THEORIES OF HEARING

A critical study of theories and experiments on sound-conduction and sound-analysis in the ear

P. J. KOSTELIJK

v Dishoeck

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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE GENEESKUNDE AAN DE RIJKSUNIVERSITEIT TE LEIDEN, OP GEZAG VAN DE RECTOR-MAGNIFICUS Dr B. A. VAN GRONINGEN, HOOGLERAAR IN DE FACULTEIT DER LETTEREN EN WIJSBEGEERTE, TEGEN DE BEDENKINGEN VAN DE FACULTEIT DER GENEESKUNDE TE VERDEDIGEN OP WOENSDAG 22 MAART 1950 TE 16 UUR

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PIETER JAN KOSTELIJK

GEBOREN TE VELSEN

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LEIDEN 1950

Promotor: Prof. Dr P. H. G. VAN GILSE

Aan mijn moeder
Aan mijn vrouw

VOORWOORD.

Het verschijnen van dit proefschrift verschaft mij de gelegenheid mijn grote erkentelijkheid te betuigen aan U, Hoogleraren, Lectoren en Privaat-Docenten, die tijdens mijn studiejaren leden waren van de Medische en Natuurphilosophische Faculteit te Utrecht voor de academische vorming, die ik van U mocht ontvangen.

Hooggeleerde van Gilse, tijdens mijn specialistische opleiding is dit proefschrift onder Uw leiding begonnen en het is mij een bizonder voorrecht, dat Gij thans mijn Promotor kunt zijn. Met grote erkentelijkheid denk ik terug aan de tijd, die ik bij U in de kliniek werkzaam heb mogen zijn. Tijdens die voor ons allen zo zorgelijke oorlogsjaren hebt Gij steeds getracht de band tussen allen die op Uw afdeling werkzaam waren te verstevigen en heb ik mogen profiteren van Uw uitgebreide kennis en rijke ervaring op het gebied der Oor-, Neus- en Keelheelkunde.

Toen de oorlogsomstandigheden het verrichten van experimentele onderzoekingen op het gebied der physische en physiologische acoustiek zeer bemoeilijkten, heb ik, op Uw aansporen, de mij door de Organisatiecommissie Gezondheidstechniek T.N.O. geboden gelegenheid tot het samenstellen van een samenvattend overzicht over theorieën en experimenten betreffende de gehoorzin gaarne aanvaard.

Gij, hooggeschatte Promotor, hebt steeds mijn belangstelling voor de problemen der acoustiek aangewakkerd en mij aangespoord deze vaak hopeloos schijnende taak tot een einde te brengen. Voor deze steun ben ik U ten zeerste erkentelijk.

Een woord van bizondere dank moge hier worden gericht aan de Organisatiecommissie Gezondheidstechniek T. N. O. en in het bizonder aan de Geluidcommissie dezer Organisatie, voor de financiële en morele steun, waardoor het mogelijk werd, dat dit overzicht als afzonderlijk rapport der Commissie en tevens als proefschrift kon verschijnen.

Bij de uitwerking der physische problemen mocht ik grote hulp ondervinden van de waarnemend Voorzitter van de Geluidcommissie T.N.O. Dr Ir C. W. Kosten, alsmede van Drs J. J. Groen en Mevrouw E. Kraak-Cramer, waarvoor ik hen op deze plaats gaarne mijn erkentelijkheid wil betuigen.

Het secretariaat van de Organisatiecommissie Gezondheidstechniek T.N.O., alsmede de Universitaire Pers Leiden breng ik bizondere dank voor hun medewerking bij de technische uitvoering dezer publicatie.

Met dankbare herinnering denk ik terug aan de prettige samenwerking tijdens mijn assistentschap met mede-assistenten, zusters en ander personeel van de Oorheelkundige Afdeling van het Academisch Ziekenhuis te Leiden, waarbij ik in het bizonder denk aan Mejuffrouw Nieuwenhuyse, Zuster Molenkamp, alsmede aan de heren Brouwer en Piena.

Tenslotte mag ik allen, die op enigerlei wijze aan het tot stand komen van dit proefschrift hun medewerking hebben verleend van harte dank zeggen voor hun zeer gewaardeerde hulp, zonder welke de uitvoering van deze taak mij vrijwel onmogelijk zou zijn geweest.

Oegstgeest, Maart 1950

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CHAPTER I

INTRODUCTION

The explanation of the sense of hearing is undoubtedly one of the most difficult problems in science. Numerous otologists, anatomists and physiologists, as well as many physicists have been engaged in solving this problem. The great amount of clinical experience and the vast number of experiments, the observations of which often were conflicting, have led to the formation of a great many theories of hearing.

This has made it hitherto practically impossible to come to any one theory capable of explaining all the characteristics of the sense of hearing.

In order to arrive at a classification of all the facts and data available, it will be necessary to analyse the different processes which go to form the auditory sensation.

Whereas in the case of the cutaneous senses and the special senses of taste and smell, the stimulus affects the sensory elements directly, in the case of the senses of vision and hearing the stimulus has first to pass through a series of media before arriving at the sensory organ proper. The various physical constants of these conductive systems will influence the nature of the stimulus, and changes in these constants may alter the final perception of this sensory stimulus. Only after the physical energy has been transferred into nervous energy will the impulse pass along the nerve to the cerebral cortex, where a final interpretation of the stimulus takes place. The whole process can therefore be divided schematically into three stages, namely:

1. the transference of the physical energy of the stimulus to the sense organ proper. In the ear this is achieved by the sound-conducting system, which consists of the tympanic membrane, the chain of ossicles, and the fluid of the inner ear. The air in the middle ear, the membrane of the foramen

rotundum and the membranes suspended in the cochlear fluid also have to be considered as part of this system.

2. the conversion of the physical energy into nervous impulses by the sense organ of CORTI ("transformation system").

3. the conduction of nervous impulses along the nerve-tracts to the nerve centres in the auditory cortex.

In studying the sense of hearing we shall have to decide with which of the above systems certain peculiarities of this sense are connected. In early days this study was almost entirely limited to the sound-conducting system, including the basilar membrane, and most of the auditory theories of that time attempted to deduce the function of the ear chiefly from the anatomical structure and the physical characteristics of this system. Whereas the function of the middle ear in man could be traced with some degree of certainty, it was almost impossible, on account of the minute dimensions and inaccessibility of the cochlear system, to examine the physical and biological peculiarities of the inner ear apparatus. Thus many contradictory hypotheses were formed concerning the function of the inner ear, but the values of the various physical constants of this organ (e.g. the viscosity and density of the fluid, damping, mass, and elasticity of the basilar membrane), were frequently estimated arbitrarily. von BÉKÉSY in his ingenious investigations, making use of an extremely accurate experimental and microscopical technique, was the first to try to correlate all these physical characteristics of the inner ear in order to lead to a better insight into the working of this part of the auditory organ.

After the anatomical discovery of the spiral organ by ALPHONSE CORTI in 1851, its function in relation to the normal process of hearing was soon recognized. Though, later on, some doubt was expressed as to the absolute necessity of an intact organ of Corti for the perfect sense of hearing (WITTMAACK (2), RUNGE, KEPES, v. GILSE) we may now assume that the integrity of this organ is indispensable for the normal function of the organ of hearing. At first conclusions regarding the function of the organ of Corti could be drawn only from the study of the microscopical structure of this organ after the death of the human being. Since experimental physiology was still in its infancy and no reliable method for testing thg hearing in animals existed it was only in the human being that a functional examination of hearing could be made.

And it was only possible after the death of the human being that a correlation between this functional examination and the pathological-anatomical changes in the organ of hearing could be established. Drawing conclusions about the function of an organ from its microscopical structure, however, is only possible to a certain extent, and owing to technical difficulties, this is particularly limited in the case of the hearing organ. The investigations of HAMBERGER et al., however, seem to have opened the way to correlate the results of functional tests with biochemical changes in the nerve-cells of the cochlear and vestibular ganglia.

Not until methods were developed which permitted the testing of hearing in animals, was the way opened to a closer study of the physiology of hearing. Since the experimental technique was at first limited to the examination of the sound-conducting system, it was practically impossible to investigate the inner ear and the auditory nerve in the same manner. Only the discovery of the electrical activity of the cochlea and the auditory nerve, by WEVER and BRAY (1), opened the way to a better understanding of the function of the inner ear, and central interpretation of the nerve impulses. As the following chapters will touch repeatedly upon these animal experiments, the principal methods are now described briefly.

1. *the acoustic reflexes* — animal experiments have revealed that certain groups of muscles contract in response to sound impulses of sufficient intensity. Preyer, for instance, described in rodents the so-called pinna-reflex, consisting of a short contraction of the auricle which can be recorded on a kymograph. Of much greater importance, however, appeared to be the contractions of the intra-tympanic muscles in response to sound stimuli (acoustic reflex contraction). This reflex has been studied by a great many authors (KATO, KOBRAK (1, 2, 4), LORENTE DE NÓ (1, 2), PHILIP, HALLPIKE and several others).

It was shown that in various animals both muscles respond to sound impulses of sufficient intensity, the reflex mechanism of the stapedius muscle being the more sensitive (KATO). The strength of contraction at a certain intensity-level of the stimulus varies widely in different animals and individuals, but as in each individual it is directly proportional to the intensity of the stimulating sound, this reflex may be used as an index of auditory function. Any alteration in the perception of sound impulses will change the rate of contraction of the intra-tympanic muscles. Since even in response to a unilateral stimulus the reflex appears in both ears, the cochlear function in one ear may be studied by the contractions of the muscles in the opposite ear.

LÜSCHER (1) demonstrated the stapedius reflex in man; and many subsequent investigations have contributed to the elucidation of the characteristics of this particular auditory reflex contraction. (KOBRAK (2); LINDSAY, KOBRAK and PERLMAN; POTTER; PERLMAN and CASE (1)).

2. *the vestibular reflexes* — another form of motor reflex is the reaction first described by TULLIO (reaction of Tullio). If, in an animal, the pigeon for instance, the static organ is opened by making a fistula in one of the semicircular canals, movements of the head and eyes result as a reaction to sound impulses of sufficient intensity. These experiments have been confirmed and carried further by several others. Though this reflex cannot be considered as a means of measuring the cochlear function, because it is still maintained after total abolition of the cochlea, it may well serve as a means to examine the hydrodynamic behaviour of the inner ear before and after the sound-conducting apparatus has been subjected to various kinds of surgical interventions (HUIZINGA, v. EUNEN).

3. *the conditioned reflexes* — when, in an animal a certain stimulus evokes a certain reflex and simultaneously a sound impulse is delivered, the animal, after some time and practice, will exhibit the reaction only when the sound impulse is given and the original stimulus is omitted (PAVLOV). This method appeared well suited for studying the physiology of hearing (CULLER, BROGDEN et al., DWORKIN), and has, for instance, brought forward evidence for a cerebral tonal localization (ADES, METTLER and CULLER).

4. *electrical phenomena* — In 1930 WEVER and BRAY (1) reported upon their classical experiments in which electric potential oscillations could be derived from the auditory nerve of an anaesthetized animal in response to sound waves activating the ear. The next year ADRIAN (1) showed that these potential waves could be easily detected from the area of the foramen rotundum by opening the auditory bulla. The investigations of DAVIS et al. (1934) soon showed that two different phenomena had to be distinguished:

a. the electrical response of the cochlea (cochlear activity, cochlear potentials, cochlear response, cochlear microphonics) — as this phenomenon disappears after the death of the animal, WEVER and BRAY concluded that it must be of a biological nature. The characteristics of the sound impulse, such as frequency, intensity and phase, are almost accurately followed by the electric potentials generating in the cochlea and spreading to adjacent areas, such as the foramen rotundum and the cochlear nerve. The cochlea thus works as a type of microphone (microphonic action of the cochlea).

DAVIS and his co-workers interpreted the cochlear response as arising in the sensory cells of the organ of Corti as a result of mechanical distortion of these cells (piezo-electrical effect). Contrary to this hair-cell theory, stands the theory that these cochlear potentials have a purely physical origin in movements of fluids, or polarized membranes in the inner ear (EYSTER, BAST and KRASNÒ, HALLPIKE and RAWDON-SMITH (2), FIORI-RATTI and MANFREDI). The many investigations which have since been carried out have established, with a fairly high degree of certainty, that the cochlear potentials have their origin in the hair-cells of the organ of Corti (STEVENS and DAVIS, HINNEN, WALZL (1), JUUL).

Though the cochlear microphonics may not be considered as an absolute measure of the hearing sensation of the animals, since, even with total dissection or destruction of the auditory nerve, the electrical activity of the cochlea remains unchanged (GUTTMANN and BARRERA (1, 2), RAWDON-SMITH and HAWKINS), it must be regarded as a highly valuable means of measuring the cochlear function during life. The influence of alterations in the sound-conducting apparatus as well as in the sensory organ can easily be studied by this method. (Summaries: STEVENS and DAVIS, KELLAWAY).

Since it is fairly clear that the structures responsible for the cochlear microphonics are an essential link in the process of hearing, any marked alteration in these structures will result in a similar alteration in the auditory acuity. The attempts to correlate the hearing sensation in animals, as measured by the conditioned reflex method, with the occurrence of cochlear microphonics, as well as the study of cochlear activity in man (PERLMAN and CASE (2), LEMPERT et al. — cochleogram) may carry us towards the solution of how close the relationship is, which exists between the cochlear microphonics and the hearing sensation.

A similar effect to that which can be derived from the cochlea may be elicited by the crista in the ampulla of the static organ, if an opening is made in the corresponding semicircular canal and a sound wave activates the ear (BLEEKER). This microphonic action of the crista has nothing to do with the cochlea, as it can also be generated if the cochlea is destroyed or extirpated.

b. action currents of the auditory nerve — these action-currents in general exhibit the same phenomena which electrophysiology has already demonstrated in all other sensory nerves (ADRIAN, (2)). The further study of these action-currents has of recent years furnished valuable data regarding the manner in which the sound impulses are conducted to the central nervous system by the nerve fibres of the auditory nerve (WALZL (2), WOOLSEY and WALZL, TUNTURI, GALAMBOS and DAVIS (1, 2)).

It is not intended, however, to enter further into these investigations here since they are but indirectly concerned with the subject under discussion. In the following chapters, after a short summary of the principal anatomical facts, an attempt will be made to give a review of the historical development of the theories of hearing leading up to our present knowledge as far as it concerns the first phase of the auditory process. At the same time a distinction will be made between:

1. Theories and experiments respecting the sound *transmission* in middle and inner ear.
2. Theories and experiments respecting the sound *analysis* by the auditory organ.

CHAPTER II

THE STRUCTURE OF THE INNER EAR AND THE CHARACTERISTICS OF THE INNER EAR FLUIDS

Since most theories of hearing are based on the various anatomical features of the organ of hearing the principal facts regarding these features, as far as they are in relation to its function, will now be described.

From the anatomical point of view the ear may be divided into three parts (fig. 1):

1. External ear, which includes the auricle and the external auditory meatus. According to v. BÉKÉSY (4) the average volume of the external auditory meatus amounts to 1.04 cc and the average depth to about 2.7 cm.

