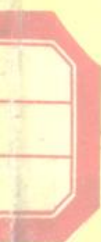


An Introduction to the Physiology of Hearing

James O. Pickles



An Introduction to the Physiology of Hearing

James O. Pickles

*Department of Physiology,
University of Birmingham,
Birmingham, England*



1982



ACADEMIC PRESS

A Subsidiary of Harcourt Brace Jovanovich, Publishers

LONDON NEW YORK

PARIS SAN DIEGO SAN FRANCISCO SÃO PAULO

SYDNEY TOKYO TORONTO

01/86/9
ACADEMIC PRESS INC. (LONDON) LTD
24-28 Oval Road,
London NW1

U.S. Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue,
New York, New York 10003

Copyright © 1982 By ACADEMIC PRESS INC. (LONDON) LTD

All Rights Reserved

*No part of this book may be reproduced in any form by photostat, microfilm, or
any other means without written permission from the publishers*

British Library Cataloguing in Publication Data

Pickles, J.O.

An introduction to the physiology of hearing.

1. Hearing 2. Psychoacoustics

I. Title

612'.85 QP461

ISBN 0-12-554750-1 Hardback

ISBN 0-12-554752-8 Paperback

LCCN 81-69596

Phototypesetting by Oxford Publishing Services, Oxford
Printed in Great Britain by St Edmundsbury Press, Bury St Edmunds

Preface

The last fifteen years have seen a revolution in auditory physiology, but the new ideas have been slow to gain currency outside the circle of specialists. Undoubtedly, one of the main reasons for this has been the lack of a general source for non-specialists, and it is hoped that the present book will introduce recent thinking to a much wider audience.

Whilst the book is primarily intended as a student text, it is hoped that it will be equally useful to teachers of auditory physiology. It should be particularly useful to those teaching physiology to medical students, because general texts of physiology aimed at medical students commonly contain only a small section on hearing, which is based on material that is 20 or more years out of date. The increasing concern about the extent of hearing loss in the community should increase the attention paid to auditory physiology in the medical curriculum.

The majority of the book is written at a level suitable for a degree course on the special senses or as a basis for a range of postgraduate courses. It is organized so as to be accessible to those approaching the subject at a number of levels and with a variety of backgrounds. Chapter 1 on the physics and analysis of sound contains elementary information which should be read by everyone. Those who need only a brief introduction to auditory physiology may then read only Chapter 3 on the Cochlea. Those whose interests lie in the psychophysical correlates may read Chapters 1 to 4, and then turn to Chapter 9. Those who are interested in clinical aspects may read Chapters 1 to 3, part of Chapter 4 (as indicated), and then Chapter 10. Chapter 5, which explores the newer ideas on cochlear physiology, is written at a more advanced level than the rest of the book, and if desired may be omitted without affecting the understanding of the other chapters. Chapters 6, 7, and 8, on the brainstem, cortex, and centrifugal pathways should appeal primarily to specialist physiology students, although the latter part of Chapter 7 on the cortex, and some parts of Chapter 8 on centrifugal pathways, contain much material that should be of interest to students of physiological psychology.

Only the most elementary knowledge of physiology is assumed, and even

such basic concepts as ionic equilibrium potentials are explained where appropriate, so that the book should be accessible to those with only a small background in physiology. The treatment is nonmathematical, and only a few very elementary algebraic equations appear. In Chapter 3, some of the reasoning behind theories of cochlear mechanics is explained verbally for the benefit of those without mathematical training. I have found that for those *with* such training, this approach makes the subject more, rather than less, confusing. I can only apologize to them, and refer them to the several excellent accounts that have already appeared at their own level (e.g. Zwislocki, 1965; Dallos, 1973a; Schroeder, 1975; Geisler, 1976; Steele, 1976; and Dallos, 1978).

I should like to express my thanks to colleagues who read and commented on sections of an earlier version of the manuscript, and in particular to G. R. Bock, S. D. Comis, J. L. Cranford, L. U. E. Kohllöffel, O. Lowenstein, B. C. J. Moore, G. F. Pick, H. F. Ross, I. J. Russell, R. L. Smith, and G. K. Yates. I am also grateful to D. Robertson for supplying the micrographs of Fig. 3.4, and to T. L. Hayward for help with the illustrations. The book was written while I was a member of the Neurocommunications Research Unit at Birmingham University, and I am grateful to my colleagues in the Unit, S. D. Comis and H. F. Ross, for many helpful discussions, and to everyone, in this university and elsewhere, who dealt patiently with a continual series of small queries.

