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Physiological Acoustics

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TO JULIUS LEMPERT

Preface

HEARING consists of a complex series of events beginning with the application of physical vibrations to the ear and ending with a perception of sound. We are concerned here with the initial portion of this series, in which the ear's operations are simply acoustic: in which sound vibrations impinge upon the exterior part of the ear, are transmitted inward to the sensory cells of the cochlea, and produce a mechanical stimulation of these cells. The further processes in the sensory cells and in the elements of the auditory nervous system are electrophysiological in nature and lie beyond the boundaries of physiological acoustics. It must be said, however, that though these further processes are not the immediate matter of our discussion they are ever present in the background to stimulate and guide our thinking about the primary problems of sound reception.

As indicated here, our field embraces only auditory reception, and we have not included any discussion of the non-auditory effects of sonic or ultrasonic vibrations, such as the disruptive and thermal effects that may be observed in isolated cells and small organisms.

The treatment begins, in the first three chapters, with a consideration of the anatomy of the ear, the physical nature of sound, and the methods that have been developed for the study of auditory processes. The discussion in these early chapters is largely on an elementary level and serves to introduce many of the terms and principles that will be employed later on. Also the presentation here of the chief methods of investigation simplifies the later description of specific experiments. This introductory part of the book leads up to a consideration of the conditions underlying the ear's sensitivity, and thus brings into focus the problem of the basic function of the middle ear mechanism.

This functional problem and the manner of its solution then come in for searching study, and lead to a formulation of the principles governing the operation of the middle ear as a mechanical transformer. We thus confront the problem of how energy in the form of aerial waves is effectively utilized by the ear.

Following this examination of the general problem of the ear's handling of vibratory energy we take up more specifically the efficiency and fidelity of the process. The question of distortion in the ear is given detailed attention because the opinion has long prevailed that the middle ear is the seat of aural distortion and there has been much reluctance to accept the contrary view, to which our evidence leads, that this structure carries out its task with great fidelity and that it is the sensory cells of the inner ear that introduce distortion into the sounds that we hear.

A major problem, and one given the most particular consideration, is how sounds enter the cochlea and how they act upon its internal structures in producing their patterns of sensory stimulation. After a discussion of the trends of present thinking on this problem we present what we regard as the simplest and most satisfactory theory of this process.

Two chapters are devoted to derangements of the conductive mechanism and the forms of deafness that result. Special attention is given to otosclerosis, one of the most frequent causes of conductive deafness and of singular interest because its symptoms have finally yielded to otologic treatment.

In the final chapters we bring together many of the facts and principles developed earlier and seek to evaluate them further and to show the present status of our knowledge in this field.

Near the end of the book is a glossary of abbreviations and symbols, and thereafter are a number of appendixes containing physical, mathematical, and anatomical data that are commonly useful in connection with auditory problems. There is also a list of references containing the sources specifically mentioned in the text.

The discussion of the various topics is systematic: the existing facts and the more credible opinions are reviewed critically, the points of agreement and conflict are indicated, and our interpretations and evaluations are given. Many of the results that are presented here represent our own investigations carried out over a number of years. Some of the more recent experiments were designed expressly to answer questions raised in the writing of this book, and several of these experiments are reported here for the first time. Chief among these new experiments are the following: (1) an experimental test of the drum-lever hypothesis (page 87), (2) the location of the rotational axis of the cat's ossicular chain (page 101), (3) the lever action of the ossicles (page 105),

(4) further experiments on the locus of distortion in the ear (page 163), (5) the electrical conductivity of the cochlea (page 282), and (6) a further study of the patterns of response in the cochlea as shown by electrical potentials (page 310). In addition, new data are given on the practical limits of drum membrane displacement (pages 89, 149), the constancy of the ossicular lever ratio (page 153), the maximum tension of the cat's stapedius muscle (page 193), and the lengths of the fluid pathways of the cochlea (page 286). Also, further results are presented (page 271) on our experimental test of the traveling wave theories, an investigation also stimulated by the preparation of this book but which has already been reported in current journals. In connection with all these experiments we gratefully acknowledge the assistance given by a contract with the Office of Naval Research and also the assistance of Higgins funds allotted to Princeton University.