2. Middle ear, consisting of a cavity filled with air separated from the external ear by the tympanic membrane, to which is attached the chain of ossicles, namely the hammer or malleus, the anvil or incus and the stirrup or stapes.

The pressure in this cavity under normal conditions is equal to that of the atmospheric pressure of the external ear, and is regulated by means of the Eustachian tube. As the acoustic properties of the tympanic membrane are mainly determined by the cushion of air within the tympanic cavity, a slight change of its pressure may cause an important alteration in the acoustic impedance of the membrane. To the malleus and to the stapes are attached two small muscles, the M. tensor tympani to the malleus and the M. stapedius to the stapes. A contraction of the stapedius muscle may cause a slight displacement of the stapes (LÜSCHER). No displacement of the malleus or the tympanic membrane has, however, been observed in the acoustic reflex contractions of the tensor tympani in man (WAAR).

3. Internal ear, which consists of two parts, the static organ, or vestibule together with the three semicircular canals, and the cochlea, which is a spirally coiled tube, wound round an axis for two and a half turns (fig. 2). In some animals the number of turns of the cochlea is greater, that of the guinea-pig, for instance, has four turns.

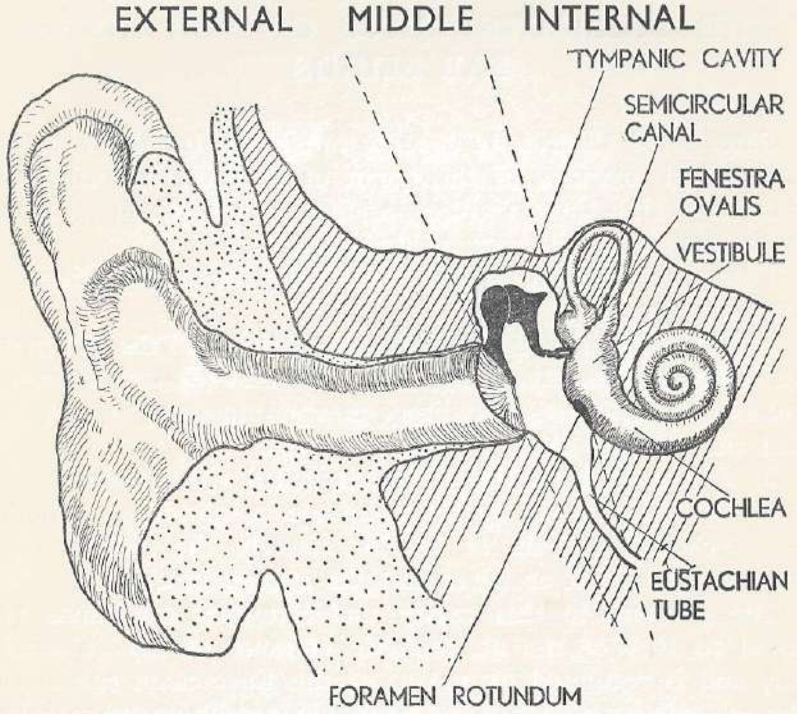

Fig. 1. Schematic diagram of the structures of the external, middle and internal ear.

Briefly the inner ear is contained in a complete cavity of the temporal bone, known as the osseous labyrinth, which is filled with fluid known as perilymph, and in this fluid is suspended the membranous labyrinth, a series of communicating sacs and ducts, containing another fluid, the endolymph (fig. 5).

Two openings in the osseous labyrinth or the labyrinthine capsule lead from the middle ear into the inner ear. These openings are known as the fenestra ovalis or oval window and the foramen rotundum or round window. Whereas nearly the whole of the fenestra ovalis is occupied by the footplate of the stapes, a flexible elastic membrane is stretched in the bony ring of the foramen rotundum. On account of the membranous connection of the stapedial footplate with the margin of the fenestra ovalis, the stapes can make a to and fro movement. Because this fixation is much stronger at one side than at the other, the stapes does not move like a piston in a cylinder, but makes a pivoting movement, with the axis of rotation at the lower posterior pole (fig. 8). The movements of the stapes in connection with its shape have been elaborately studied by Stuhlman (2, 3) and Fumagalli.

The cochlear partition.

The cochlea, throughout almost its entire length, is divided into two separate parts by a partition, partly bony, partly membranous. At the apex of the cochlea the membranous part of the partition is deficient, so that an opening is formed between the two separate portions of the tube. This opening, measuring about 0.1 sq. mm is called the helicotrema (fig. 2). The bony part of this partition is in the form of a shelf, the osseous spiral lamina, and is attached to the axis of the spiral, called the modiolus, whereas the membranous portion stretches from the free border of the osseous lamina to the outer wall of the canal. This membrane is known as the basilar membrane, and, as it is of great importance in most theories of hearing, a more detailed description of its anatomical features is necessary.

The basilar membrane consists of three layers, two covering layers and one intermediate layer. Since the investigations of Hensen (1863) and Nuel (1872) it is generally held that this intermediate layer consists of a great number of adjacent fibres running radially in a homogeneous ground substance. Ayers (1) and Shambaugh (1) described in the human specimen not one, but four layers of fibres, three of which ran in a radial direction and a fourth which ran at right angles to the other three. In some animals (cat and rabbit) two layers of fibres do occur, separated by a homogeneous substance (Held (3)).

As the result of anatomical investigations Hardesty (1) assumed that the fibres were built up of numerous fibrils, tightly connected with each other through a richly branched network of connective tissue, so that the whole layer of fibres showed a great resemblance to a very thin tendinous plate. Because the fibres in the outer part of the basilar membrane are much thicker than those in the inner part, the membrane is divided into two zones, the zona pectinata and the zona arcuata. In the latter the fibres are thin and branched, forming a delicate network, whereas, under ordinary microscopical technique the much thicker fibres of the zona pectinata are distinctly separated from each other. According to Retzius (1884) there are approximately 24.000 fibres in the zona pectinata, whereas Hensen estimated this number at 13.400. The whole layer of fibres may be lacking at the base of the

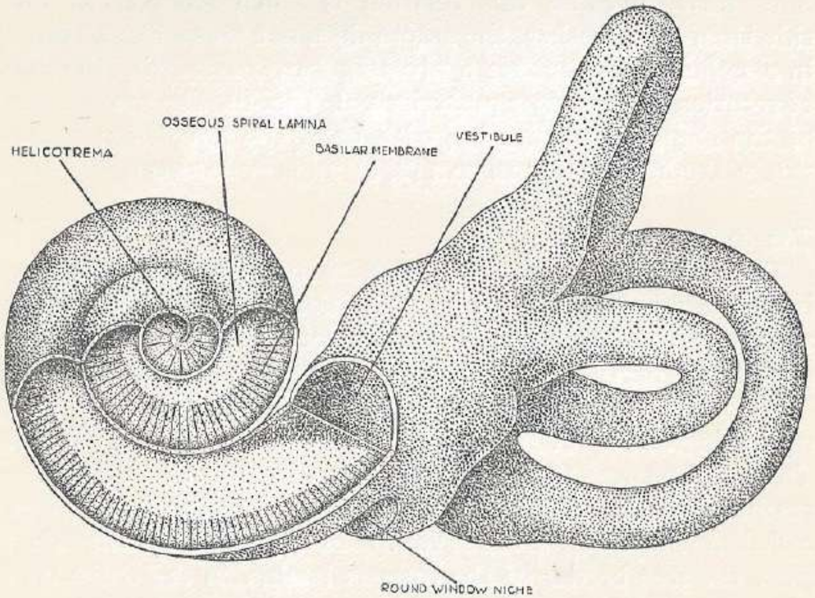

Fig. 2. Lateral view of the osseous labyrinth. The lateral wall of the cochlea with the oval window has been partly removed to show the cochlear partition and the helicotrema.

cochlea as well as at the helicotrema. Mygind, who has investigated a great number of labyrinths regards these fibres, however, as being a histological artefact.

Dimensions of the basilar membrane.

1. length — Hensen, in 1865, adopted an average length of 33.5 mm. By making use of Guild's reconstruction method, Hardy investigated 68 cochleae of individuals varying in age from 10 weeks to 85 years. By measuring along the line of the pillar cells, she found the average length to be 31.52 mm, with a variation from 25.26 mm to 35.46 mm.

Using an entirely different method, Keen (2) estimated the length in man to be 32 mm, measured along a line indicating the attachment of the basilar membrane to the spiral ligament.

2. width — Whereas the width of the cochlear canal gradually decreases from base to apex, the basilar membrane grows wider as the bony part of the partition tapers away (fig. 2). The investigations of Guild (2) and Wever, however, have shown that at a considerable distance from the apex (from half to one turn) the basilar membrane instead of growing wider tapers away rapidly again, and that its width at the apex may vary considerably in different individuals.

The accounts relating to the width at different places of the membrane vary considerably in the works of various authors. In 1863 Hensen recorded for the newly-born a variation in width between base and apex of 0.041 to 0.495 mm, this being a 12-fold increase in width. Keith and Held only found a 3-fold increase. Wever, who investigated a great many human cochleae by the graphic reconstruction method of Guild (1), found the width at the basal turn to be fairly constant (about 80 micra) but that great variations occurred in other parts of the membrane. An average of the maximal width was found to be 0.498 mm, with a variation from 0.423 to 0.651 mm. Thus his measurements, with a 6¼-fold increase, lie between those of Hensen and later authors.

Wever pointed out that a theory of hearing which postulates a differentiating rôle for the width of the basilar membrane, must allow for a wide range of normal variation in the apical region.

	base	middle	maximum
Hensen..........	0.041		0.495
Retzius	0.210	0.340	0.360
Keith	0.160		0.520
Held	0.176	0.304	0.480
Wever	0.080		0.498

The cochlear duct.

A very delicate membrane, Reissner's membrane, stretches from the inner spiral shelf to the outer wall of the canal. At base and apex the basilar membrane and Reissner's membrane are connected, giving rise to a separate closed canal, which, on cross section, shows a triangular form (fig. 3).

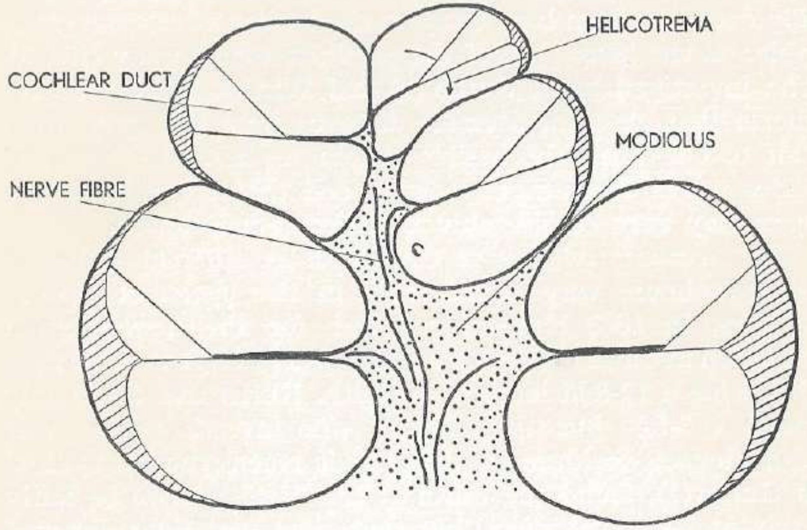

Fig. 3. Diagram of axial section of the cochlea.

The size of this canal, known as the scala media or cochlear duct, seems to vary little in different species of animals (Keen, (2)). At birth the cochlea has already reached its

definite form and adult size (Anson et al.), a fact which may possibly be related to the wave-length of the acoustic frequencies.

The scala media is filled with a viscid fluid, the endolymph, differing in physical as well as in chemical characteristics from the perilymph, which fills up the remaining part of the original tube. These parts are known as the scala vestibuli and the scala tympani. Thus two separate spaces are formed, both filled with fluid, the perilymphatic and the endolymphatic space (fig. 5). According to Zwislocki the cross-sectional area of the scala vestibuli and scala tympani in the same individual varies considerably at various distances from the fenestra ovalis (fig. 4).

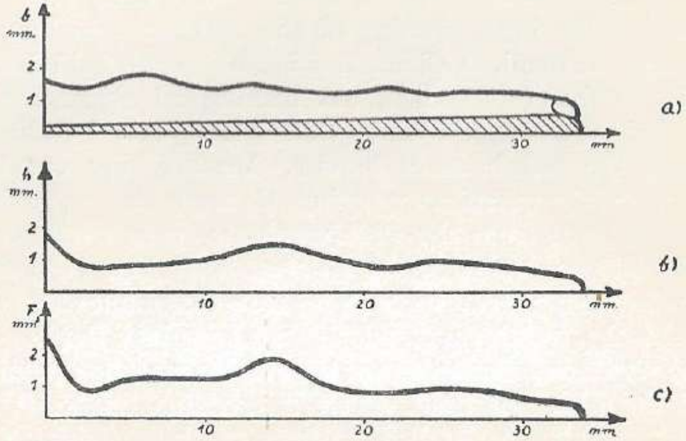

Fig. 4. Dimensions of the scala vestibuli in relation to the distance from the oval window. (After Zwislocki)

a. parallel to the basilar membrane; the lined area indicates the basilar membrane
b. perpendicular to the basilar membrane
c. the approximately calculated cross-sectional area.

The perilymphatic and endolymphatic fluid systems of the inner ear.

The perilymphatic space of the inner ear is connected with the subarachnoid space at the base of the brain by a small canal. As early as 1761 Cotugno showed that the bony canal, the cochlear aqueduct, forms a free communication between the two spaces, but the question as to whether the membranous canal, the ductus perilymphaticus, which passes through the aqueduct, is open to the passage of fluid, has long been disputed. Although most investigators have maintained that a free communication exists between the perilymphatic and subarachnoid spaces (a.o. Perlman and Lindsay, Ahlén), Waltner again questions the patency of the cochlear aqueduct. In human temporal bones a barrier membrane was found, separating the inner opening of the cochlear aqueduct from the scala tympani. A direct flowing of spinal fluid into the cochlea is therefore denied, but histological evidence points to a fluid exchange, if any, that takes place by diffusion through the membranous barrier. Another tiny canal, the ductus endolymphaticus, passing through the aquaeductus vestibuli, leads from the endolymphatic space to the saccus endolymphaticus outside the petrous bone (fig. 5). This sac forms a blind pouch, so that no free communication exists between the endolymph and the cerebrospinal fluid.

The very small dimensions of the cochlea and the exceedingly small quantities of fluid which it contains, make it very difficult to give a detailed analysis of these fluids. Nevertheless some data respecting their physical and chemical attributes have been obtained. In the pigeon Rossi found the viscosity of perilymph in relation to water to be 1.7, that of endolymph 2.9, whereas SzÀsz demonstrated that the refraction of the perilymph is less than that of the cerebrospinal fluid.