July 1981

J. O. Pickles
Birmingham

Contents

Preface	v
Contents	vii
 I. The Physics and Analysis of Sound	1
A. The nature of sound	1
B. The decibel scale	3
C. Impedance	4
D. The analysis of sound	6
E. Linearity	8
F. Summary	9
 II. The Outer and Middle Ears	10
A. The outer ear	10
B. The middle ear	14
C. Summary	22
D. Further reading	23
 III. The Cochlea	24
A. Anatomy	24
B. The mechanics of the cochlea	34
C. The electrophysiology of the cochlea	48
D. Summary	68
E. Further reading	70
 IV. The Auditory Nerve	71
A. Anatomy	71
B. Physiology	72
C. Summary	104
D. Further reading	106
 V. Mechanisms of Transduction and Excitation in the Cochlea	107

A. Introduction	107
B. Mechanisms of transduction	108
C. Active movements in the cochlea: the evoked cochlear response	126
D. Hair cells and neural excitation	130
E. The linearity of cochlear function	134
F. Frequency selectivity and the second filter	143
G. Summary	150
H. Further reading	153
 VI. The Brain Stem Nuclei	 154
A. Considerations in studying the central nervous system	154
B. The cochlear nuclei	156
C. The superior olivary complex	168
D. The ascending pathways of the brainstem	177
E. The inferior colliculus	178
F. The medial geniculate body	184
G. Brain stem reflexes	188
H. Summary	191
I. Further reading	193
 VII. The Auditory Cortex	 194
A. Organization	194
B. The responses of single neurones	202
C. Behavioural studies of the auditory cortex	211
D. Hypotheses as to the function of the auditory cortex	223
E. Summary	225
F. Further reading	227
 VIII. The Centrifugal Pathways	 228
A. Introduction	228
B. The olivocochlear bundle	229
C. Centrifugal pathways to the cochlear nuclei	240
D. Centrifugal pathways in higher centres	246
E. Summary	249
F. Further reading	250
 IX. Physiological Correlates of Auditory Psychophysics and performance	 251
A. Introduction	251
B. The absolute threshold	257
C. Frequency resolution	253

D. Frequency discrimination	264
E. Intensity	269
F. Sound localization	277
G. Speech	279
H. Summary	284
I. Further reading	285
 X. Sensorineural Hearing Loss	 286
A. Types of hearing loss	286
B. Sensorineural hearing loss of cochlear origin	287
C. A cochlear prosthesis?	295
D. Summary	300
E. Further reading	301
 Appendix	 302
References	303
Index	328

I. The Physics and Analysis of Sound

Some of the basic concepts of the physics and analysis of sound, which are necessary for the understanding of the later chapters, are presented here. The relations between the pressure, displacement and velocity of a medium produced by a sound wave are first described, followed by the decibel scale of sound level, and the notion of impedance. Fourier analysis and the idea of linearity are then described.

A. The Nature of Sound

In order to understand the physiology of hearing, a few facts about the physics of sound, and its analysis, are necessary. As an example, Fig. 1.1 shows a tuning fork sending out a sound wave, and shows the distribution of the sound wave at one point in time, plotted over space, and at one point in space, plotted over time. The tuning fork sends out a travelling pressure wave, which is accompanied by a wave of displacement of the air molecules making them vibrate around their mean positions. There are two important variables in such a sound wave. One is its frequency, which is the number of waves to pass any one point in a second, measured in cycles per second, or hertz (Hz). This has the subjective correlate of pitch, sounds of high frequency having high pitch. The other important attribute of the wave is its amplitude or intensity, which is related to the magnitude of the movements produced. This has the subjective correlate of loudness.