Our thanks are offered to many friends who have stimulated and aided us in this work. Because the actions of the ear are often made clear and meaningful only in a contemplation of its aberrations and failures, we feel fortunate in having received over many years the benefits of a close association with Dr. Julius Lempert, Dr. Philip E. Meltzer, and other members of the Lempert Institute of Otology, and through both discussion and experiment in their company of having come face to face with many of the clinical problems of hearing. We are indebted to Dr. Stacy R. Guild of the Johns Hopkins Otological Research Laboratory for supplying us with photographs of the drawing of the cochlea shown as Plate 3 and of the human stapedius muscle shown as Plate 7, and to both Dr. Lempert and Dr. Dorothy Wolff of the Lempert Institute of Otology for making available to us the sections of the tensor tympani muscle shown in Plates 5 and 6. Dr. Lempert also loaned us the original drawings for Plates 8 and 9. The frontispiece is from "Three Unpublished Drawings of the Anatomy of the Human Ear" by the late Max Brödel, reproduced with the permission of the publishers, the W. B. Saunders Company. And finally we express our appreciation to Suzanne Wever, who carried out the exacting task of typing the final copy of the manuscript.

E. G. W. and M. L.

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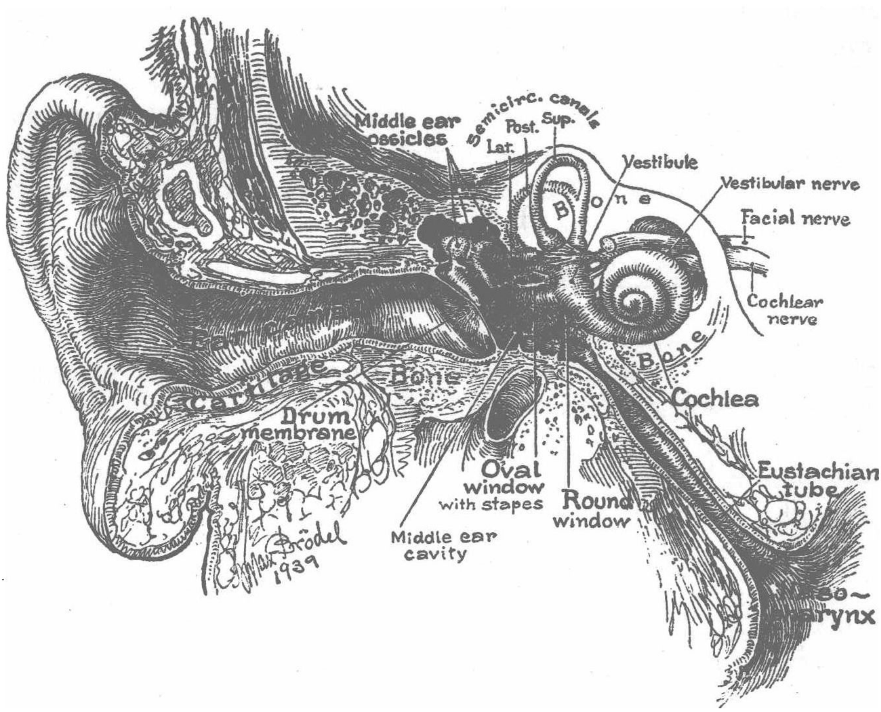
PART I

Introduction


Middle ear ossicles
Semicirc. canals
Lat.
Post.
Sup.
Vestibule
Vestibular nerve
Facial nerve
Bone
Cochlear nerve
Cochlea
Cartilage
Bone
Drum membrane
Oval window with stapes
Round window
Middle ear cavity
Eustachian tube
Max Brödel 1939

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The Ear and Its Structure

HEARING is the result of two kinds of processes, one mechanical and the other physiological. Sounds outside the body strike the external ear and are conducted through the peripheral auditory apparatus to the deep-lying sensory cells, and so far their actions are purely mechanical. In these cells, however, an important transformation takes place. A new action arises that is not mechanical, but as far as we can ascertain is electrochemical. Electrochemical likewise are all the further processes by which the sensory changes, or rather other changes that are representative of them, are relayed onward through the complicated pathways of the nervous system.

In this book we are concerned with the first part of this chain of events, the mechanical part, which constitutes the principal field of physiological acoustics. In the chapters to follow we shall study the ear as a piece of acoustical apparatus and evaluate its service in bringing the vibratory energy of the outside world into play with the final receptor cells of the cochlea.