According to v. Békésy (1) the viscosity of the perilymph is 0.0197 c.g.s. (at 20° C. water has a viscosity of 0.0101 c.g.s.) and the density 1.034 grams/cc. at 37° C. The osmotic pressure of the fluids has been measured by Aldred, Hallpike and Ledoux. They found an average osmotic pressure (expressed in gram/NaCl. per 100 Gr. of water) of 1.058 for the endolymph and 1.046 for the perilymph. For the cerebrospinal fluid and the blood, values were found of 1.017 and 0.994 respectively. On account of technical difficulties which prevail regarding the measurements of the endolymph, these authors, however, assume that endo- and perilymph are virtually isosmotic at a level equivalent to about 1.052 % NaCl.

The question of the origin and circulation of both fluids forms a very difficult problem. As regards the endolymph, it is generally agreed that this fluid is at least partly secreted by the stria vascularis.

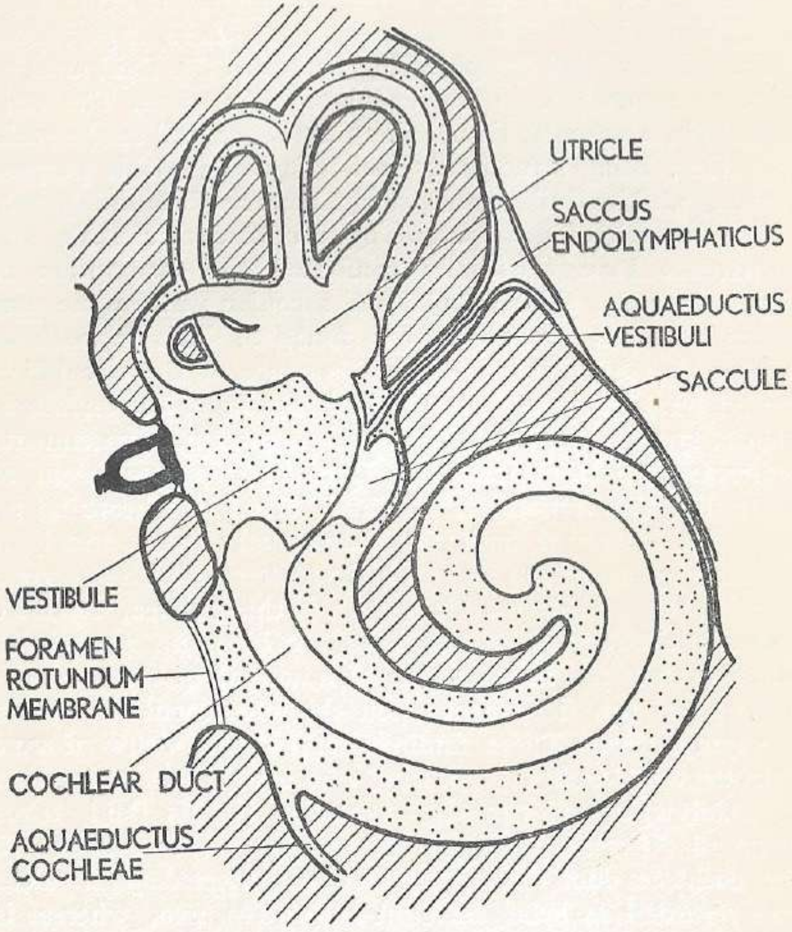

Fig. 5. Schematic diagram of the membranous labyrinth and the perilymphatic space (After Werner).

Guild (3) injected a solution of iron-salts into the cochlear ducts of living guinea-pigs, and the distribution throughout the endolymphatic space in each case was studied by the precipitation of Prussian blue granules, after the use of acid in the fixation fluid. Since these granules were eventually recovered in the saccus endolymphaticus, it became apparent that there was a flow of endolymph from the ductus cochlearis through the ductus reuniens and the ductus endolymphaticus to the saccus, where, in the loose vascular tissue of its wall, resorption of the fluid occurred. Since these experiments make a flow of endolymph highly probable, this fluid must be secreted somewhere in the endolymphatic space. The stria vascularis, a vascular tissue along the outer wall of the cochlear duct, being structurally well adapted for this purpose was regarded by Guild as the principal source of the endolymph.

The investigations reported by Siirala, Secrétan and Andersen have essentially confirmed the assumption of Guild, that the epithelium of the saccular wall in the pars intermedia has an absorptive function. This hypothesis implies that an obstruction to this route of the circulation should be followed by a general distension of the endolymphatic system, in front of this obstruction. Experiments performed by MacNally and Lindsay, however, seem to contradict this hypothesis of Guild. The latter, working on monkeys, destroyed both the saccus and ductus endolymphaticus by means of a fine drill. Even after a period of several months the endolympathic system in the cochlea, vestibule and semicircular canals was found to be quite normal, indicating that the maintenance of a normal quantity of endolymph is not dependent upon the integrity of the saccus endolymphaticus. These findings support the vieuw of von Fieandt and Saxén (1, 2, Saxén) who stated that absorption of endolymph, and particles suspended in this fluid, takes place ad different places of the endolymphatic system. In the cochlear duct the epithelium of the external spiral sulcus was regarded as being such an absorptive area, whereas it was stated that in the static labyrinth the absorptive function was carried out by the epithelium of the saccus endolymphaticus. On the other hand, Lurie (3) showed that in congenitally deaf dogs an extensive atrophy of the stria vascularis was associated whit a collapse of the ductus cochlearis and saccule, but that the endolymphatic system of the utricle and semicircular canals showed no sign of collapse. It is thus highly improbable that the stria vascularis exists as the sole source of the endolymph fluid.

This controversy may again be explained by the investigations of v. Fieandt and Saxén. For, according to these writers, secretion of endolymph not only occurs in the stria vascularis, but also in the marginal epithelium of the saccule and the utricle, as well as in the plana semilunata of the cristae in the semicircular canals.

The source, flow and ultimate fate of the perilymph is also not adequately explained. According to Werner three possibilities of the origin of the perilymph must be considered, namely:

1. the perilymph being derived from the endolymph by way of diffusion through the walls of the membranous labyrinth.
2. the perilymph being formed as a transudate from the perilymphatic blood-vessels (e.g. from the modiolus).
3. the perilymph being derived from the fluid in the subarachnoid space.

Numerous experiments have been carried out, in which various dyes, iron-salt solutions and solutions containing particles in suspension have been injected into the bloodstream, and the subarachnoid space, and their distribution throughout the inner ear studied (Ahlén, Perlman and Lindsay, Gisselsson). On the grounds of new experiments performed on rabbits, Altmann and Waltner state that the perilymph is mainly derived from the cerebrospinal fluid, reaching the perilymphatic space principally through the ductus perilymphaticus, and to a lesser extent through the internal auditory meatus. Gisselsson arrives at a similar conclusion on account of his experiments upon the passage of fluorescein to the labyrinthine fluids.

Although the last possibility is the one most generally accepted, the analytical studies of Aldred et al., which demonstrated that the endolymph and perilymph are virtually isosmotic, leave the possibility of a derivation of the perilymph from the endolymph. The experiments of Altmann c.s., in which iron salt solutions easily penetrated Reissner's membrane lend credit to the assumption that a passage of fluid through the walls of the membranous labyrinth is possible. Resorption of perilymph was thought to take place in the tissue spaces of the spiral ligament and the crista spiralis, from where the fluid passes into the venous system. These findings are thus largely in accordance with the earlier experimental results obtained by Quix and v. Egmond.

The organ of Corti and the tectorial membrane (fig. 6).

In the ductus cochlearis, resting on the basilar membrane, is the organ of Corti. This structure consists of a framework of supporting cells, between which hair-cells are situated.

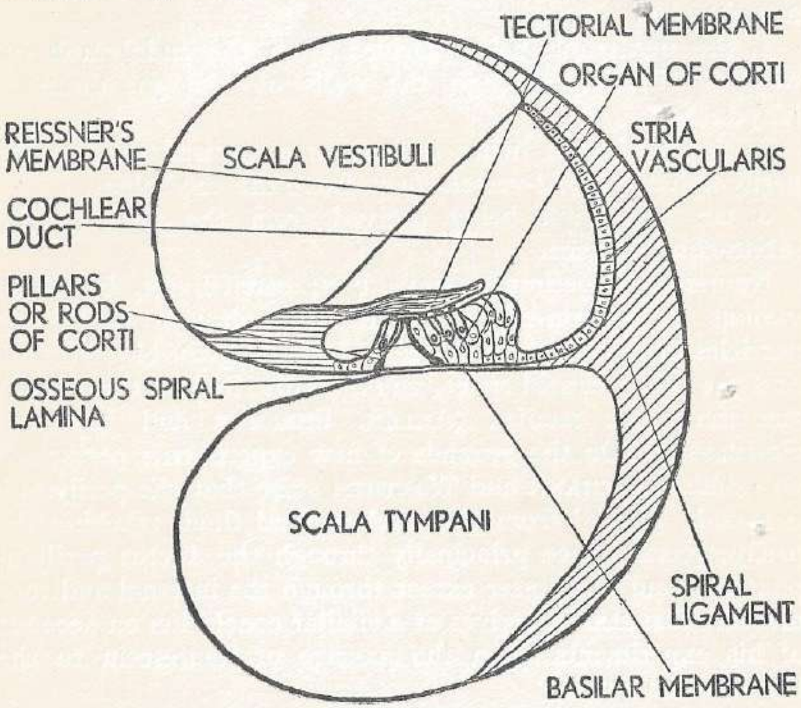

Fig. 6. Diagram of cross section of a cochlear turn with the organ of Corti.

These cells derive their name from the hairs, or cilia, projecting from their surface. The hair-cells are divided into two rows by the pillars or rods of Corti, forming the inner and outer pillars of the tunnel of Corti. There is one row of inner hair-cells and from three to five rows of outer hair-cells.

Resting on the hair-cells is the membrana tectoria. This membrane is attached at its inner margin to the superior lip of the osseous lamina. It is a semifluid structure, probably consisting of keratin in gelatinous form, in which are embedded delicate fibres of uniform size (Hardesty (1, 2)). According to Hardesty its density is only slightly greater than that of the endolymph in which it is submerged. The true nature of the tectorial membrane is still unknown, as post-mortem coagulation, as well as fixation and preparation for microscopical study, may greatly alter the colloidal structure of the mass. The membrane is narrow and thin in the lower part of the basal turn, but widens and thickens towards the apex of the cochlea (according to Hardesty (2) in the pig the size of the membrane near the apex is nearly a hundred times greater than its size near the beginning of the basal coil).

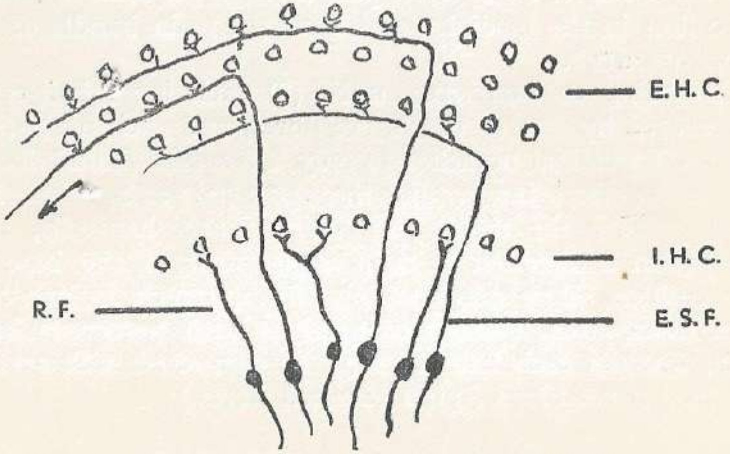

Fig. 7. Diagram of the innervation of the organ of Corti (After Lorente de Nó).
E.H.C. — external hair-cells;
I.H.C. — internal hair-cells;
R.F. — radial fibres;
E.S.F. — external spiral fibres.

Whether the membrane is co-extensive with the spiral organ, as was originally held by Retzius and also accepted by Kishi, Shambaugh (1, 3), Prentiss and Wittmaack (3), or whether it is merely floating on the tiny hairs of the spiral organ (Hardesty, Held) is still an open question.

In a recent contribution on the structure of the tectorial membrane DE VRIES has shown that the membrane does not end with a free margin, but that it is most probably attached to the cells of Hensen by means of a very delicate network („Randfasernetz").

The innervation of the hair-cells.

The hair-cells are connected with the fine terminals of the nerve-fibres. These fibres pass through the osseous lamina, to collect in the modiolus and form the main bundle of the cochlear nerve.

According to LORENTE DE NÓ (3) each inner hair-cell is innervated by one or two nerve-fibres, and each nerve-fibre gives off terminal branches to only a few cells (radial fibres). The nerve-fibres innervating the outer hair-cells, when they have reached the radial level of the outer hair-cells, turn sharply in a direction at right angles towards the base of the cochlea. They may continue for as much as one half turn downwards, making connections with numerous hair-cells, whereas each hair-cell may be connected with several of these nerve-fibres (spiral external fibres.)

CHAPTER III

HISTORICAL SURVEY OF THE THEORIES OF HEARING UP TO THE MIDDLE OF THE 19TH CENTURY

An idea was formed about the function of the hearing organ with the aid of anatomical findings at a very early date. At the beginning of the 16th century the knowledge of the structure of this organ scarcely went beyond the tympanic membrane. Only by the notable investigations of the Italian anatomists of the Renaissance was the knowledge of the macroscopical structure of the auditory organ considerably enlarged.

Andreas Vesalius (1514—1564) gave a description of the tympanic membrane and the ossicles, of which only the hammer and the anvil were known; it was he who introduced the names of malleus and incus respectively for the two ossicles, and recognized the promontory with its two windows. His description of the inner ear and the auditory nerve was, however, still very superficial and incomplete. Giovanni Ingrassia (1510—1580) at the same time, with other Italian anatomists, discovered the third ossicle, the stirrup or stapes. He also pointed out that sound-vibrations were capable of being conducted to the hearing organ via the teeth.

The greatest anatomical discoveries in this field, however, were performed by the anatomists Fallopius and Eustachius. The first (1523—1563) described the oblique position of the tympanic membrane and gave to the middle-ear cavity the name of "tympanum". He divided the inner ear into two cavities: the vestibule with the semicircular canals and the snail-shell, for which he introduced the names respectively of "labyrinth" and "cochlea". According to Fallopius the cochlea started at the foramen rotundum and consisted of three turns. He was the first to describe the osseous spiral lamina, and he already pointed out the fact, that the inner ear, with respect to form and size shows little change after birth.

A better description of the inner ear than Fallopius had given, came from Bartholomeus Eustachius (1510—1574). He recognized the cochlear galleries and gave a detailed description of the modiolus with the osseous and the membranous spiral lamina, and he also accurately described the anatomy and function of the auditory tube (called after him, the Eustachian tube) and the tensor tympani muscle. ("Epistola de auditus organis" 1563).

The structure of the membranous labyrinth was still unknown, and it was held that the spaces of the inner ear were filled with air instead of with fluid ("aër ingenitus or aër implantatus").