If the sound wave is in a free medium, the pressure and velocity of the air vary exactly together, and are said to be in phase. The displacement however lags by a quarter of a cycle. It is important to understand that the pressure variations are around the mean atmospheric pressure. The varia-

2 An Introduction to the Physiology of Hearing

tions are in fact a very small proportion of the total atmospheric pressure — even a level as high as 140 dB SPL (defined on p. 4), as intense as anything likely to be encountered in everyday life, makes the pressure vary by only 0.6%. The displacement is also about the mean position, and the sound wave does not cause a net flow of molecules.

The different parameters of the sound wave can easily be related to each

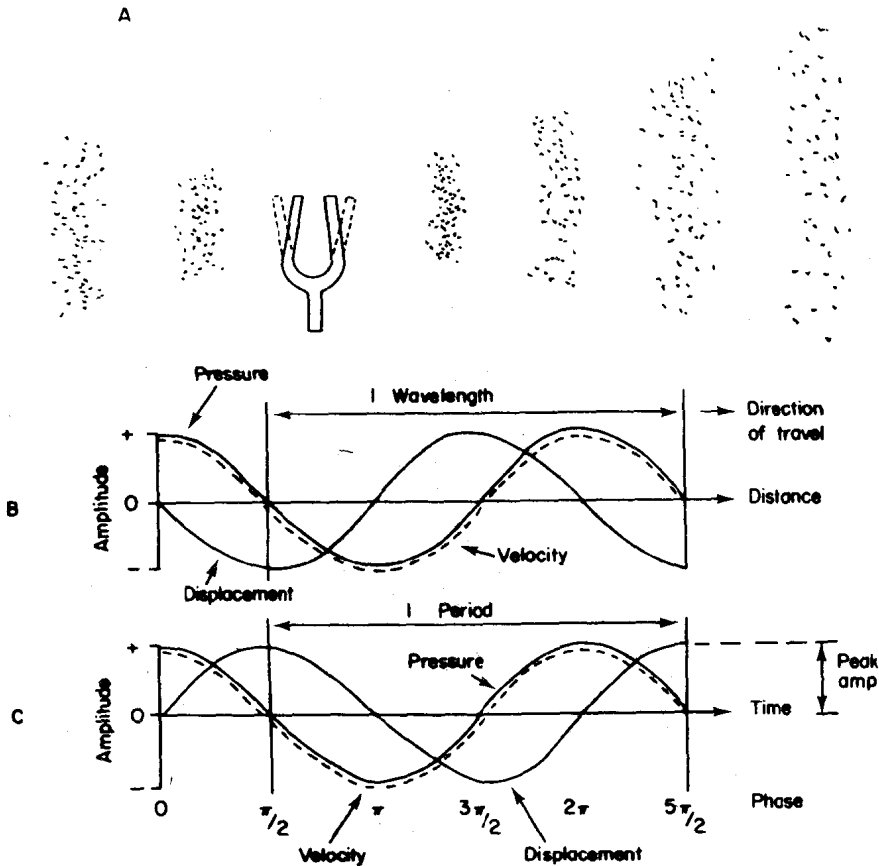


Fig. 1.1 A. A tuning fork sending out a sound wave.

B. The variation of the pressure, velocity, and displacement of the air molecules in a sinusoidal sound wave are seen at one moment in time. The variations are plotted as a function of distance. The pressure and velocity vary together, and the displacement lags by a quarter of a cycle.

C. The same variation is plotted as a function of time, as measured at one point. Because times further in the past are plotted to the right of the figure, the curve of displacement is here plotted to the *right*, not to the left as in part B, of the pressure curve. The phase increases by 2π (or 360°) in one cycle. The sound wave is defined by its peak amplitude and its frequency.

other. The peak pressure above atmospheric (P) and the peak velocity of the sinusoid (V) are related by:

$$P = RV \quad (\text{Equation 1})$$

where R is a constant of proportionality, called the *impedance*. It is a function of the medium in which the sound is travelling, and will be dealt with later.

The intensity of the sound wave is the amount of power transmitted through a unit area of space. It is a function of the *square* of the peak pressure, and, by equation 1, also of the square of the peak velocity. It in addition depends on the impedance; for a sine wave,

$$\text{Intensity } I = P^2/2R = RV^2/2 \quad (\text{Equation 2})$$

In other words, if the intensity of a sound wave is constant, the peak pressure and the peak velocity are constant. They are also independent of the frequency of the sound wave. It is for these reasons that the pressure and velocity will be of most use later.

