of the vibration and is measured in hertz (previously called "cycles per second") after the German physicist Heinrich Hertz (1857–1894), celebrated for his experimental discovery of radio waves. The quantity ω_0 is called the angular frequency of the natural oscillation, and is measured in radians per second. Clearly, from (2.3), the frequency of the motion increases if the particle is made lighter or the spring stiffer—a physical insight that we need to keep in mind. Note that, if we know the mass *m* and measure the free oscillation frequency ω_0 , then (2.3) gives us the spring stiffness β . Finally, θ is called the phase of the oscillation and indicates in just what part of the cycle the system is at t = 0. The phase is measured in radians, but can be referred to in degrees provided we remember to convert back to radians for calculations.

Since there are still two parameters a and θ to be determined, we need to know two independent pieces of information about the system. These might be

the displacement x_0 and the velocity v_0 at time t = 0. Substituting these values in the general solution (2.2), we easily find that

$$a^{2} = x_{0}^{2} + \left(\frac{v_{0}}{\omega_{0}}\right)^{2}$$
 and $\tan \theta = -\frac{v_{0}}{\omega_{0}x_{0}}$. (2.5)

This then specifies the solution completely.

We remarked above that we could have carried out this discussion using in (2.1) the trial function $a \sin(\omega_0 t + \theta')$ rather than a cosine function, and indeed the interpretation of the solution would have been just the same. The only difference would have been in the phase constant or, equivalently, in the choice of the zero of time. The two solutions are identical if we choose $\theta' = \theta + \pi/2$. It is simply a matter of convenience which form we use and, in this book, we shall keep consistently to the form (2.1).

2.2 Choice of Units

It is possible to carry out calculations in acoustics in a variety of different systems of units, provided we are absolutely consistent about it. Older books often use the c.g.s. system and, indeed, we may feel that its fundamental units are of more nearly appropriate size for problems in sensory biology than are other systems. There are, however, considerable advantages to be gained from consistent use of the SI system, now standard in almost all of science. Indeed, when dimensions are given in microns (micrometers) and masses in milligrams, it is just as easy to convert to meters and kilograms as to anything else. We have therefore used the SI system exclusively in this book, and we must warn against the random use of other units if the results of calculations are to be correct. Details of these units are given in Appendix C.

In the case of the simple oscillator it is easy to think of the mass and convert it to kilograms. The force constant β for the spring is less familiar, however. Its value must be given in the appropriate SI units, which are newtons per meter, since the force F_E is in newtons and the displacement x in meters. The examples at the end of the chapter give some practice in performing the necessary calculations.

2.3 Complex Notation

We now discuss a mathematical device that may seem unnecessarily complicated at this stage, but that leads to immense simplification in all our later discussion. It is therefore worthwhile to spend a little effort to master the ideas. It is as well to remember, from the outset, that the development is a piece of pure mathematics in which we explore the consequences of particular formal assumptions, so that we should not be worried by the assumption of "imaginary" numbers with particular

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unusual properties—they exist only within the framework of the mathematical theory that defines them. More detail is given in Appendix A.

We know that the exponential function exp nt or e^{nt} can be differentiated with respect to t to give

$$\frac{d}{dt}e^{nt} = ne^{nt}.$$
(2.6)

Let us try $x = ae^{nt}$ as a solution to equation (2.1). Substitution and use of (2.6) twice shows that this is a satisfactory solution provided that

$$n^2 = -\beta/m = -\omega^2. \tag{2.7}$$

The problem is that the right-hand side of this equation is negative, while if n is an ordinary number then its square is necessarily positive.

We can get over this difficulty, and in doing so extend the domain of mathematics, by introducing a symbol j defined by the relation

$$j^2 = -1.$$
 (2.8)

Clearly j cannot be an ordinary number, but is a new sort of number that has been traditionally called an imaginary number. There is a related imaginary number i defined by

$$i = -j \tag{2.9}$$

which similarly satisfies the equation $i^2 = -1$. We could develop our discussion in terms of either *i* or *j*. Traditionally physicists and mathematicians have used *i*, while engineers have used *j*, and books on acoustics may use either. In this book we shall use *j*, because some of our methods will turn out to be closely related to those of electrical engineering, but it is possible to convert any result to the other convention by simply writing -i for *j* wherever it occurs.