At that time there was no question of a well-founded theory of hearing and the indications in that direction did not go beyond the statement, that the tympanic membrane and the ossicles were set into vibration by sound (Eustachius).

In 1587 the first monograph about the organ of hearing "De auditus instrumento" of Volcher Koyter (1534—1600) was published. Although this work does not give a deeper insight and only consists of a compilation of the conceptions of earlier investigators, it presents a good representation of the position of science at that time. According to Koyter the sensation of sound was elicited by the sound collected by the pinna, reinforced in the external auditory canal and transmitted to the oval and round windows by the tympanic membrane and the ossicles. He held that in the cochlea, as in musical instruments, the sound was intensified and propagated by the presence of the "aër ingenitus", picked up by the branches of the auditory nerve and transmitted furthe on.

In comparison with the 16th century the first half of the 17th century brought few important discoveries about the structure of the ear. The conceptions regarding the physiology of hearing at first did not go further than the views of Koyter, but later on they were considerably widened on account of a better understanding of the physical properties of sound, and of its propagation in different media.

Only the appearance in 1683 of the work of the French anatomist Guichard Joseph Duverney (1648—1730) entitled: "Traité de l'organe de l'ouie, contenant la structure, les usages et les maladies de toutes les parties de l'oreille" brought an entirely new advance in the field of otology.

In his description Duverney mentioned nearly everything that could be achieved with the methods of preparation available at that time. The vestibule with the semicircular canals, the two and a half turns of the cochlea and the modiolus with the spiral lamina were so accurately described, that later times could add but little to his description. According to Duverney the spiral lamina originates in the vestibule, and the continuation of the osseous spiral lamina into a membranous partition, already suggested by Eustachius and again described in 1600 by Julius Casserius (1561—1616) was confirmed by Duverney: "The spiral lamina, being attached to the centre with its base, and with its other extremity to the wall of the canal opposite the centre, divides this canal (cochlea) in two by means of a very delicate membrane, much thinner than the lamina, which does not continue in the same level, but somewhat lower than the lamina".

He also described accurately the passage of the auditory nerve in the modiolus with its small ramifications in the spiral lamina. The presence of a communication between the two galleries of the cochlea as described independently by Thomas Willis (1622—1675) and Jean Méry (1645—1722) was denied by Duverney.

In his physiological descriptions Duverney clearly indicated the inner ear as the place where the sensation of sound originated, because in this organ a structure was found which was able to vibrate with the different tones according to the principle of resonance. In this idea he was supported by the French physicist Mariotte: "This lamina is not only capable of receiving the vibrations of the air, but its structure makes it appear credible that it is able to answer to all their different characters: for it being larger at the beginning of its first convolution than it is at the extremity of the last, where it finishes as in a point, and its other parts diminishing proportionately in bulk, we may suppose that the larger parts may be vibrated without the others participating in that vibration, and therefore are capable of receiving none but the slower undulations which consequently answer to grave tones and that on the contrary its narrower parts being agitated, their undulations are quicker and consequently answer to acute tones, in the same manner that the larger parts of a steel spring form its slowest undulations and answer the grave tones and so its narrower parts form quicker and more frequent vibrations and consequently answer to acute tones. So that in short the spirits of the nerve, which expanded over its substance, receive different impressions which represent in the brain the different appearances of tones according to the different vibrations of the lamina spiralis". Because of the difference in size between the ampulla and the semicircular canals, Duverney also attributed a hearing function to these structures.

On three points the theory of Duverney-Mariotte is in conflict with modern conceptions, because it assumes:

1. that the sound-vibrations in the inner ear are propagated by air;
2. that the low tones are perceived in the basal turn of the cochlea and the high tones in the apical turn;
3. that the semicircular canals and the vestibule are concerned with the interpretation of sound.

The opinion of Antonio Valsalva (1666—1723) differed from that of Duverney in that he looked upon the membranous part of the cochlear partition, as opposed to the bony spiral lamina, as being the essential organ of sound-perception. In his work "Tractatus de aure humane" which appeared in 1704, he described the spiral lamina as consisting of rather thick, easily broken bone, attached to the modiolus and a thinner membranous part, which he called the "zona". According to Valsalva this "zona cochlea" was composed of the finest terminations of the auditory nerve. Like Duverney, Valsalva attributed to the semicircular canals an acoustic function and he still held the opinion that the labyrinth was filled with air, although he had already noticed the presence of fluid in the inner ear. He also suggested the use of the words scala vestibuli and scala tympani instead of the old words "upper" and "lower" galleries. Although apart from Valsalva, Vieussens (1699), Cassebohm (1735) and Morgagni (1740) had recognized the presence of fluid in the inner ear, it was Domenico Cotugno (1736—1822), who in his work "De aquaeductibus auris humanae internae anatomica dissertatio" (1760) was the first to prove that the whole cavity of the inner ear was filled with fluid and he definitely broke with the existing theory of the "aër ingenitus". That this theory held sway for such a long time can probably be explained by the fact, that up to the beginning of the 18th century, it was assumed that a liquid, because of its incompressibility, was not able to transmit sound-vibrations. Not until 1742 was it definitely shown by Mollet that this assumption was wrong, and Cotugno made use of this fact in his physiological descriptions of the hearing organ. According to him the sound-vibrations were transmitted to the labyrinthine fluid via the stapes, which in turn set the spiral lamina into vibration. Cotugno for the first time noticed and described correctly how the long "chords" of the spiral membrane were situated at the apex and the shortest "chords" at the base of the cochlea. Like Duverney Cotugno assumed that these "chords" were set into resonance by the sound-vibrations.

Apart from the fact that Cotugno was the first to recognize the importance of the labyrinthine fluid as well as that of the cerebrospinal fluid, he also was the discoverer of both aqueducts of the inner ear (cochlear and vestibular aqueducts) and recognized their significance in connection with the flow of the intralabyrinthine fluid.

That at the time of Cotugno the resonance-hypothesis was fairly generally spread, may also appear from what Albrecht van Haller (1708—1777) in his work "Primae lineae physiologiae in usum praelectionum academicorum" (1747) wrote about the function of the organ of hearing:

"The following conjecture is attractive. Since the lamina spiralis forms a triangle ending in a sharp point toward the tip, one may conceive that the lamina contains an indefinite number of chords, continually shortening in their length, and thus harmonically resounding the various high and deep sounds as they vibrate to the numerous sounds, namely the longest chords in the base of the cochlea with the sonorous sounds, and the shortest chords nearer the tip with the sharp sounds". Haller referred to what his famous teacher Boerhaave in 1740 wrote in his "Praelectiones academicae": "But we have such an indefinite number of chords, that they may vibrate harmoniously with innumerable tones: the longest chords with the lowest tones, those of medium length with the middle tones and the shortest with the high tones".

Boerhaave himself mentioned Claude Perrault (1613—1688) as the original founder of this theory. Although Perrault knew of the osseous spiral lamina which he described as being very thin and flexible (and which he named "membrane spirale") he failed to recognize the membranous partition, so that he assumed that both galleries communicated over their entire length. In his "Essays de Physique" (2nd volume entitled "on sound"), which appeared in 1680 Perrault, after describing the anatomical situation of the osseous spiral lamina, wrote about the function of the cochlea: ". . . . and indeed, this situation seems very favorably to the function which this organ must have, that is to be easily brought into vibration by the movements of the air which cause the sound".

A definite statement of a resonance-theory of perception of sounds of different pitch was also made by Petrus van Musschenbroek in 1729 (Shaxby).

The notable anatomical discoveries of Cotugno were little appreciated, for instance, more than a century elapsed before the existence of the aqueducts was confirmed; and also his conception about the gradually increasing length of the "fibres" is nowhere found to have been confirmed during this period.

Though in the second half of the 18th century the resonance-hypothesis is mentioned in several works about the hearing organ, owing to the deficient knowledge of microscopical anatomy, the vibrating function was either attributed to the nerve fibres or to the elastic bone fibres in the spiral lamina.

Through the development of experimental physiology in the 19th century criticism soon rose against this conception and physiologists like Magendie, Joh. Müller and E. H. Weber ardently disputed the resonance-hypothesis, so that at last it was totally discredited.

In 1817 e.g. Magendie wrote in his "Précise élémentaire de physiologie":

"The osseo-membranous partition, which separates the two scalae of the cochlea, has given rise to a hypothesis, which no one believes at the present day".

And Harless, describing the science in the middle of the 19th century wrote in the "Handbook of Physiology" of R. Wagner (1847): "When we finally try out the possibility of a direct perception of the various tones, we must at first break with a conception, already disputed by Joh. Müller, and which maintains, that the nerve fibres with their different lengths, e.g. on the spiral plate of the cochlea, are compared with strings of variable length, whereby the nerves themselves are considered as the musical instruments and the tone-perceiving chords at the same time. When a particular arrangement for the perception of different tones at all exists in the hearing organ, it can only be looked for outside the nerves in their direct neighbourhood".

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CHAPTER IV

THEORIES AND EXPERIMENTS ON THE CONDUCTION OF SOUND IN THE EAR

From the foregoing chapter it may be concluded that up to the middle of the last century, little was known about the function of the inner ear. Through lack of microscopical technique the detailed structures had still escaped notice. The old conception respecting some resonating structure was purely theoretical, and experimental physiology was still in its infancy. A theory which was able to explain the propagation of sound-waves in the inner ear did not exist. In 1851, however, E. H. **Weber** made a statement which may be considered as the beginning of experimental physiology of the inner ear. Because of its historical significance Weber's statement will be partly quoted here:

"He demonstrates, that the air-borne sound-waves are not conducted by the external ear, tympanic membrane and ossicles to the membranes suspended in the labyrinthine fluid in the form of compressions and rarefactions, but that for this purpose the following mechanism exists, which structure and mode of action has not yet been acknowledged. With the tympanic membrane is connected a lever-system, consisting of hammer and anvil, of which the axis of rotation passes through the points of attachment of the processus Folianus and short crus of the incus. Both ossicles are connected by an articulation, which however, is so constructed that no differential movement is possible in a plane perpendicular to this axis, so that they can only move as if no articulation existed and the ossicles formed one bony mass. The transverse vibrations of the tympanic membrane set up by the vibrating particles of the air, are communicated by this lever-system to the other lever-arm (long process of the incus) connected

with the stapes, which is attached by its base in the oval window and consequent to the transverse vibrations of the tympanic membrane moves to and fro. Such a movement would, however, be impossible if the incompressible fluid filling up the osseous labyrinth had no way of escape. For this purpose a second opening in the labyrinth, the round window, closed by a delicate membrane exists, which, corresponding to the movement of the stapes is moved in and out by the pressure-variations of the fluid. The movement of this membrane may even be observed by the naked eye, if the stapes is moved in the oval window. In this movement of the stapes, which is communicated from the oval to the round window, the whole labyrinthine fluid necessarily participates. The vibrations of the fluid set in motion the in this fluid suspended parts of the membranous labyrinth and the nerves embedded in this structure. The spiral lamina of the cochlea is stretched in the labyrinthine fluid between the oval and round window, and the vibrations in passing to the round window have to traverse the membrane of the spiral lamina and thus encounter the nerve-terminals embedded in this lamina".

So Weber still held the opinion that the nerve-terminals ended freely in the basilar membrane. In the following year Alphonse Corti published his excellent investigations concerning the hearing apparatus of mammals, in which he described the finer construction of the lamina spiralis membranacea and the sense organ, the organ of Corti, resting upon it. In this structure he not only discovered the pillar cells, but also the cylindrical hair-cells, and he was the first to describe the tectorial membrane resting upon this organ. **Helmholtz** (2) accepting Weber's explanation and attaching great value to the tympanic membrane and the ossicular chain for the conduction of sound in the ear, gave to many points a physico-mathematical explanation of this theory. In this way the original conception of Weber found an important expansion and what may be called: "the theory of Weber-Helmholtz" originated.

This theory has held sway for almost a century, despite much criticism on various points.

Weber assumed that the reactions of sound in the ear at physiological intensities would be the same as those observed in his specimen. Weber's experiment, however, must be looked upon as a very rough imitation of these indubitably very small movements. Pohlman (1, 2, 3, 4) especially has constantly criticized Weber's interpretation of the mechanics of the inner ear. He is certainly correct where he states that: "the fact that one opens a door by pushing on it, does not mean that it will open when one says "Boo", or in other words the conclusions of Weber and Helmholtz may not be valid for sound-vibrations of physiological intensity, and the whole question must be submitted to a further critical examination. For this purpose the various hypotheses upon which the theory has been founded must be considered separately and their value estimated with regard to the great number of clinical and experimental data which have since been established. These various hypotheses may be delineated as follows (fig. 8):

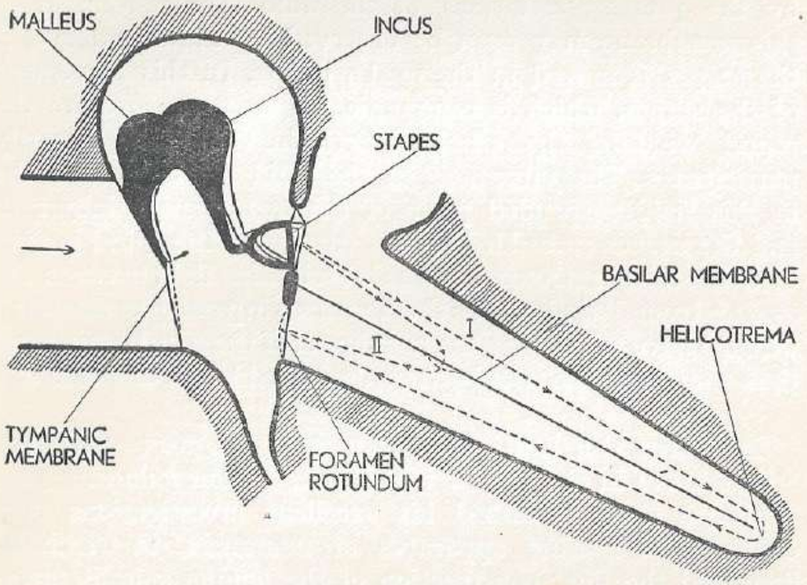

Fig. 8. Schematic diagram of the vibratory movements of the tympanic membrane, the ossicles and the structures of the inner ear. Instead of coiled the cochlea is represented as a straight double canal (After Stevens and Davis).

I. The air-conducted sounds set the tympanic membrane into vibration;
II. The vibrations of the tympanic membrane are conducted to the inner ear by the chain of ossicles;
III. Owing to the peculiar construction of the tympanic membrane and ossicles the sound-vibrations are conducted to the inner ear with increased force;
IV. The vibrating movement of the stapes induces a movement of the fluid in the inner ear;
V. This periodic displacement of the fluid brings about a movement of the basilar membrane;
VI. The membrane of the round window serves as a way of escape for the pressure exerted on the cochlear fluid;
VII. The membrane of the round window is the only way of escape for this pressure;
VIII. The labyrinthine fluid is incompressible;
IX. The bony capsule of the labyrinth has to be considered as a non-elastic container.