Unlike the above parameters, the peak *displacement* of the air molecules does vary with frequency, even when the intensity is constant. For constant sound intensity, the peak displacement is inversely proportional to the frequency:

$$D = \frac{1}{2\pi f} \sqrt{\frac{2I}{R}} \quad (\text{Equation 3})$$

where D is the peak displacement, and f is the frequency. So for sounds of constant intensity, the displacement of the air particles gets smaller as the frequency increases. We can see correlates of this when we see a loud-speaker cone moving. At low frequencies the movement can be seen easily, but at high frequencies the movement is imperceptible, even though the intensities may be comparable.

B. The Decibel Scale

We can measure the intensity of a sound wave by specifying the peak excess pressure in normal physical quantities, e.g. newtons/metre², sometimes called pascals. In fact it is often more useful to record the RMS pressure, meaning the square Root of the Mean of the Squared pressure, because such a quantity is related to the energy (actually to the square root of the energy) in the sound wave over all shapes of waveform. For a sinusoidal waveform the RMS pressure is $1/\sqrt{2}$ of the peak pressure. While it is perfectly possible to use a scale of RMS pressure in terms of N/m², for the purposes of physiology

and psychophysics it turns out to be much more convenient to use an intensity scale in which equal increments roughly correspond to equal increments in sensation, and in which the very large range of intensity used is represented by a rather narrower range of numbers. Such a scale is made by taking the ratio of the sound intensity to a certain reference intensity, and then taking the logarithm of the ratio. If logarithms to the base 10 are taken, the units in the resulting scale, called Bels, are rather large, so the scale is expressed in units 1/10th the size, called decibels, or dB.

$$\text{Number of dB} = 10 \log_{10} \left(\frac{\text{Sound intensity}}{\text{Reference intensity}} \right)$$

Because the intensity varies as the square of the pressure, the scale in dB is 10 times the logarithm of the *square* of the pressure ratio, or 20 times the logarithm of the pressure ratio:

$$\text{Number of dB} = 20 \log_{10} \left(\frac{\text{Sound pressure}}{\text{Reference pressure}} \right)$$

It only now remains to choose a convenient reference pressure. In physiological experiments the investigator commonly takes any reference he finds convenient, such as that, for instance, given by the maximum signal in his sound stimulating system. However, one scale in general use has a reference close to the lowest sound pressure that can be commonly detected by man, namely, 2×10^{-5} N/m² RMS, or 20 μ pascals RMS. In air under standard conditions this corresponds to a power of 10^{-12} watts/m². Intensity levels referred to this are known as dB SPL.

$$\text{Intensity level in dB SPL} = 20 \log_{10} \left(\frac{\text{RMS Sound Pressure}}{2 \times 10^{-5} \text{ N/m}^2} \right)$$

We are then left with a scale with generally positive values, in which equal intervals have approximately equal physiological significance in all parts of the scale, and in which we rarely have to consider step sizes less than one unit. While we often have to use only positive values, negative values are perfectly possible. They represent sound pressures less than 2×10^{-5} N/m², for which the pressure ratio is less than one.

C. Impedance

Materials differ in their response to sound; in a tenuous, compressible medium such as air a certain sound pressure will produce greater velocities of movement than in a dense, incompressible medium such as water. The

relation between the sound pressure and particle velocity is a property of the medium and was given in equation 1 by Impedance $R = P/V$. For plane waves in an effectively infinite medium the impedance is a characteristic of the medium alone. It is then called the *specific impedance*. In the SI system, R is measured in $(\text{N/m}^2)/(\text{m/sec})$, or N sec/m^3 . If R is large, as for a dense, incompressible medium such as water, relatively high pressures are needed to achieve a certain velocity of the molecules. The pressure will be higher than is needed for a medium of low specific impedance, such as air.