Equation (2.8) contains nearly all we need to know about imaginary numbers. Mathematics is a formalism that follows from basic definitions such as this equation, and all we need to do is follow the rules. Since imaginary numbers such as j or 3.7j are different from ordinary numbers such as 1 or 3.7, they must be kept separate from them. A general number, traditionally called a complex number, has a real part and a complex part and is written a + jb, for example. In this book, to avoid confusion, we shall print the symbols for all complex numbers in **bold italic typeface**. Other books may not use this convention, relying upon the context to indicate whether the number is real or complex, or may use a different convention. Complex numbers can be added or multiplied, simply remembering to apply the definition (2.8). Complex numbers can also be divided one into the other, but the details are a little more complicated and are set out in Appendix A.

It turns out, as again we show in more detail in Appendix A, that there is a close relationship between the ordinary trigonometric sine and cosine functions and the exponential function with an imaginary argument. The connection is expressed by the result

$$e^{j\theta} = \cos\theta + j\sin\theta \tag{2.10}$$

where we take θ to be real. This leads to the inverse relations

$$\cos\theta = \frac{e^{j\theta} + e^{-j\theta}}{2} \quad \text{and} \quad \sin\theta = \frac{e^{j\theta} - e^{-j\theta}}{2j}.$$
 (2.11)

Finally we note a further definition, that of the magnitude or absolute value of a complex number. If z = a + jb, then the magnitude of z, written as |z| or simply as z, is defined to be

$$|z| = z = |a + jb| = (a^2 + b^2)^{1/2}.$$
 (2.12)

This is almost as though real and imaginary numbers are geometrically at right angles to one another, and indeed a diagram in which complex numbers are drawn on a plane with the x axis representing their real component and the y axis their imaginary component is often useful. This too is discussed in Appendix A. From this definition (2.12) and (2.10) it follows that

$$|e^{j\theta}| = (\cos^2\theta + \sin^2\theta)^{1/2} = 1$$
 (2.13)

for any real θ .

This digression into complex number notation finally allows us to write formal solutions for the displacement x and velocity v = dx/dt in the simple oscillator problem, which is defined by the equation (2.1), as

$$\mathbf{x} = a e^{j(\omega_0 t + \theta)} \qquad \mathbf{v} = j \omega_0 \mathbf{x} = a \omega_0 e^{j(\omega_0 t + \phi)} \qquad \phi = \theta + \pi/2 . \tag{2.14}$$

The second form for v comes about from (2.10), from which we see that $e^{j\pi/2} = j$. These complex expressions, because they contain j, are mathematical constructs that require interpretation when applied to physical systems. Indeed they have no physical meaning at all until we have decided how this interpretation is to be made.

Comparing the first of (2.14) with (2.10), we see that the complex expression contains two versions of the simple oscillation (2.2) that we identified as the physical solution to the simple oscillator problem. The real part gives the cosine version and the imaginary part the sine version, though with the same value of θ so that the two are always 90° out of phase. We need only one of these versions, and we adopt the convention of always choosing the real part to represent the physical quantity. We could just as easily have chosen the imaginary part, with

the symbol *j* removed, but the convention is to take the real part, just as we chose a cosine rather than a sine in (2.2). This interpretation now allows us to identify *a* as the amplitude, ω_0 as the angular frequency, θ as the phase angle of the displacement, and ϕ as the phase angle of the velocity. We shall usually write all oscillatory quantities in forms similar to (2.14), with the time variation $e^{j\omega t}$ included. Sometimes, however, it is convenient to omit this factor and refer to what remains, for example $a = a e^{j\theta}$, as a complex amplitude.

The reason for adopting what looks like a great deal of mathematical sophistication only to arrive back at our original simple result is that it saves us a great deal of difficulty when we must treat more complicated physical situations. If we represent physical quantities as complex numbers, as in (2.14), then the single symbol x or v includes information about amplitude, frequency, and phase, and these are all dealt with correctly and automatically by the procedures of complex algebra. It is easy, for example, to multiply together two or more exponential functions, since we simply add their arguments, whereas the multiplication of two or more cosine functions generates sines and cosines of sum and difference angles, which are very difficult to keep track of.