HISTORICAL ORIENTATION

To gain perspective on our field of study we begin with a historical survey. The early Greeks, like Empedocles in the fifth century B.C., conceived of sounds much as we do today as vibratory movements propagated through the air, and they were aware of the fact—as indeed anyone may discover for himself—that hearing is the result of the passage of these vibrations into the ear,

Beyond this elementary fact, however, Empedocles and his followers had little understanding of the hearing process. They suffered from two serious handicaps. Primarily, their knowledge of the ear's anatomy was woefully limited. They knew about the drum membrane and the tympanic cavity beyond it, but the other, deep-lying structures escaped their notice. Therefore it was natural for them to regard the tympanic cavity as the seat of hearing.

Secondly, in their consideration of the hearing process the ancient Greeks were further handicapped by an idea that then dominated all sensory theory and in fact pervaded all scientific thinking of the time. This idea, known as the principle of resemblances (by which all causes of phenomena are sought in similarities of substance and form) is found almost universally among primitive peoples as the basis of incantations and magic. It forms the basis of homeopathic medicine as the belief that a disease symptom may be made to vanish by doing something that by itself produces that same symptom. For example, a fever is treated by applying heat and frostbite by rubbing with snow. This magic principle as applied to sensation led to the assertion that "like is perceived by like," and as applied to hearing it meant that for anyone to perceive the vibrations of the air outside the body it was necessary for him to have within the ear another quantity of air of a special sort, the "implanted air." This air, supposedly introduced into the tympanic cavity at the birth of the individual and retained there throughout life, was considered as resounding in some way to the motions of the air outside and thereby giving an impression of sound.

Galen,* toward the end of the Greek period (about A.D. 175), took a step forward by recognizing the importance of nerve excitation in the sensory processes in general, and he knew about the auditory nerve, having seen its bundle of fibers passing out of the internal auditory meatus to the brain. Thus he shifted the seat of hearing from the tympanic cavity inward to what he conceived as an expansion of the auditory nerve and called the "neural membrane." However, he had no knowledge of the inner ear itself and, what is more remarkable, he seems to have had no acquaintance with the drum membrane either, but this membrane may well have been absent in the old, poorly preserved skulls that he must have used for study. The "neural membrane" he located at the end of an oblique and tortuous passageway that evidently comprised

* For Galen's works, in Latin translation, see the list of references at the end of the book.

In general, this list is to be consulted whenever an author's name is mentioned. When more than one title is listed after an author's name, each is given a number, and a particular title is referred to in the text by adding its number, italicized and within parentheses, after the name. Sometimes an author's name is mentioned without a number even though the listing will be found to contain more than one title; in such a case all the titles are pertinent to the point under discussion.

the external auditory meatus and its expansion into the middle ear cavity. He still retained the old belief in the implanted air and only transferred it to a more remote locus; lying deep in the passageway it now served as an intermediary agency, the means by which the "neural membrane" was stimulated.

DISCOVERY OF THE CONDUCTIVE MECHANISM

No progress was made in the theory of the action of sound on the ear until the sixteenth century, when the great anatomists of that age, in the course of their comprehensive scrutiny of the human body, brought to light most of the heretofore hidden parts of the ear. By the middle of that century the essential features of the conduction apparatus were well recognized. The two larger ossicles were discovered first, but by whom is not known. Berengario da Carpi in 1514 mentioned them briefly, and later, in 1543, Vesalius described them in detail and gave them their present names of malleus and incus. Then Ingrassia (1546) discovered the third ossicle, the stapes, and the two windows of the cochlea. Fallopius (1561) carefully described the ossicles and their articulations, and also distinguished the two principal divisions of the inner ear and gave them their present names of cochlea and labyrinth.

Eustachius (1564) described the tensor tympani muscle and the tube connecting the tympanic cavity with the pharynx, now known by his name. Both of these structures had been seen earlier without any clear comprehension of their functions. The second tympanic muscle, the stapedius, was first accurately described by Varolius (1591).

After the principal parts of the middle ear had been identified it became possible for Coiter in 1566 to present the first systematic account of the transmission of sound by the ear. In his book, *De auditus instrumento*, which has the distinction of being the first treatise dealing exclusively with the ear, he traced the path of vibrations from their entrance into the external auditory meatus through the drum membrane and the auditory ossicles to the cochlea and the labyrinth. He believed also in an alternative path, by way of the air of the tympanic cavity, which he thought was excited by the movements of the malleus. In this connection he argued against the implanted-air hypothesis, pointing out that the opening of the Eustachian tube to the pharynx made it impossible for the tympanic contents to have any distinctive characteristics. In the cochlea and labyrinth, which he considered to be filled with air, the sounds became amplified "as in a musical instrument" and their movements affected the terminal twigs of the auditory nerve.