The impedance will concern us when we consider the transmission of sounds from the air to the cochlea. Air has a much lower impedance than the cochlear fluids. Let us take, as an example, the transmission of sound from air into a large body of water, such as a lake. The specific impedance of air is about 400 N sec/m^3 , and that of water $1.5 \times 10^6 \text{ N sec/m}^3$, a ratio of 3750 times. In other words, when a sound wave meets a water surface at normal incidence, the pressure variation in the wave is only large enough to displace the water at the boundary by $1/3750$ of the displacement of the air near the boundary. However, continuity requires that the displacements of the molecules immediately on both sides of the boundary must be equal. What happens is that much of the incident sound wave is reflected; the pressure at the boundary stays high, but because the reflected wave is travelling in the opposite direction to the incident wave it produces movement of the molecules in the opposite direction. The movements due to the incident and reflected waves therefore substantially cancel, and the net velocity of the air molecules will be small. This leaves a net ratio of pressure to velocity in the air near the boundary which is the same as that of water.

One result of the impedance jump is that much of the incident power is reflected. Where R_1 and R_2 are the specific impedances of the two media, the proportion of the incident power transmitted is $4 R_1 R_2 / (R_1 + R_2)^2$. At the air-water interface this means that only about 0.1% of the incident power is transmitted, corresponding to an attenuation of 30 dB. In a later section (p. 15) we shall see how the middle ear converts a similar attenuation in the ear to the near-perfect transmission estimated as occurring at some frequencies.

Finally, in analysing complex acoustic circuits, it is convenient to use analogies with electrical circuits, for which the analysis is well known. Impedance in an electrical circuit relates the voltage to the rate of movement of charge, and if we are to make an analogy we need a measure of impedance which relates to the amount of medium moved per second. We can therefore define a different acoustic impedance, known as acoustic ohms, which is the pressure to move a unit *volume* of the medium per second. Acoustic ohms will not be used in this book, and where necessary, values will be converted from the literature, which is done by multiplying the number of acoustic ohms by the cross-sectional area of the structure in question.

D. The Analysis of Sound

Figure 1.2 shows a small portion of the pressure waveform of a complex acoustic signal. There is a regularly repeating pattern with two peaks per cycle. The pattern can be approximated by adding together the two sinusoids shown, one at 150 Hz, and the other at 300 Hz. Such an analysis of a