The various hypotheses mentioned above will now be further commented upon, both from a theoretical and an experimental point of view.

I. The oscillations of the tympanic membrane in response to air-conducted sounds.

Since it is impossible to observe with the naked eye periodic movements taking place in less then 1/10 of a second the attempts at direct visualization of the vibrations of the membrane, even with the use of high optical magnification, have never met with great success.

Waar used a microscope in observing the tympanic membrane of human beings, but even at a magnification of 146 × he failed to notice any oscillatory movements of the membrane in response to very strong sound stimuli. To visualize the rapid movements of the tympanic membrane at the audible frequencies we have to make use of the method of stroboscopic observation. With this method a light source illuminating a vibrating object is interrupted in nearly the same frequency as the vibration frequency of the sound source. The result is an apparent slow movement of the vibrating object making direct observation possible. **Mach** and **Kessel** (1, 2) in using a specially constructed speculum with a magnification of 40 × were the first to employ this method in their investigations on the human tympanic membrane and the sound-conducting system of fresh human cadavers. Thus **Kessel** (1874) succeeded in observing the acoustic oscillations and mode of vibration of the membrane in fresh cadaver-specimens at physiological intensities. In later years **Lucae** (1901) applied the stroboscopic method to the clinical examination of the ear.

Recently this method has been made useful by **Perlman** (2) in a simple manner for clinical application. It appeared that the posterior portion of the tympanic membrane moved much more than the anterior part (Mach and Kessel computed a ratio of approximately 4 : 1). The greatest excursion was to be seen between the umbo and the posterior-superior portion of the annulus. The least movement was made by the malleus. Its movement was, however, always in the same phase as the movement of the pars tensa (Perlman: "The drum in response to an acoustic stimulus entering the canal does not appear to move with equal excursions but does appear to move in equal phase"). The acoustic oscillations of the tympanic membrane have recently been registered with the aid of stroboscopic light and moving picture-film by **Kobrak** (7).

Besides this direct observation various indirect methods have been designed to demonstrate the vibrations of the tympanic membrane. **Köhler** for instance, had a very small mirror stuck to his tympanic membrane and recorded photographically the movements of this membrane in response both to air- and to bone-conducted sounds. In a similar way **Wada** attached small mirrors to various parts of the tympanic membrane of different animals, and was able to record its vibrations.

The fact that we may not draw the same conclusions from experiments with dead and living material becomes evident when we learn that in the experiments of Wada the tympanic membrane of the pigeon, which vibrated with tones of a certain intensity when alive, did not respond to the same tones of same intensity after its death. A similar effect was obtained by Wada after severing the M. tensor tympani. In recent studies on the vibrations of the tympanic membrane and the sound-conducting apparatus, **Perlman** (5,6) made use of a very sensitive equipment to register the oscillations of this system. Electronic means, used by physicists for detecting minute acoustic displacements, were adapted to the special conditions prevailing in the ear. A piece of metal foil of 2 sq. mm was made to adhere to the surface of the tympanic membrane, and a capacitive probe was advanced towards the foil at a distance of 1 mm. With this equipment it was possible to record the oscillations of various parts of the tympanic membrane, in response to various frequencies, on the screen of a cathode-ray oscilloscope.

A very ingenious method of demonstrating the vibrations of the tympanic membrane, and at the same time obtaining an impression of the amplitudes occurring at the auditory threshold, was employed by **Wilska**.

Whereas in all the above-mentioned experiments the tympanic membrane was set into vibration by a sound-source, Wilska succeeded in inducing movements of the membrane mechanically in the living. A light wooden shaft, 8 cm long, was fastened at one end to the umbo of the tympanic membrane and at the other to the moving coil of an electro mechanical transducer, which was tightly fixed to the side of the subject's head. The electro-dynamic system was driven by a sinusoidal alternating current with a frequency ranging from 45 to 9.000 c/s. The strength of the current needed to generate a just-audible tone was measured. The amplitude of the wooden shaft was determined separately with the aid of a microscope at the same magnitude of current. In this way only amplitudes down to 0.001 mm could be measured. Since the amplitudes for most frequencies at the threshold of hearing are much smaller, only the amplitudes at low frequencies could be determined, whereas the values for the higher frequencies had to be extrapolated. Thus it was calculated that in the region where the ear is most sensitive (2000—3000 c/s) the amplitude of the tympanic membrane at the threshold of hearing amounts approximately to: 0.0045 mμ or less than the diameter of a hydrogen molecule. At 2000 c/s it amounts to 10^{-9} and at 10.000 c/s $5 \, . \, 10^{-9}$ cm

With a similar technique Frenckner has also attempted to obtain an impression about the amplitude of vibration of the tympanic membrane. The only difference from Wilska was that the membrane was set into vibration by sound-waves. In the first series of experiments the free end of a shaft was observed under a microscope and magnified 600 times. It was not possible, however, either with direct observation or with the different methods of registration attempted, to obtain any decided measure of the magnitude of the reactions.

In a second series of experiments use was made of the much more sensitive micro-oscillometer.

When the measuring coil, fastened to the rod, vibrates in a magnetic field, the electric energy produced in the coil is amplified and a certain reading can be taken from the output-meter: "After the ear has given a certain reading in the output-meter, it is replaced by an ear-phone, whose membrane takes the place of the tympanic membrane. The rod is fastened between the membrane and the measuring coil. The ear-phone is fed from the audio-frequency generator with the same frequency as that used in testing the ear. The audio-frequency voltage of the ear-phone is regulated until the output-meter gives the same reading as that obtained in the test with the ear. The amplitude of the vibration is measured with a microscope mounted over the glass rod. The value thus obtained may then be considered equal to the amplitude of the vibrations in the tympanic membrane in the test with the ear itself, as the measuring coil in the micro-oscillometer gives the same potential in both cases. With this apparatus it was possible to read vibrations to 0.000007 mm at 1000 c/s".

This size of the movements varies greatly according to the point at which the glass rod is fastened, but it varies even more according to the frequency of the tone which produces the vibration.

It appears that tones which lie at a level with the membrane's own oscillations, thus around 1000 c/s produce many times greater amplitudes than others, probably because of resonance-phenomena. In a normal case, in which the glass rod was attached about midway between the umbo and margo in the normal light reflex, a movement of 0.00013 mm was obtained with 1100 c/s, and in another in which the glass rod was fastened directly in front of the umbo, the value of 0.000015 mm was obtained with 500 c/s. These values are not claimed to bee xact measurements of the amplitude of the vibration of the tympanic membrane. They only suggest the approximate size of what has to be reckoned with. Frenckner, for instance, does not say what intensity of sound stimulus must be employed to obtain these amplitudes.

From all these experiments, however, we may well draw the conclusion that the tympanic membrane executes oscillatory movements as a reaction to sound impulses, and that the amplitudes of these vibratory motions are extremely small.

II. The vibrations of the tympanic membrane are transmitted by the chain of ossicles to the inner ear.

Whereas it has long been accepted that the vibrations actually follow this route there has always been contention in the literature regarding the manner in which these vibrations are transmitted to the oval window. Opposing the opinions of Savart, Joh. Müller, and others, who assumed that the sound-vibrations were propagated by the chain of ossicles in the form of compressions and rarefactions (Bezold), was the view taken by Weber who stated that this conduction took place by a mass movement of the whole apparatus.

Helmholtz (2) concurred with this latter conception, and explained mathematically that, considering the small dimensions of the ossicles relative to the wave-lengths of the acoustic frequencies (for a tone of 40.000 c/s the wave-length in bone is approximately 50 mm) every point in the chain must always be in the same phase of vibration and that the system must therefore be regarded as one mass moving as a whole. Although this view must be considered as the one most generally accepted, in the more recent otological literature the conception of molecular vibrations is again met with (Philip), it being held that owing to the very small amplitudes initiating a sound-sensation, there can be no mass movement. Because, we have only to deal with mass movements in acoustics, there can only be a quantative and not a qualitative difference between mass and molecular vibrations. The amplitudes may thus very well be of molecular dimensions.

The first experiments demonstrating the vibrations of the chain of ossicles in response to sound-waves were made by POLITZER (2). By fixing tiny hairs on hammer and anvil, vibration curves of the ossicles were registered on a rotating cylinder. To avoid the load with such small levers BUCK (1870), in Helmholtz's laboratory, used tiny luminescent points upon the ossicles whereby the vibration curves appeared to have the form of Lissajous figures. MACH and KESSEL (2) studied the movements of the ossicles stroboscopically. In the later investigations of FRANK, KRAINZ, DAHMANN and PERLMAN (3) small mirrors were mounted on the different ossicles and the results registered by means of light-beam levers, whereby Frank and Broemser demonstrated that loading of the ossicles with these small mirrors of negligible mass had little influence upon the moment of inertia.

DAHMANN, by attaching minute mirrors to the ossicles at their centres of rotation, was thus able to measure the angular displacement of the rotation-axis of the ossicles in response to static pressure-variations in the outer ear canal, and to sound stimuli of physiological intensity. In this way Dahmann demonstrated the following facts:

1. All the ossicles respond with measurable vibrations to both high and low tones.

2. All the ossicles may move in several planes, one plane 'however' predominating, namely that corresponding to the in- and outward movement of the handle of the malleus and the long process of the incus.

3. As far as moderate pressure-variations are concerned, malleus and incus have one common axis of rotation extending from the anterior ligament of the malleus to the fan-shaped ligament of the incus. With stronger stimuli small sideways movements may occur, thus illustrating that the ossicles may vibrate with several axes of vibration.

4. As long as weak stimuli are used, and the amplitude of vibration of the ossicular chain remains small, so that the stapes can readily follow these movements, and as long as the elastic capsular tissues connecting the ossicles offer more resistance than the attachment of the stapes in the oval window, the whole chain vibrates as one solid unit. But as soon as the amplitude of the tympanic membrane and malleus exceeds the limited rate of mobility of the stapes, a decrease of amplitude from the malleus via the incus to the stapes is observed. The frictional resistance of the stapes is then greater than the forces set up by the elastic tissue connecting the ossicles. In the transmission of more powerful vibrations the ossicular chain can no longer be considered as one unit, a great deal of the acoustic energy being eliminated by differential movements between the ossicles.

The investigations of Mach and Kessel were repeated by KOBRAK (6, 7, 8) with an improved technique. In earlier experiments (5) the movements of the exposed structures of the middle ear of fresh human cadaver specimens were magnified optically. For the purpose of observation and analysis the speed of the vibrations was reduced. This was accomplished by the use of sinusoidal airpressure changes of subacoustic frequencies (below 16 c/s) and "slow motion" pictures of the acoustic frequencies (about 120 c/s). In taking the "slow motion" pictures with stroboscopic illumination a further analysis of the ossicular movements was made possible. It was shown that for moderate intensities, an increase of intensity of a tone was followed by a corresponding increase of amplitude of the ossicular movement, but at higher intensities a change of the axis of vibration was observed. These experiments again reveal the complexity of the ossicular movements in response to sounds of higher intensity. According to PERLMAN (5) the acoustic oscillations of the component parts of the sound-conducting mechanism can only be seen if the sound-intensity is sufficiently great (about 100 db) and the movements are observed with stroboscopic light. Low-frequency sounds are best used, since in general the oscillations are reduced in amplitude as frequency is raised, so that at about 1000 c/s very little is seen.

Dahmann's description of a change in the rotation-axis of the stapes at a high level of stimulation, has been confirmed by v. Békésy (7). At low acoustic pressures the stapes makes a rocking motion, like a bell-crank lever, around the posterior end of the footplate; but at high acoustic pressures a change of 90° may be observed to a rocking motion about the longitudinal axis of the footplate. This change of vibration serves as a protective mechanism, as the resulting movements of the fluid of the inner ear are greatly reduced. Perlman (4), however, using both shock pulses and sustained sound waves of high intensity could not observe this change of axis in his experiments.

All these investigations, however, were performed upon the dead ear and the question arises whether we may apply the results obtained, without reserve, to the reactions occurring in the living ear. It will thus be necessary to ascertain what factors might undergo a change in regard to the living ear.

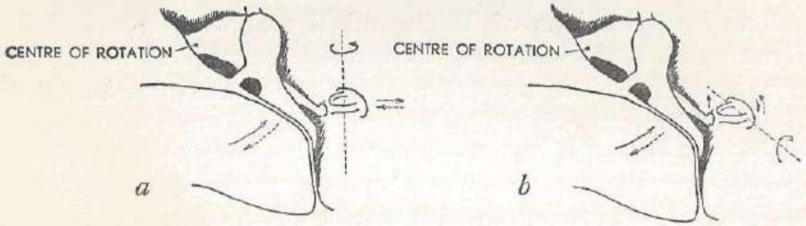

Fig. 9. Diagram of the movements of the stapes at moderate (*a*) and at very high intensities of stimulation (*b*) (After v. Békésy).

1. In all the experiments the middle-ear cavity was exposed; as long as minimum interference with the important structures is attempted, this factor will have no appreciable influence. In the living animal Wever, Lawrence and Smith showed that opening of the auditory bulla when the system remains otherwise intact has only a minor effect upon cochlear sensitivity.

2. A drop of the arterial and venous pressure to zero.

3. Change of the elastic properties of tympanic membrane, capsular and suspensory ligaments and cochlear windows. The investigations of Frank and v. Békésy (8) have demonstrated that the elasticity of the tympanic membrane is but little influenced by death. Frank measured the volume-elasticity coefficient of the tympanic membrane by placing a water column in the outer ear canal. As the walls of the canal and the fluid were regarded as incompressible, the displacements of the fluid column due to pressure-changes were considered to be equal to the volume of bulging of the tympanic membrane. It was found that the volume-displacements in the human living ear and in the fresh cadaver ear were identical.

v. Békésy demonstrated that both the resonance-frequency and the damping of the tympanic membrane remain the same after death.

4. Loss of tonus and regular reflex-contractions of the intra-tympanic muscles.

The influence of loss of this muscular activity can only be ascertained if we know its influence upon the vibration faculty of the normal sound-conducting apparatus in the living.

According to Kobrak (10) lack of muscle tonus in the cadaver has no important bearing upon the elastic qualities of the tympanic membrane; and physiological contraction of the muscles does not alter the natural frequency of the ossicular chain.

A vast number of experiments carried out on man, animals, fresh human temporal bones as well as on models, has shown, however, that a contraction of the intra-tympanic muscles may greatly influence the relative position of the ossicles, as well as their movements and the transmission of sound-vibrations to the inner ear. The results of these investigations will now be discussed in four groups, in which the influence of muscular contraction upon the sound-conducting mechanism is viewed from different angles.

1. Effect of contraction upon the relative position of the ossicles :

According to Stuhlman (3) a contraction of the tensor tympani pulls the malleus inward, upward and forward, thus applying tension to the lower segments of the tympanic membrane and to the ligaments attached to the malleus. At the same time a tension is exerted upon the capsular ligaments bridging the malleus-incus articulation, which pulls the articulating surfaces apart. Thus the coupling in this joint becomes smaller, the degree of coupling depending upon the tension exerted by the intra-tympanic muscles and the stiffness of the elastic capsular ligaments opposing this tension.