During the century following Coiter's systematic review some slight progress continued in the discovery of details of the ear's anatomy and in the understanding of its functions, but the next event of importance was the publication of DuVerney's book, *Traité de l'organe de l'ouie*, which first appeared in 1683.

DUVERNEY'S OBSERVATIONS

Joseph Guichard DuVerney was a physician of prominence in Paris, a professor of anatomy and surgery, and a medical counselor to the king. Along with these attainments, his study of the ear stamps him as a scientist of uncommon skill and discernment. This work deserves our most careful consideration, for not only is it representative of the most advanced thought of its time but it is the point of reference for much that came afterward. The problems that he raised stimulated many of the discussions and investigations of the years to follow, and certain of them are still of active concern to the student of hearing.

DuVerney began his treatment with a careful description of the anatomy of the various parts of the ear and then went on to discuss the particular functions of these parts. He was a skilled dissector, and he displayed many of the ear's anatomical features with more exactness and clarity than anyone had done before. Also he was keenly interested in how the apparatus worked and tried to explain the operations in detail. For the most part his explanations are reasonable, and sometimes they are substantiated with well-conceived tests. The anatomical mistakes that he made are understandable in view of the limitations of his observational method, for he did not have the benefit of the microscope or of means for fixing and staining tissues; these valuable technical aids were still far in the future. His functional errors, which are sometimes serious from a modern point of view, are of course to be blamed upon the primitive state of acoustic science at that time.

DuVerney regarded the external ear as a "natural trumpet" whose purpose was to collect and amplify sound waves and to convey them to the delicate parts within. He asserted that persons who have lost the auricle do not hear very well and have to resort to the use of the palm of the hand to remedy their defect. The obliquity of the external auditory meatus, he correctly pointed out, serves to protect the drum membrane against external injury and to keep out dirt and insects. This form also, he thought, serves in a fashion like the convoluted form of the concha to augment the intensity of sounds by repeated reflections.

The drum membrane is the proper receiver of sounds, he said, but is not absolutely necessary, for persons without this membrane are able to hear by applying the teeth to a vibrating instrument.

The drum membrane is tuned, DuVerney thought, by means of muscles. He mistook the external ligament of the malleus for a muscle, and so he described two muscles attached to this ossicle and serving to regulate the tension of the drum membrane. This tension is increased and relaxed according to the particular kinds of sounds to be heard; indeed, he asserted that it would be impossible for the drum membrane to take up vibrations without suitable tuning to them. He supported this position by some experiments with two lutes, and showed that on plucking a string of one lute a sympathetic vibration was set up in the other only if one of its strings was tuned to the same note or to a note in harmonic relation. He concluded that the drum membrane must be tensed for high tones and relaxed for low tones.

DuVerney sought to trace the vibrations inward to the ultimate receptors. The movements of the drum membrane are communicated directly to the malleus, then to the incus, and finally to the stapes, and thereby pass to the petrous bone and the labyrinth. Also, he admitted, it is possible to conceive that sounds pass inward by an alternative route, by way of the tympanic air, but it was his conviction that this aerotympanic pathway was much inferior to the other. Again he referred to his experiments with the two lutes, and in this connection he found that a communication of vibrations from one instrument to the other occurred readily when both were resting on a table top, but only feebly when this solid connection was broken by raising one into the air. He thus strongly favored the ossicular over the aerotympanic route of conduction. It is of further interest that his explanation of conduction from the teeth involved the ossicular route also: he traced the vibrations through the jaw bones to the temporal bones and thence through the ossicles to the inner ear.

DuVerney's further discussion is marred by the erroneous belief, which was general in his time, that the spaces of the inner ear were filled with air. This air he regarded as the implanted air of the ancients, which Perrault had located here when the old place in the tympanic cavity had been made to seem degraded by the presence of the Eustachian opening to the pharynx. DuVerney supposed that the movements of the stapes were communicated first to this air in the vestibule and finally to the air of the cochlea and semicircular canals.

DuVerney, like his immediate predecessors, regarded the bony spiral lamina as the final responsive structure of the cochlea, for, he said, it has the proper mechanical properties: it is hard, dry, thin, and brittle—the attributes well known in musical instruments as fitting them for vibration. Unlike the others, he knew about the basilar membrane, but he regarded it simply as a delicate means of supporting the bony spiral lamina on its outermost edge. Its connection with the cochlear wall he saw as dividing the spiral canal into two scalae, and as he did not know of the helicotrema he regarded this division as complete.