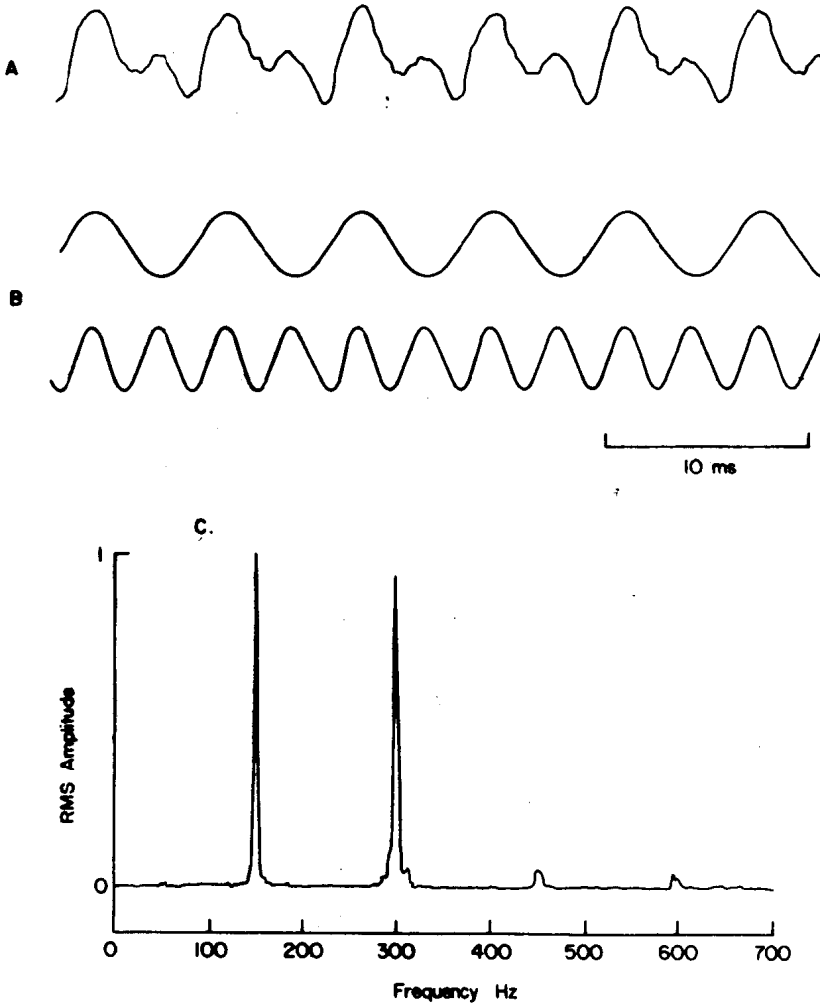


Fig. 1.2 A. A portion of a complex acoustic waveform.
 B. The waveform can be closely approximated by adding together two sine waves.
 C. A Fourier analysis of the waveform in A shows that in addition to the main components, there are other smaller ones at higher frequencies. Components at still higher frequencies, responsible for the small high frequency ripple on the waveform in A, lie outside the frequency range of the analysis, and are not shown.

complex signal into component sinusoids is known as Fourier analysis, and forms one of the conceptual cornerstones of auditory physiology. The result of a Fourier transformation is to produce the *spectrum* of the sound wave (Fig. 1.2C). The spectrum shows here that in addition to the main components, there are also smaller components, at 1/15th of the amplitude or less, at 450 Hz and 600 Hz. Such a spectrum tells us the amplitude of each frequency component, and so the energy in each frequency region.

Why do we analyse sound waves into sinusoids rather than into other elementary waveforms? One reason is that it is mathematically convenient to do so. Another reason is that sinusoids represent the oscillations of a very broad class of physical systems, so that examples are likely to be found in nature. However, the most compelling reason from our point of view is that the auditory system itself seems to perform a Fourier transform, like that of Fig. 1.2C, although with a more limited resolution. Therefore sinusoids are not only simple physically, but are simple physiologically. This has a correlate in our own sensations, and a sinusoidal sound wave has a particularly pure timbre. In understanding the physiology of the lower stages of the auditory system, one of our concerns will be with the way in which the system analyses sound into sine waves, and how it handles the frequency and intensity information in them.

Figure 1.3 shows some common Fourier transforms. In the most elementary case, a simple sinusoid, which lasts for an infinite time, has a Fourier transform represented by a single line, corresponding to the frequency of the sinusoid (Fig. 1.3A). A wave such as a square wave, similarly lasting for an infinite time, has a spectrum consisting of a series of lines (Fig. 1.3B). But physical signals do not of course last for an infinite time, and the result of shortening the duration of the signal is to broaden each spectral line into a band (Fig. 1.3C). The width of each band turns out to be inversely proportional to the duration of the waveform, and the exact shape of each band is a function of the way the wave is turned on and off. If for instance the waveform is turned on and off abruptly, sidelobes appear around each spectral band (Fig. 1.3D).

In the most extreme case, the wave can be turned on for an infinitesimal time, in which case we have a click. The spread of the spectrum will be in inverse proportion to the duration, and so, in the limit, will be infinite. The spectrum of a click therefore covers all frequencies equally. In practice, a click will of course last for a finite time, and this is associated with an upper frequency limit to the spectrum (Fig. 1.3E). Another quite different signal, namely white noise, also contains all frequencies equally (Fig. 1.3F). Although the spectrum determined over short periods shows considerable random variability, the spectrum determined over a long period is flat. It differs from a click in the relative phases of the frequency components, which for white noise are random.