In the living human being WAAR failed to observe any displacement of the tympanic membrane in response to sound stimuli even of very high intensity. A distinct inward movement of the membrane was, however, observed in persons who were able to contract the tensor voluntarily. The acoustic reflex-contraction of the tensor tympani in man must therefore be regarded as being an isometric, rather than an isotonic contraction.

In various animals, however, an acoustic reflex-contraction of the tensor causes a distinct inward movement of the tympanic membrane (KATO, PHILIP, TSUKAMOTO et al. (1936)).

POLITZER (1) demonstrated that the stapes is pressed deeper into the oval window during this tensor contraction. This inward movement of the stapes was confirmed by the experiments of WIGGERS.

In a contraction of the stapedius muscle the stapes is shifted in the incudo-stapedial joint and the capitulum moves in an inferior-posterior direction. The inferior and posterior edges of the footplate are pushed into the oval window, whilst the anterior and superior margins are forced out. Since the annular ligaments attached to the anterior margins are much longer than those attached to the posterior edge: the outward thrust is greater than the inward movement. The resultant diagonal motion of the capitulum carries the attached lenticular process of the incus with it and pushes the posterior end of the short crus of the incus into a shallow depression (fossa incudis) where a fan-shaped ligament anchors this end of the incus to the fossa in the posterior wall. This motion puts the ligaments of the malleus-incus articulation under tension, producing a loosely-coupled malleus-incus joint (Stuhlman).

The middle-ear muscles are thus exerting an antagonistic tension on the capsular ligaments of the malleus-incus articulation, but are synergistic in separating the articulating surfaces of malleus and incus. The movements of the stapes in response to a sound stimulus of sufficient intensity may be observed in the animal experiment (KATO, PHILIP a.o.) as well as in the living human being (LÜSCHER (1), PERLMAN and CASE (1)).

In Kato's experiments the reflex-contractions of the tensor caused no compensatory movements of the round window membrane, as long as the stapedius muscle functioned. As soon as this muscle was severed, however, these compensatory reactions appeared.

2. Effect of contraction upon the amplitude of movement of the ossicles:

This effect can be studied by applying tension to the exposed muscles or tendons and pulling gently in the direction of physiological contraction. The experiments of Dahmann have clearly shown that muscular traction reduces the amplitude of the acoustic oscillations. This traction mainly influences the negative phase of the movement as has been recently demonstrated again by PERLMAN (4).

These experiments on dead material were verified by TSUKAMOTO in the living rabbit. The oscillations of the intra-labyrinthine fluid in response to acoustic stimulation were greatly reduced during the contraction of the intra-tympanic muscles.

Inactivation of the muscles will therefore abolish this reduction of amplitude and the delicate cochlear structures may become exposed to excessive fluid displacements at tones of very high intensity.

KATO demonstrated that his test animals became deaf much sooner, in consequence of the impact of continuous loud sounds, when the middle-ear muscles were incapacitated than did those animals in which the muscles were left intact.

In the experiments of STEVENS, DAVIS and LURIE (1935), in which the organ of Corti was dislodged from the basilar membrane following the exposure to sounds of very high intensity, the intra-tympanic muscles were previously put out of action by the local application of chloroform.

One of the possible symptoms of facial palsy, the hyperacusis, may in this light be explained as being caused by a paralysis of the stapedius muscle, resulting in increased volume-displacements of the inner-ear fluid (PERLMAN (1)).

3. Effect of contraction upon the transmission of sound to the inner ear:

This influence has been exhaustively studied by Stuhlman(1) with an accurate 20-1 scale metal model of the ossicles. It appeared that the form of the transmission characteristic of the malleus-incus articulation, representing the relation between the angular displacement of the malleus and the force developed at the lenticular process of the incus, is strongly influenced by the degree of coupling of the malleus-incus articulation. For small deflections the displacement of the malleus proved

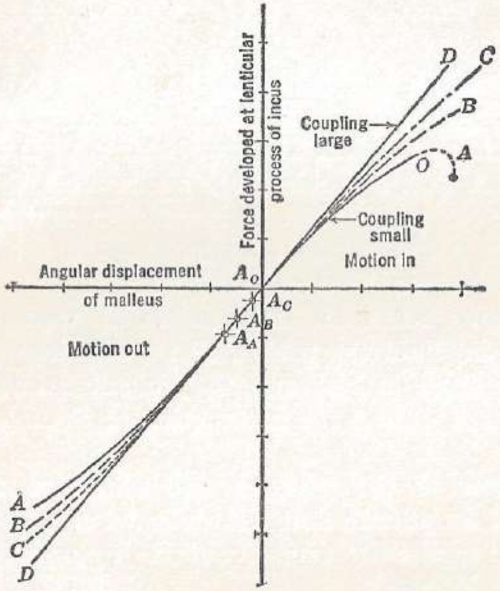

Fig. 10.

Experimental transmission characteristics of the malleus-incus coupling obtained from a 20 × model. Shift of the operating point of the characteristics from A to C shows increased coupling. The linear characteristic D indicates rigid coupling. The typical basic operating curve for the malleus-incus articulation is sigmoid shaped, as A, where the dotted line shows unstable condition attained as a result of a slight dislocation when force directed inward becomes too large (From Stuhlman, 3).

to be a linear function of the force transmitted to the lenticular process of the incus. Should the joint be closely coupled, so that no slip is possible (no action of the intra-aural muscles) the curve shows an almost linear relationship (fig. 10). With increasing intensity the shape of the transmission curve depends upon the degree of coupling of the malleus-incus articulation. A more loosely-coupled joint (increasing influence of the intra-aural muscles) produces a curve showing more asymmetrical and non-linear distortion (fig. 10 B, C). Stuhlman has thus provided evidence that a simple sinusoidal motion of sufficient amplitude, impressed at the end of the lever-arm of the malleus is transmitted to the long end of the incus, after having undergone both asymmetrical and non-linear distortion.

The effect of contraction of the muscles upon the sound-transmission to the inner ear has been investigated several times with the cochlear response method.

Hughson and Crowe (2) putting the tensor tympani under mechanical tension showed that with increasing load the transmission of low-frequency sounds was more and more suppressed. A load of 50 grams eliminated all the low tones, so that only tones above 2048 c/s were transmitted. The high tones were less affected, while if the tension was relieved the conduction immediately returned to normal. Similar results were obtained by Wiggers. During contraction of the muscles a 100 cycle tone showed a loss of 45 db, between 100 and 1000 c/s this loss decreased with increasing frequency, so that at about 1100 c/s the electrical output of the cochlea was not reduced by contraction. At 1500 c/s even augmented efficiency in the transmission system was noted.

Wever and Bray (5, 6), applying tension to the stapedius tendon found the reduction greatest for the low frequencies and growing less with increasing frequency. For the tone of 2000 c/s slight tension even increased the response.

From these animal and model experiments Stuhlman concluded that:

"Tight coupling of the malleus-incus articulation due to the relaxation of the intra-tympanic muscles and consequent close fitting of the articulating surfaces is favourable to the passage of the low-frequency, low-intensity sounds; whereas contraction of the intra-tympanic muscles, producing a looser-coupled malleus-incus joint is favourable to high-frequency, high-intensity transmission".

4. Effect of contraction upon the intralabyrinthine fluid:

TSUKAMOTO demonstrated that in the living rabbit an adequate tonal impulse caused a distinct rise of labyrinthine fluid in a capillary labyrinthine manometer. It was assumed that this rise was produced by a contraction of both the tensor tympani and the stapedius muscle and it was calculated that the displacement of the stapedial footplate averaged 0,027 mm. This effect is in seeming contradiction to the assumption that the stapedius muscle pulls the stapes outward. This controversy can, however, be explained by the experiments performed by WIGGERS. Applying the relation which DAVIS et al. discovered to exist between the polarity of cochlear response and the pressure-gradient set up by the motion of the stapes, Wiggers succeeded in analysing these movements more accurately. Davis and his co-workers established that an inward movement of the stapedial footplate, consequent to a positive pressure in the external auditory canal, generates a positive potential in the scala vestibuli and the apex, whereas a negative potential is caused on outward movement.

From fig. 11 the relations existing between the intra-labyrinthine pressure-variations and the movements of the stapedial footplate may be seen. The five slow deflections were interpreted by Wiggers as follows:

a. Contraction of the stapedius muscle — the footplate moves outward — small increase in negative potential;

b. Contraction of the tensor tympani muscle, overpowering the stapedius-contraction and forcing the footplate inward; the steep pressure-gradient at the footplate causes a steep rise of positive potential;

c. Drop of positive potential after adjustment of the cochlear fluid via the helicotrema;

d. Relaxation of stapedius muscle — the continued contraction of the tensor tympani thrusts the anterior edge of the footplate further inward, creating a second positive deflection at the apex;

e. Relaxation of the tensor tympani — the footplate returns to norma position; a negative potential is created, as the pressure in the scala vestibuli is again reduced.

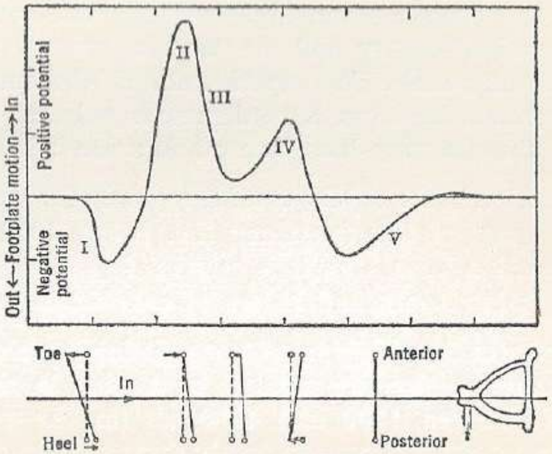

Fig. 11. Graph showing the changes in potential at the apex of the cochlea from data by WIGGERS. The lower diagram shows the correlated positions of the footplate, supposed to account for the successive changes in potential observed by WIGGERS (from STUHLMAN).

The rise of the fluid in Tsukamoto's experiments must therefore be explained as being caused by a contraction of the tensor tympani, rather than by a contraction of both muscles.

The above considerations lead us to decide upon the ultimate function of the intra-tympanic muscles in the process of hearing. It may be stated that the muscles act morphologically as antagonists, but physiologically as synergists.

For a long time two diametrically opposed hypotheses regarding their function have been advanced:

1. The *"accomodation"-theory* regarded the muscles as a

mechanism to adjust the sound-conducting apparatus to the best possible absorption of sound-energy (Mach 1863, recently again defended by Tumarkin (1)).

2. The *"protection"-theory* assumed that both muscles by their contraction protect the inner ear against strong sound-vibrations by restricting the movements of the transmission mechanism.

For a long time experimental evidence was in favour of this "protection"-theory and the "accomodation"-theory was regarded as untenable. The experiments of Wiggers, Wever and Bray et al., however, have demonstrated that the intra-tympanic muscles may have several functions:

a. Reduction in the efficiency of the system for transmitting loud tones of low frequency (i.e. below 1000 c/s); the contraction thus affords a certain degree of protection against low tones and noises of considerable intensity;

b. Increase in the efficiency of transmitting tones of medium frequency — by the increase of tension in the system tones between 1300 and 1800 c/s (in the guinea-pig) are transmitted more efficiently during contraction than during rest. In the experiments of Hughson and Crowe division of the tensor tympani tendon resulted in a marked reduction of the volume of all tones above 1024 c/s. An accomodation or "tuning up" of the auditory apparatus may thus be accepted for certain frequencies.

c. Prevention of aural harmonics — though the investigations of v. Békésy (6, 8) and Wever and Bray (4) point to the inner ear as the locus of auditory distortion, it is highly probable that the non- linearity of the middle-ear mechanism (Stuhlman) will also be responsible for the generation of aural harmonics. It was suggested by Wiggers that contraction of the intra-tympanic muscles eliminates the masking effects of low tones and their harmonics, and thus improves the auditory acuity for higher tones. In Tsukamoto's experiments the non-linear distortion of the sound-vibration was corrected by a contraction of the intra-tympanic muscles.

The afore-mentioned objections (p. 38) to experiments on dead material could largely be overcome by experiments in the living. An investigation of the mechanical properties of the entire sound-conducting apparatus in the living human being is, however, impossible. Owing to differences in structure of the middle ear in man and animals experimental physiology gives us a suggestion, but no evidence of what occurs in man. Moreover the acoustic reflex-contractions of the middle-ear muscles disappear under deep anaesthesia (Kato, Hallpike) and at physiological intensities the displacements of the ossicles are so small as to be scarcely visible.

In the living rabbit Philip was unable to observe any vibratory movement whatever of the stapes, either with low or high tones of high intensity, although movements could be observed to an amplitude of 8 μ. It is possible, however, that the rapid periodic movements, as in the case with the tympanic membrane, escaped the notice of the observer, but that with stroboscopical illumination a vibratory movement might have been seen. From these researches Philip drew the wrong conclusion that the transmission of the higher frequencies at least, might take place by molecular movement in the ossicles.

Apart from the observations of the oscillations of the ossicles in response to acoustic stimulation several experiments have indicated the importance of the ossicular chain in the transmission of the sound-vibrations to the inner ear.

von Eicken had already found that in guinea-pigs the injury to the organ of Corti after exposure to strong sound-stimuli was much less pronounced after removal of the incus than under normal conditions of the sound-conducting apparatus.

Hughson and Crowe (2) in using the cochlear response method, stated a distinct influence of interference with the joints on the output of the cochlear response. Wever, Lawrence and Smith found the elevation of threshold, resulting from disarticulation of the incudo-stapedial joint and removal of a small piece at the end of the incus, to be about 60 db on the average.

van Eunen found in the pigeon a considerable reduction of the reaction of Tullio after severing the columella (the only ossicle in birds, directly connecting the tympanic membrane with the oval window) without injuring the columella-footplate.

It may thus be assumed that the chain of ossicles is in some way of great importance for the transmission of the sound-vibrations from the tympanic membrane to the inner ear.

Long before Weber assigned to the membrane of the round window the function of compensatory area for the vibrating fluid column of the inner ear, it was supposed that the sound-vibrations entered the inner ear through the round window, and the term "membrana tympani secundaria" was introduced. This view was already held by Duverney (1683), Schellhammer (1684) and Scarpa (1791), and later defended by Joh. Müller, Claudius and recently again by Mac Naughton Jones and Popper. This view seemed to be confirmed by the experiments of Weber-Liel, who severed the incudo-stapedial joint and slightly dislocated the incus.

In response to sound-stimulation distinct excursions of the round window membrane were observed, disappearing as soon as the glass covering the tympanic cavity was removed.

Weber-Liel thus concluded that the round window membrane could be set into vibration mechanically by the air of the tympanic cavity. Kleinschmidt likewise assumed that the membrane could transmit sound-vibrations much more easily by means of the closed air-chamber of the middle ear than by the system of ossicles which, in view of the rapid vibrations, would have too great an inertia.