In the sections that follow, and indeed throughout this whole book, we shall come to appreciate the power and simplicity of this complex notation applied to problems involving waves and vibrations. It is very far from being just a demonstration of mathematical sophistication.

2.4 Damping

To bring the simple oscillator a little closer to physical reality, we must allow for some imperfections in its behavior. The most important of these is the introduction of energy losses, either through imperfection in the spring or because of viscous losses in the medium through which the mass is moving. For our present purposes it does not matter which of these forms of loss we consider, for in each of them the force opposing the motion is proportional to the velocity of the oscillating particle. This is quite different from the loss forces arising from sliding friction, which are nearly independent of all but the sign of the velocity until the particle is brought to rest.

We can represent the viscous drag forces by a term $F_R = -\gamma dx/dt$ added to the right-hand side of the equation of motion (2.1) so that, after rearrangement, it can be written

$$m\frac{d^2x}{dt^2} + \gamma\frac{dx}{dt} + \beta x = 0.$$
(2.15)

To solve this equation we assume a solution in the form of an exponential, $x = ae^{nt}$ where a is real and n may be complex. If we substitute this into (2.15), then we



Figure 2.2 The decay behavior of a simple damped oscillator, with natural frequency ω_0 and damping constant α , as a function of the normalized damping α/ω_0 . For small damping $(\alpha/\omega_0 < 1)$, the decay is oscillatory; if $\alpha/\omega_0 = 1$ the damping is critical and the displacement tends to zero in the shortest possible time; if $\alpha/\omega_0 > 1$ the return to zero displacement is prolonged.

can simply divide out the amplitude a and we are left with a quadratic equation for n, which is simply solved to give $n = j\omega' - \alpha$ where

$$\omega' = \omega_0 \left[1 - \frac{\alpha^2}{\omega_0^2} \right]^{1/2} \qquad \alpha = \frac{\gamma}{2m}$$
(2.16)

and $\omega_0 = (\beta/m)^{1/2}$ as before. The motion is then given by

$$\boldsymbol{x} \approx a e^{-\alpha t} e^{j \omega t} \tag{2.17}$$

and α is called the damping coefficient of the oscillator. If the damping is small, in the sense that $\alpha/\omega_0 \ll 1$, then $\omega' \approx \omega_0$, but if the damping is large the frequency may be significantly lowered. If $\alpha/\omega_0 = 1$, the damping is termed critical, and the mass returns to rest without any oscillation at all. For damping greater than the critical value, the return to rest is slower still. This behavior is illustrated in Fig. 2.2.

All real oscillators are damped to some extent, and the damping of springs made of biological material is generally very much higher than that of the metal springs found in mechanical systems. We defer more detailed comparisons until we have a model that is more directly related to a real system.

2.5 The Sinusoidally Driven Oscillator

A damped oscillator simply settles down to its stationary equilibrium position after a time long compared with the reciprocal of the damping coefficient α . The situation is then completely uninteresting unless something happens to excite the oscillator into motion again. In the next few sections we examine how this happens, starting with the simplest case in which the oscillator settles down into a steady-state vibration under the influence of a sinusoidal external force.

Suppose the oscillator has mass *m*, restoring force constant β and damping γ , so that its natural frequency is $\omega_0 = (\beta/m)^{1/2}$ and its damping constant $\alpha = \gamma/2m$. Let the external force have magnitude *F* and frequency ω so that, using complex notation, we can write it as $Fe^{j\omega t}$ with the zero of time chosen so that the phase of the force is zero. The equation of motion is

$$m\frac{d^2\mathbf{x}}{dt^2} + \gamma\frac{d\mathbf{x}}{dt} + \beta\mathbf{x} = F e^{j\omega \mathbf{x}}$$
(2.18)

or, dividing by m,

$$\frac{d^2x}{dt^2} + 2\alpha \frac{dx}{dt} + \omega_0^2 x = (F/m)e^{j\omega x}.$$
(2.19)