The stapedial movements he conceived as entering the upper or vestibular scala and acting upon the spiral lamina from above. At the same time, in line with his somewhat grudging admission of the aerotympanic route, he supposed that the vibrations along this path entered the round window and beat upon the spiral lamina from below. Such double action, he thought, ought to give particularly vigorous stimulation.

DuVerney mentioned that some students had doubted that the semicircular canals served as a primary receptor for sounds, and according to them had only the accessory function of reinforcing the entering sounds by resonance. However, he took the position that this part of the labyrinth was a true acoustic receptor. His reasons were plausible: the canals have a suitable structure, they are served by the same nerve, and certain animals, such as birds, have no cochlea yet they hear with these other organs.

Despite his inclusion of the semicircular canals as a part of the hearing organ, DuVerney placed the main emphasis upon the cochlear apparatus, and he went on to describe the tapered form of the spiral lamina and to develop his theory that by reason of its varying width this structure is differentially tuned to the range of audible frequencies. Because this bony lamina is wider at the basal end of the cochlea and narrower toward the apex, he located the low tones in the base and the high tones in the apex.

FURTHER DEVELOPMENTS OF AUDITORY THEORY

Two further developments were necessary to bring this conception of sound conduction in the ear close to its modern form. The first was the discovery that the cochlear spaces are filled with fluid. Several persons had noticed that fluid was present in these spaces, but Cotugno in 1760 was the first to maintain that only fluid is present: that it fills the whole space. Meckel provided the conclusive evidence for this view by an ingenious experiment. He exposed some fresh specimens of human temporal bones out of doors in freezing weather and observed that the labyrinth when opened was filled with ice. This proof of the pervasiveness of the labyrinthine fluid sounded the end of the implanted-air hypothesis by crowding it out of its last reposing place.

The next and most important development was the identification of the true auditory receptors. DuVerney had considered the spiral lamina as ideally suited to be a resonator and he thought that the auditory nerve fibers were expanded upon its surface. But two influences led away from this position and toward the acceptance of a soft structure. One was a classical bias in favor of the "neural membrane" that Galen had spoken of, with a little of the magic of the old principle of resemblances to reinforce it; thus Valsalva argued that a soft tissue ought to be served by a "soft" part of the auditory nerve. This argument becomes intelligible when we recall that classically the sensory and motor nerves had been designated as soft and hard respectively. Valsalva thus was referring to the sensory—i.e., auditory—division of the auditory-facial bundle that was then regarded as one nerve. He characterized these soft sensory tissues in the labyrinth as a whole as the "zona cochleae," which is his name for the membranous spiral lamina.

The second influence was derived from the growing interest in the process of resonance and the search for resonating structures in the ear. DuVerney had indicated only a broad kind of selectivity for the spiral lamina, but as time went on this conception grew more and more specific. Haller in 1751, in reporting what is evidently the interpretation of DuVerney's theory that was then current, spoke of the spiral lamina as made up of a series of strings of varying lengths.

Cotugno brought these two influences together. He accepted from Valsalva the idea of a membrane as the receptor and conceived this membrane as made up of a series of vibrating strings. This conception of the basilar membrane as a resonator and as the final receptor organ met with general acceptance during the latter part of the eighteenth century. Further progress had to await the discovery of finer details of cochlear anatomy.

The anatomists had achieved this much in the understanding of the ear by the methods of gross dissection and by viewing with the unaided eye or with simple lenses. Then about 1830 the compound microscope, which had long been known in principle, was made into a practical instrument through improvements in the art of lens-making. Thereby a new world of objects was brought into view, and soon the ear claimed its share of searching study.

With the aid of this new instrument, Huschke in 1835 made out several new features of the cochlear structure. He saw the limbus and its outward extension as the vestibular lip, and distinguished these parts from the bony spiral lamina, whose outer edge he now called the tympanic lip. Reissner discovered a new membrane, now known by his name, which runs all along the cochlea and divides the space on the vestibular side of the basilar membrane into two parts, the scala vestibuli and the cochlear duct. The cochlear duct contains endolymph, a fluid entirely separate from the perilymph of the vestibular and tympanic scalae.

The most important event of this period was Corti's discovery, in 1851, of the complex sensory structure lying on the basilar membrane. He saw the tectorial membrane, the hair cells, and the "rods" of Corti, and made out in considerable detail the relations of these new parts and others that had already been recognized.

Many investigators took part in the elaboration of further details, and by the end of the century the picture was well filled in. Retzius and Held made outstanding contributions, especially to our knowledge of the forms and positions of the hair cells and