Already from a comparative anatomical point of view it is very improbable that the round window is the way for the sound-vibrations to enter the inner ear. There are different species of vertebrates (amphibians and reptiles) in which the round window is lacking, whereas in most vertebrates an oval window and a perilymphatic duct are always present (Tumarkin, (2)). The pressure-escape takes place here through an opening into the cranial cavity. During the course of evolution this saccus perilymphaticus migrates to the pharynx, and the tubo-tympanic cleft. If in this trend the entodermal

mucous membrane is reached then the foramen rotundum appears (de Burlet, Tumarkin (2)). The cochlear aqueduct narrows more and more and the foramen rotundum takes over the function for the equalisation of pressure. The aqueduct is thus phylogenetically older than the foramen rotundum (de Burlet). With the lower orders of animals where there is a large epitympanic space with many additional cavities (as in birds, crocodiles and some species among the mammals with a large bulla tympanica) or where the epitympanic space is connected by a wide opening with the pharynx, it does not seem probable that the round window membrane plays any important rôle in the transmission of sound to the inner ear. It is therefore illogical to assume suddenly this route in the human, and other forms of vertebrates, with a small epitympanic space.

Only very few experiments have been performed concerning the possible rôle of the round window in the transmission of sound. Link, using fresh human temporal bones, investigated how far the membrane could be set in motion by sound-vibrations. By placing a wall of plastic material between the round window and the rest of the tympanic cavity the former was isolated without the transmission mechanism being affected. The vibration amplitude of the round window membrane, when the sound was conducted via the external auditory meatus and tympanic membrane, proved to be absolutely unaltered, although any possibility of the sound being transmitted to the membrane via the air of the middle ear was precluded. At the same time Link was able to demonstrate that the membrane exhibited no vibrations when the sound-source produced a tone of very high intensity, in the immediate proximity of the round window membrane. Moreover the previously mentioned experiment of Weber-Liel was repeated. After interrupting the incudo-stapedial articulation the long crus of the incus was slightly dislocated. When the audiometer tone was transmitted to the inner ear via the external auditory meatus and tympanic membrane the round window membrane was set into vibration, although the amplitude was less than before the manipulation.

As long as there was any contact between incus and stapes, however, vibrations in the latter were observed, although these were smaller than those of the round window membrane. But whenever the incus was removed, no excursions were observed, either of the stapes or of the round window membrane, although the amplitude of the tympanic membrane with the hammer became appreciably larger by the removal of the damping influence of the incus.

In this connection must also be mentioned the various experiments in which the round window membrane was isolated from the middle-ear cavity, by plugging the niche with some material, and the influence upon the hearing function tested (see page 69). These experiments, indicating that blocking of the niche has little influence upon the cochlear function, make it appear highly improbable that the round window membrane has under normal conditions any important function in the delivery of sound-vibrations to the inner ear.

The question, however, rises whether under abnormal conditions the sound-waves may enter the inner ear by way of the round window. **Frank**, who studied the problem of sound-transmission via the middle ear, mathematically and empirically (with models and preparations), stated that when the sound-pressure acts equally upon both fenestrae there cannot be any movement of the cochlear fluid. This is only possible if the round window lies at a sufficient distance from the oval window. Since the distance between the two windows is small the resulting pressure-difference will also be rather small (v. **Békésy** (16)). Another contingency according to Frank, is that the round window will be protected from the interference of air-borne sound-waves. This screening is effected in his opinion, in two ways, viz.:

1. By way of the tympanic membrane and the chain of ossicles, whereby an orderly delivery of the vibrations to the oval window is effected;
2. By the position of the round window membrane behind the wall of the promontory in a deep niche, the fossula fenestrae cochleae. Since the dimensions of the niche are small, relative to the wave-lengths of the audiofrequencies, this screening is the more effective the higher the frequency is.

Although various cases are known of patients who, after a so-called radical mastoid operation (whereby tympanic membrane, malleus and incus have been removed) still retained a fairly good hearing function, most of them experience a great loss of hearing, especially in the low-tone range. The same holds good for cases where an inflammation of the middle ear has left a great defect in the tympanic membrane. Now, it has long been known that these patients, as a rule, report improved hearing when the environment of the round window is isolated from the rest of the cavity of the middle ear by means of a wet plug of cotton-wool, or a drop of fluid (artificial tympanic membrane).

In this way **Bárány** obtained improved hearing by covering the round window with mercury, and **Hughson** (1, 2) putting the results of his animal experiments into practice, achieved in patients, with or without defect of the tympanic membrane, a hearing improvement in various types of deafness by applying periosteal grafts of tissue in the round window niche. In such cases it is probable that, according to Frank's supposition, the screening effect will be enlarged, since a total immobilisation of the round window membrane by the presence of a remaining air-cushion between prosthesis and membrane is hardly conceivable. v. **Békésy** (7), now, has endeavoured to show that in cases with one normal ear and the other ear lacking tympanic membrane and ossicular chain, the sound-vibrations do enter the inner ear through the round window. For this purpose he used the subjective directional hearing. When the sound-vibrations set in motion the basilar membrane via the round window, its phase of vibration will be opposite to the phase of vibration when the sound-waves are carried in by a normal ossicular chain. This phase-difference has no influence upon the sensation of sound, but it has upon the directional hearing. To the normal ear a tone of 200 c/s was directed, while to the other ear a tone of the same loudness, but slightly different frequency (200, 3) was delivered. Under these conditions the observer experienced a tone that seemed continually to shift its position as the phase of the sound-waves reaching the two ears varied, and which seemed to make a circular movement round the head, so-called "Drehtöne". If the observer was asked to indicate in which direction the apparent source of sound was moving, it was shown that the direction of movement in the abnormal ear was opposite to that in the normal. When the abnormal ear was then provided with an artificial tympanic membrane, touching the promontory, the sound-source now moved in both ears in the same direction, indicating that the phase-relations were restored to normal.

Apart from the fact that the auditory localization besides being dependent on a phase-difference, depends mainly on a difference in intensity, POHLMAN (4) has advanced against this hypothesis that in cases of progressive fixation of the ossicular chain, when the amount of sound-energy conducted through the oval window will exactly equal that conducted through the round window membrane, the patient must be deaf to both air- and bone-conducted sounds, because no differential pressure in the two scalae would be developed. Later, as the fixation becomes more pronounced, the hearing acuity should again return to some degree as the round window takes over the function. A case of this variety, however, has never been reported. The same holds true for the experiment of v. BÉKÉSY. A theoretical position of the prosthesis might be conceived in which the sound-energy acting on both windows will be equal and no hearing sensation can be elicited.

This controversy has been experimentally analysed by LÖWY (1). It was shown, employing the cochlear response in animal experiments, that interference with the sound-conducting mechanism causes a gradual shift of the aural microphonic, but that a sudden reversal of phase does not exist. In another series of experiments LÖWY (2) analysed the action of the pellet-type of artificial tympanic membrane. Löwy believed the mechanism in the improvement of the response to be composed of two effects:

a. a screening effect and *b*. an increase in the stiffness of the vibrating system.

Recently two sets of experiments have brought forward evidence that the round window may form an alternative path for the sound-waves to enter the inner ear.

In a first series of experiments, performed by WEVER, LAWRENCE and SMITH the output of cochlear potentials in response to stimuli applied to the cochlea, either by way of the round window or by way of the oval window, was compared. After removal of the middle-ear structures, in which only the footplate of the stapes remained in the oval window, a sound tube was alternately sealed over the oval and the round window. The cochlear response from both windows was remarkably similar in form, the differences between the two response-curves never exceeding 4 db. The sound-transmission via the oval window was in general slightly favoured.

These experiments indicate that when the middle-ear mechanism is absent the cochlea may be stimulated, almost as readily by way of the round window as by way of the oval window.

In a second series of experiments, carried out by KOBRAK (12) the oscillations of the incus in fresh human temporal bones were recorded in response to sound stimuli conducted by tube to the round window (fenestral sound conduction).

At the same intensity-level of the sound stimulus the vibrations of the incus were about equal in ossicular and fenestral conduction.

In the living animal, in which the tensor reflex of the opposite ear was used as an indicator of cochlear function, it was shown that a good reflex was obtained for sounds conducted into the round window niche.

Clinical and experimental evidence thus points to the round window as an alternative path for the sound-vibrations to gain access to the cochlear fluid.

III. Owing to the peculiar structure of the tympanic membrane and the ossicular chain the vibrations of the membrane are transferred with increased force to the fluid of the inner ear.

Since the fluid of the inner ear is a much denser medium than the air, it requires considerable force to transmit the vibrations of the air to the fluid of the labyrinth. HELMHOLTZ (1) attributing great value to the system of tympanic membrane and ossicular chain in the transference of sound-waves, formulated this as follows: "In this transference of the vibrations of air into the labyrinth it must be observed that although the particles of air themselves have a comparatively large amplitude of vibration, yet their density is so small that they have no very great moment of inertia, and consequently when their motion is impeded by the drumskin of the ear, they are not capable of presenting much resistance to such an impediment or of exerting any sensible pressure against it. The fluid in the labyrinth, on the other hand, is much denser and heavier than the air in the auditory passage, and to move it rapidly backwards and forwards, as in sonorous oscillations, a far greater exertion of pressure is required than was necessary for the air in the auditory passage. On the other hand the amplitude of the vibrations performed by the fluid in the labyrinth is relatively very small, and extremely minute vibrations will in this case suffice to give a vibratory motion to the terminations and appendages of the nerves, which lie on the very limits of microscopic vision".

"The mechanical problem which the apparatus within the drum of the ear had to solve, was to transform a motion of great amplitude and little force, such as impinges on the drumskin, into a motion of small amplitude and great force, such as had to be communicated to the fluid of the labyrinth".

The middle-ear apparatus is thus represented as a type of impedance-matching transformer.

According to HELMHOLTZ (2) this transformer action is accomplished by three mechanisms, viz.:

1. By the peculiar structure of the tympanic membrane. The fibrous layer of this membrane is built of circular and radial fibres. Its form resembles a shallow cone, slightly curved towards the periphery. This form was considered by Helmholtz as being caused by the elastic circular fibres curving the non-elastic radial fibres outward. Helmholtz, now suggested that a relatively large deflection of the membrane, in the direction of the pressure exerted upon it, causes a relatively small displacement of the malleus-handle (manubrium). In his opinion the excursions of the free portion of the tympanic membrane are at least 3 times greater than those of the handle of the malleus. From this he deduced mathematically that a slight pressure on the convexity, in other words, on the middle of the radial fibres, already exercises considerable pressure upon the malleus-handle, whereby the radial fibres act as long lever-arms ("tympanic membrane lever hypothesis").

FRANK has shown, however, that if the tympanic membrane be considered as a membrane under tension, only part of the pressure exerted on the membrane is transferred to the handle of the malleus.

Moreover, v. BÉKÉSY (9) has demonstrated that the elasticity of the tympanic membrane is the same in different directions. If the membrane was pressed on with a fine probe this caused a fairly round impression, whereas in membranes stretched more tightly in one direction an elliptical impression results.

The mode of vibration of the tympanic membrane has been studied anew by v. BÉKÉSY (9) with a special method. By means of a probe whose end-surface consisted of a condenser about 1 sq.mm he was able to measure the amplitude of a nearby surface from a change of capacity in the condenser. He was thus able to detect movements as small as 10^{-6} cm. At a distance of about 0.5 mm from the object only the amplitude of a surface of about 1 sq.mm could be measured. By determining the contours of uniform amplitude over the tympanic membrane it was found that the membrane, up to a frequency of 2400 c/s, vibrates as a rigid cone, rotating round an axis at its upper margin. As a consequence of this rotation the amplitude of the membrane becomes greatest at the edge of the tympanum opposite this axis of rotation (see fig. 12).

It means that the membrane at this point, as in a dynamic loudspeaker, must be freely movable. Indeed v. Békésy found a fold of the membrane, with a radius of curvature of 0.5—0.8 mm at the lowest margin of the tympanic membrane, allowing great excursions of this part (fig. 13). It enables the conic part of the membrane to move without noteworthy deformation. v. Békésy determined the stiff part of the membrane to be 55 sq.mm against a total surface of 85 sq.mm. The results of these investigations are thus largely at variance with Helmholtz's opinion that the convexity of the tympanic membrane plays any important rôle in the amplification of forces delivered to the malleus.

2. By the peculiar structure of the chain of ossicles which acts as a lever-mechanism ("ossicular lever hypothesis").

If malleus and incus are considered as forming one close unit, rotating around a common axis, perpendicular to the plane of these ossicles, this unit may act as a lever-system. Helmholtz assumed its axis of rotation as passing through the anterior suspensory ligaments of the malleus to the point of fixation of the short crus of the incus (fig. 14). Since the long crus of the incus is shorter than the long crus of the malleus, its amplitude of movement will be smaller than that of the malleus handle.

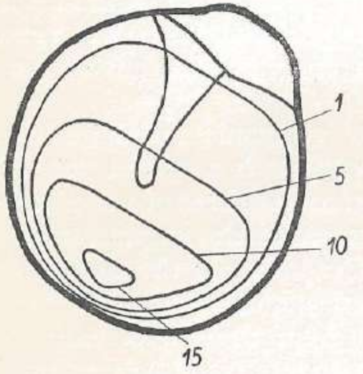

Fig. 12.

Contours of uniform amplitude of the tympanic membrane below 2000 c/s (After v. Békésy).

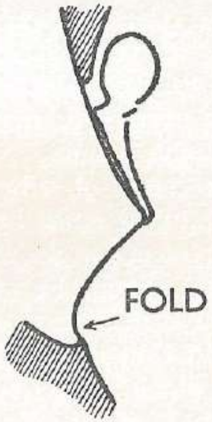

Fig. 13.

The mobile fold at the margin of the tympanic membrane which permits the central part to move as a rigid cone. (After v. Békésy).

Helmholtz computed that on inward movement the displacement of the lenticular process of the incus was 2/3 of that of the end of the malleus-handle, and that consequently the force acting upon the stapes would be 1.5 times greater than the force exerted upon the manubrium of the malleus.

The efficiency of such a lever-system will, however, be largely dependent on the degree ow coupling between the ossicles. In his experiments with a model of the middle ear, Stuhlman (1) found this ratio to be 1.27 to 1 if the malleus-incus articulation was closely coupled. If the joint was loosely coupled the centre of rotation of malleus and incus, on inward motion, was located at the lower edge of their articulating surfaces. The ratio of the lever-arms was nearly 2 to 1. On outward motion a similar centre developed at a diagonally opposite point just below the superior edge of the incus. The ratio of the lever-arms now became 1 : 1.