In the steady state, it is obvious that the displacement x must vary sinusoidally with frequency ω , and we need to find the amplitude of that motion and its phase relative to the exciting force. To do this, we assume that $x = ae^{j(\omega x + \theta)}$ as usual and substitute this in (2.19). Dividing out the common factor $e^{j\omega x}$ then gives the result

$$ae^{j\theta} = \frac{(F/m)}{(\omega_0^2 - \omega^2) + 2j\omega\alpha}.$$
(2.20)

To find the amplitude a we take the absolute value of each side of this equation, giving

$$a = \frac{(F/m)}{\left[(\omega_0^2 - \omega^2)^2 + 4\omega^2 \alpha^2\right]^{1/2}}$$
(2.21)

To find the phase θ involves a little more algebra, but simplifies to

$$\tan \theta = \frac{-2\omega\alpha}{\omega_0^2 - \omega^2}.$$
 (2.22)

Here θ is the phase angle of the displacement x relative to the exciting force F.

This somewhat involved bit of algebra has given us the results we need in the form of equations (2.21) and (2.22). We now need to see what they mean in physical



Figure 2.3 Response of a simple oscillator, with natural frequency ω_0 and Q value as shown, to an exciting force of constant amplitude as the frequency ω is varied. The first panel shows the displacement amplitude response a, and the second panel the phase response θ of the displacement.

terms. The most obvious question to ask of the present system is: what is the amplitude of the motion as the frequency is varied, keeping the magnitude of the external force constant? The answer is given by equation (2.21), and typical response curves are shown in Fig. 2.3(a). As is clear from the equation, the amplitude is a maximum when $\omega = \omega_0$, a condition known as resonance. The amplitude response at low frequencies tends to a constant value, while at high frequencies it declines steeply as $1/\omega^2$. Two curves are plotted in the figure, one for $\alpha = 0.1$ and one for $\alpha = 0.3$.

Another way in which to display these results, and one that is more often used, is to plot not the displacement amplitude *a* but rather the velocity amplitude $v = \omega a$. The change to the formula (2.21) is obvious, simply amounting to multiplying by ω , and the effect on the response curves is shown in Fig. 2.4(a). The response maximum is still very close to ω_0 but the curve has now a nearly symmetrical bell shape, going to zero in the limit of both low frequencies, where the response is proportional to ω , and of high frequencies, where the response varies as $1/\omega$.

To describe these curves, and particularly their variation as the damping is changed, it is usual to define a quality factor, denoted by Q, for the resonance. The definition relates to the amplitude or velocity response curves and, provided the damping is not too large, the Q value is defined to be the ratio of the frequency of the peak response divided by the full-width $\Delta \omega$ of the curve at the two points where its amplitude is $1/\sqrt{2} \approx 0.707$ times the peak value (also called the half-power full



Figure 2.4 Response of a simple oscillator, with natural frequency ω_0 and Q value as shown, to an exciting force of constant amplitude as the frequency ω is varied. The first panel shows the velocity amplitude response v, and the second panel the phase response ϕ of the velocity.

width, since power is proportional to the square of the amplitude). This leads immediately to the result

$$Q = \frac{\omega_0}{\Delta \omega} = \frac{\omega_0}{2\alpha}.$$
 (2.23)

In the case of very large damping $\Delta \omega$ becomes uncertain, and so Q is defined quite generally as $\omega_0/2\alpha$. The situation of critical damping, referred to in Fig. 2.2 in relation to the decay of free vibration, corresponds to $\alpha/\omega_0 = 1$ and thus to Q = 0.5. The Q value for a vibrator is found by measuring the frequency response curve and dividing the resonance frequency ω_0 at the response peak by the peak full-width $\Delta \omega$.

If we plot the displacement and velocity response curves using logarithmic scales for both frequency and response axes as shown in Fig. 2.5, then the behavior is seen to be particularly simple. The "skeleton" of the response is the two straight lines, shown dotted in the figure. Superimposed upon their intersection is a peak of height Q times the value of the response at the intersection, the width of the peak being inversely proportional to Q. We shall often use this sort of logarithmic plot in the later development.