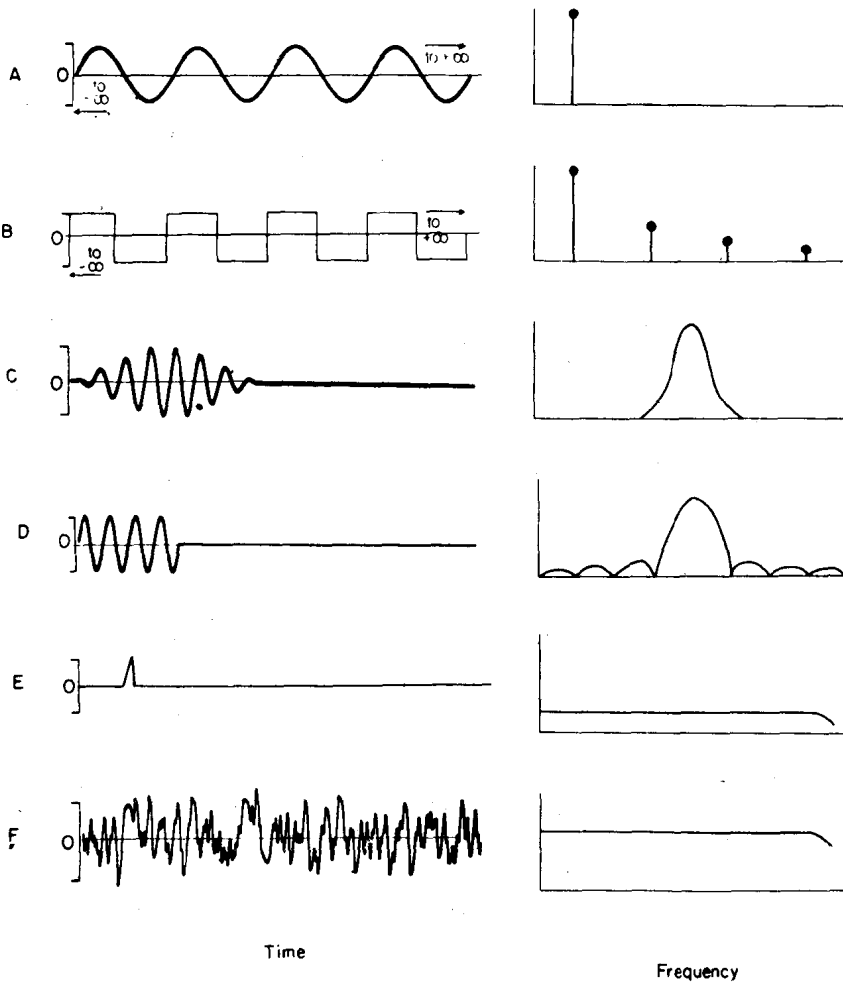


Fig. 1.3 Some waveforms (left) and their Fourier analyses (right).

A. Sine wave. B. Square wave (in these cases the stimuli last an infinite time, and have line spectra, the components of which are harmonically related). C. Ramped sine wave. D. Gated sine wave. E. Click. F. White noise.

E. Linearity

One concept which we shall meet many times, is that of a *linear* system. In such a system, if the input is changed by a certain factor k , the output is also changed by the same factor k , but is otherwise unaltered. In addition linear systems satisfy a second criterion, which is that the output to two or more

inputs applied at the same time, is the sum of the outputs that would have been obtained if the inputs had both been applied separately.

We can therefore identify a linear system as one in which the amplitude of the output varies in proportion to the amplitude of the input. A linear system also has other properties. For instance, the only Fourier frequency components in the output signal are those contained in the input signal. A linear system never generates new frequency components. Thus it is distinguished from a non-linear system. In a non-linear system, new frequency components are introduced. If a single sinusoid is presented, the new components will be harmonics of the input signal. If two sinusoids are presented, there will, in addition to the harmonics, be intermodulation products produced; that is, Fourier components whose frequency depends on *both* of the input frequencies.

In the auditory system, we shall be concerned with whether certain of the stages act as linear or non-linear systems. The tests used will be based on the properties described above.

F. Summary

1. A sound wave produces compression and rarefaction of the air, the molecules of which vibrate around their mean positions. The extent of the pressure variation has a subjective correlate in loudness. The frequency, or number of waves passing a point in a second, has a subjective correlate in pitch. Frequency is measured in cycles per second, known as hertz (Hz).
2. The particle velocities produced by a pressure variation depend on the impedance of the medium. If the impedance is high, high pressures are needed to produce a certain velocity.
3. When a sound pressure wave meets a boundary between two media of different impedance, some of the sound energy is reflected.
4. Complex sounds can be analysed by Fourier analysis, that is, by splitting the waveforms into component sine waves of different frequencies. The cochlea seems to do this too, to a certain extent.
5. In a linear system, the output to two inputs together, is the sum of the outputs that would have been obtained if the two inputs had been presented separately. Moreover, in a linear system, the only Fourier frequency components that are present in the output are those that were present in the input. Neither is true for a non-linear system.