In biological systems, the oscillators we meet have relatively small Q values, in the range from 1 to about 30. Metallic vibrating systems such as tuning forks

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or gongs may have Q values of several hundreds, while specially prepared systems such as vibrating quartz crystals can have Q values of many thousands. Systems with high Q values have sharp response peaks, giving large response at the peak frequency, but small bandwidth. Conversely, systems with low Q values have modest peak response but broad bandwidth. In fact there is always a trade-off as expressed by the relation

$$(\text{peak response}) \times (\text{bandwidth}) = \text{constant}.$$
 (2.24)

We shall later find that a law of this kind is quite general.

We can look at the phase response $\theta(\omega)$ or $\phi(\omega)$ of the oscillator in much the same way, using equation (2.22). As far as the displacement response is concerned, $\theta \rightarrow 0$ at low frequencies, so that the displacement is exactly in phase with the force. At the resonance $\omega = \omega_0$, $\theta = -\pi/2$ or -90° , and at very high frequencies $\theta = -\pi$ or -180° . The phase change takes place essentially over the width of the response peak near ω_0 , as shown in Fig. 2.3(b). The phase $\phi(\omega)$ of the velocity response has a similar variation but, because $v = j\omega x$ and $j = e^{j\pi/2}$, we find that $\phi = \theta + \pi/2$. This means that the velocity is exactly in phase with the external force at the resonance frequency ω_0 . The variation in phase for the velocity response is shown in Fig. 2.4(b).

Figure 2.5 Logarithmic plot of (a) the displacement response and (b) the velocity response, for a simple oscillator, with natural frequency ω_0 and Q value as shown, to an exciting force of frequency ω . Note the straight dotted lines of the skeleton that show the asymptotic response for ω well away from ω_0 . The peak response at resonance is Q times the skeleton response.



2.6 Impedance and Admittance

We now define two quantities which, in various guises, will be immensely important in our development of the subject. It is clearly necessary to be able to describe the response of a system to an applied force, and this is most usefully specified for oscillatory systems by supposing that the force has oscillatory behavior with frequency ω and amplitude *F*. It turns out to be best to deal with the velocity response *v* of the system, rather than the displacement response, so that altogether we can write

$$F = F e^{j\omega t}$$
 and $v = v e^{j\phi} e^{j\omega t}$. (2.25)

We define the mechanical admittance $Y^{(M)}(\omega)$ at frequency ω to be the complex quantity

$$Y^{(M)}(\omega) = \frac{v}{F} = \frac{v}{F} e^{j\phi}$$
(2.26)

with the superscript (M) implying "mechanical" to differentiate this admittance from acoustic admittance, which we shall meet later. From (2.20), an explicit expression for the admittance is

$$Y^{(M)}(\omega) = \frac{j\omega}{m[(\omega_0^2 - \omega^2) + 2j\omega\alpha]}.$$
 (2.27)

The magnitude $|Y^{(M)}|$ of the mechanical admittance is, except for a constant factor, the quantity illustrated in Figures 2.4 and 2.5(b). It measures how easy it is to cause the mass of the oscillator to move at a given frequency. The admittance itself is, however, a complex quantity. It does not have a physical existence like a pressure or a displacement, but is rather an operator that converts one such physical quantity (force) into another (velocity). Because of its complex nature it generally introduces a phase shift into this conversion, so that this phase shift appears between the two physical quantities that it connects. Note that at resonance, when $\omega = \omega_0$, the admittance as given by (2.27) is a real quantity and, by (2.26), $\phi = 0$ and the velocity is in phase with the force.

The mechanical impedance is a related quantity, just the reciprocal of the admittance,

$$Z^{(M)}(\omega) = [Y^{(M)}(\omega)]^{-1} = \frac{F}{v}.$$
 (2.28)

and is often used for convenience in some contexts. $Z^{(M)}(\omega)$ is given explicitly by taking the reciprocal of the complex expression in (2.27). The impedance, too, is real at the resonance frequency ω_0 but has a minimum rather than a maximum