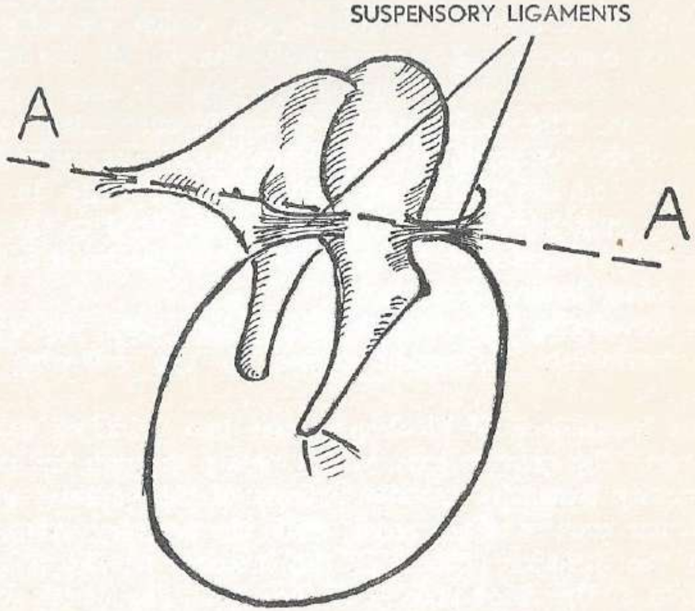

Fig. 14. The axis of rotation passes through the centre of gravity of the ossicles.

The determination of the lever-ratio will, however, not only depend upon the degree of coupling of the ossicles, but also upon the exact knowledge around which axis of vibration the ossicular chain moves.

The vibratory mechanism of the sound-conducting apparatus was recently again subjected to an extensive study by Fumagalli. The structure of the tympanic membrane and the middle-ear system and their mechanisms of vibration were studied in different mammal species from a morphological point of view. It was demonstrated that the incudo-malleolar joint in man and other mammals constitutes a diarthrosis, developing very soon into an ankylosis. For the small displacements occurring in sound-vibrations malleus and incus may be considered as one unit, whereas for larger displacements (mechanical injuries) the joint may retain a certain degree of elasticity. In rodents the joint is either a synchondrosis (rabbit) or a synostosis (guinea-pig), which excludes any mobility between the ossicles mutually. In all the species examined the incudo-stapedial joint, however, was a mobile diarthrosis. The hammer-anvil block is suspended to the walls of the tympanic cavity by the anterior process of the hammer and the short crus of the anvil. Only in man and the guinea-pig is the anterior process fixed to the tympanum by means of a ligament, in other species it is fixed by a bony lamina (synostosis).

In considering these morphological data with the results of experiments Fumagalli comes to the following conclusions:

The hammer-anvil block possesses two principal axes of rotation. The gravity axis, which passes through the centre of gravity from the anterior process of the hammer to the lenticular process of the anvil, while the rotatory axis passes from the anterior process of the hammer to the point of fixation of the short process of the anvil. The whole system can vibrate alternately around either one or other of these axes. The anterior process of the hammer must, in all species, be considered as the pivot upon which the system moves and through which pass both the gravity and the rotatory axes. In cases of small vibrations the system vibrates around the gravity axis. The elastic ligaments of the posterior anvil joint do not check the displacements of the short process, as long as these movements are smaller than the limit set by the ligaments or the surface of the articulation. As soon as the size of the displacements becomes larger than this limit the joint becomes automatically blocked and the system starts vibrating around the rotatory axis.

A detailed analysis of the lever-systems of both axes showed that the ratios of the lever-arms had the following values:

for the rotatory axis: man 1.3, dog 1.3, ox 2.6, horse 2.0
for the gravity axis: ,, 10.0, ,, 16.7, ,, 12.7, ,, 22.7

A change in these vibrating axes will therefore result in strong variations for what concerns the ratios between the lever-arms. It is assumed that this change takes place gradually and that under normal conditions the chain vibrates around an infinite number of intermediate axes, between the gravity and the rotatory axes.

Almost all investigators, who have studied the vibratory mechanism of the ossicular chain, have demonstrated that the excursions of the ossicles in response to sound-vibrations gradually decrease in size from the malleus through the incus to the stapes. Dahmann showed, however, that if the system malleus-incus together with the tympanic membrane was separated from the labyrinth in the incudo-stapedial joint the amplitude of the long crus of the incus was the same as that of the umbo. Similar results were obtained by Perlman (5), who demonstrated that the stapes moves with a much greater amplitude when driven by an intact chain, after removal of the elastic, restoring force of the annular ligament.

From his experiments Dahmann came to the conclusion that the decrease in amplitude of the positive phase of the sound-wave cannot be caused by the lever-mechanism, but that the mobility of the joints and the resistance of the annular ligament of the stapes are largely responsible for this reduction of amplitude (see p. 36).

From all these experimental data the conclusions may be drawn that the vibration-mechanism of the ossicular chain is very complex and variable, that an accurate determination of the ratio of amplitudes and lever-arms is extremely difficult and that it is still questionable whether the reduction in amplitude, if existing at all, plays any important rôle in the transfer of pressure from the tympanic membrane to the fluid of the inner ear, or whether it is caused by the resistance of the middle-ear system.

3. Of far greater importance seems to be the difference in cross-sectional area between the tympanic membrane (85 sq.mm) and the footplate of the stapes (the hydraulic ratio). According to the measurements of WRIGHTSON and KEITH, which have been confirmed by STUHLMAN (1) the average area of the stapedial footplate is 3.2 sq.mm. Frank already had stated that on account of the relatively large area of the membrane, in comparison with the area of the stapedial footplate, a 20-fold increase in force might be expected, though this force might be considerably reduced by a fairly good mobility between the ossicles.

This pressure-transformation by the middle-ear mechanism and the tympanic membrane has been experimentally checked by v. BÉKÉSY (9).

In fresh human temporal bones access to the vestibule of the labyrinth was obtained through the internal auditory meatus. The same capacity probe as was used in determining the amplitude of the tympanic membrane, was inserted close to the vestibular side of the stapedial footplate. A sound-pressure was delivered simultaneously to the tympanic membrane and to the footplate. The pressure needed to keep the stapes at rest was measured and correlated with the pressure of the same frequency delivered to the tympanic membrane. It was shown that up to a frequency of 2400 c/s the sound-pressure needed to keep the stapes at rest was about 20 times greater than the sound-pressure at the tympanic membrane.

v. Békésy states that the transfer of pressure from the tympanic membrane to the footplate of the stapes is independent of frequency up to 2400 c/s and represents a 20-fold increase in force.

The physical problems related to this transformer-action of the middle ear will be discussed in more detail in Chapter VII.

IV. By the vibrations of the stapes the fluid of the inner ear is set in motion.

Weber introduced the principle of mass movement of the cochlear fluid, i.e. the pressure-pulse momentarily spreading over the fluid, which is displaced in its entirety. The physical explanation of this view was that the wave-lengths of compression-waves are large in proportion to the size of the cochlear system (in water for 20000 c/s-7.25 cm). For this reason it was held that all parts of the column of fluid were in the same phase of vibration. It is difficult to say, if this is in agreement with Helmholtz's original conception. He indeed spoke of "a sort of wave movement", but he did not state the true nature of this movement. According to the adherents to the resonance-theory the mass movement of the fluid would set the basilar membrane in transverse vibration. Opposed to this theory is the group of the so-called "wave-theories" (TER KUILE, RANKE and others), who assume that a travelling wave travels up the vestibular scale.

Whether we accept the one possibility or the other, a certain quantity of fluid will have to be displaced, and this must have an outlet somewhere for the pressure exerted upon it. To demonstrate the fluid displacements in the cochlea at physiological intensities of sound is, on account of the very small amplitudes involved, a problem presenting utmost difficulties. The investigations of POLITZER (1), HELMHOLTZ (2), BEZOLD and others had already proved that displacements in the labyrinthine fluid occur with pressure-variations in the auditory meatus (measured with glass capillary manometers inserted into the semi-circular canals of the labyrinth). All the investigations revealed that when the air in the meatus was compressed the manometer recorded a rise of the fluid. In the living rabbit TSUKAMOTO found with this technique a rise of the fluid in response to an adequate tone stimulus. According to him this rise was caused by a contraction of the intra-tympanic muscles (see page 44).

Although the capillary manometrical methods may give us a record of the static pressure-variations in the ear, yet, since the sinusoidal fluid displacements in a capillary decrease with constant pressure proportionate to the frequency, they furnish no insight into the rapid dynamic pressure changes of the audiofrequencies. Capillaries cannot be used for measurements in audiofrequencies, but only for static pressure-measurements.

An attempt has now been made to demonstrate the movement of the fluid in the labyrinth with the aid of vestibular reactions. Since it is generally accepted that a fluid movement in the endolymph canal is the adequate stimulus for the cristae in the semi-circular canals, the induced vestibular reactions may be used as an index of this fluid movement. Under normal conditions, however, a sound-impulse will cause no movement of the fluid in the vestibular organ. Behind the oval window is situated the vestibulum from which issue several canals, namely the semi-circular canals and the scala vestibuli of the cochlea (fig. 5). Each of the 3 semi-circular canals empties into the vestibulum not merely at its beginning but also at its end, and both lie close to each other. An inward movement of the stapes will thus exercise an equal pressure on the beginning and end of the fluid column in the canals. The fluid remains at rest. When, however, an opening is made in one of the semi-circular canals thus forming a way of escape for the perilymph, then a flow of fluid can be easily produced. In patients with a fistula in one of the semi-circular canals BENJAMINS was able to obtain distinct vestibular reactions to sound. This was still easier when in test animals (e.g. the pigeon) an opening was made in one of the semi-circular canals (reaction of Tullio).

Since the head reactions initiated in this way disappear again immediately as soon as the fistula is closed, HUIZINGA explains the reaction as being caused by a fluid displacement, exerting a pressure against the crista of the canal.

After removal of the plug, the reaction appears again immediately. The fistula thus would perform a similar function to the membrane of the round window in the cochlea. If the operational cavity with the fistula was isolated from the external auditory canal, so that the sound-vibrations were prevented from reaching the new fistula, the reaction remained unaltered (VAN EUNEN). In this connection mention must also be made of the interesting facts that have been established during recent years in the operation on patients suffering from so-called "otosclerosis". In patients afflicted with this disability the impairment of hearing is mainly due to a fixation of the stapes by a newly formed bony mass. Consequently the possibility of bringing the cochlear fluid into motion by way of the ossicular chain is greatly reduced. As soon as a new fenestra has been created somewhere in the vestibular part of the labyrinth, or in the promontory, a sudden improvement in hearing is achieved.

In creating this new fenestra mobility of the perilymph is reestablished and a shuttle-action of the fluid between the two windows again becomes possible. It is generally understood that the new window acts as a new entrance for the sound-vibrations into the labyrinth, but evidence supports the view that the possible route may be: tympanic membrane-air of the tympanic cavity-round window-labyrinth. Making use of the method of the "Drehtöne", described by v. Békésy (see page 51), MOL, for instance, found a definite phase-reversal in cases, which had undergone succesfully the fenestration-operation. This makes it highly probable that in these cases the newly created opening does not act as a new oval window (fenestra nov-ovalis), but as a compensatory area for the vibrating labyrinthine fluid, or as a new round window in the sense of Weber. When the new opening (which is usually made in the horizontal semi-circular canal) closes again by the growth of new bone, the improvement in hearing is lost, and only a revision of the operational area may sometimes restore the hearing again. From this evidence it seems necessary, that a shuttle-action in the fluid of the labyrinth between the two windows is essential to audition.

By means of the reaction of Tullio, VAN EUNEN was able to observe the influence upon the sound-transmission of manipulations on the conduction-apparatus of the pigeon. First of all he established that the optimum of the reaction was attained in the frequency region of 600—800 c/s. A sound-intensity of 70 db in this region was needed to excite a reaction. For higher and lower frequencies greater intensities were required to obtain movements of the head. The curve representing graphically the threshold values for the frequency range from 100—3200 c/s always had a characteristic form, and showed a certain conformity with the human audiogram.

The optimum of the reaction, however, lay much lower than the region of highest sensitivity in man, which, according to van Eunen, might be explained by the fact that the upper-limit of hearing in the pigeon is much lower than in man (WEVER and BRAY (2)). Section of the columella-stem without damaging the stapedial footplate led to a great reduction of response. The same effect resulted from removal of the tympanic membrane and fixation of the columella-footplate in the oval window. In all these cases the curve was shifted to higher values and this was the case for all frequencies. Blocking of the round window had no appreciable effect upon the reaction.

Van Eunen's experiments are thus all in favour of a sound-transmission through the ossicular chain and oval window, and make it seem highly improbable that the sound-waves under normal circumstances enter the inner ear through the round window.

On human temporal bones v. BÉKÉSY (1) observed stroboscopically movements of the labyrinthine fluid and the basilar membrane, but the intensities required were so high that the stapes was disrupted by the vibrations of the electro-magnetically driven tuning fork placed on the stapes.

The whirlpool movements of the labyrinthine fluid, which v. Békésy observed in his specimen, have also been demonstrated by LEONARDELLI in the guinea-pig; and KOBRAK (9) was able to register and measure the amplitude of fluid-vibration in the cochlea of human temporal bones at various frequencies and intensities of a tone.

Finally, as evidence of a possible displacement of the fluid mention must be made of the experiments in which the movements of the round window membrane in response to sound-vibrations are registered. These movements will be discussed in detail sub. 6.

V. The movements of the fluid set the basilar membrane into vibration.

If, according to the fairly generally accepted conception, it be assumed that the fluid is incompressible and surrounded by rigid bony walls, then there is but one possible way for it to evade the pressure of the stapes namely, by bulging the membrane of the round window into the middle-ear cavity.

For this purpose the fluid has a choice of two routes (fig. 8), namely:

1. Through the narrow opening (helicotrema) in the apex of the cochlea;
2. Via the scala vestibuli, membrane of Reissner and ductus cochlearis, through the basilar membrane to the scala tympani.

The slow equalisation of pressure would then take place via the helicotrema, while the very small diameter of the helicotrema and the high frictional resistance of the perilymph make a volume-displacement of the fluid through the helicotrema impossible for the rapid periodic displacements of the fluid in sound-vibrations.

Direct evidence of a vibrational movement of the basilar membrane is extremely difficult to obtain. In the experiments of v. BÉKÉSY (1) the cochlea was exposed over a large area, and the vibrations of the membrane were followed stroboscopically. As stated above, however, very high intensities of stimulation were required. In his experiments on guinea-pigs LURIE (1) found a disruption of the whole organ of Corti from the basilar membrane after exposure of the animals to sounds of very high intensity. This was taken as evidence of the vibrations of the membrane.

MYGIND, however, points out that the chloroform used for the purpose of eliminating the influence of the intra-tympanic muscles may already have caused great alterations in the histological structure of the organ of Corti.

It is questionable whether, from these experiments with abnormally loud tones, conclusions may be drawn respecting the reactions occurring in the basilar membrane under normal conditions. When other ways of escape are open to the fluid, it would not seem impossible that movements in the fluid might appear without the basilar membrane being set into motion.

VI. The membrane of the round window serves as a low-resistance pathway for the vibrating fluid of the inner ear.

The movements of the round window membrane have been repeatedly studied on human temporal bones. In 1841

WEBER (1) seems first to have pointed to the round window membrane as a probable compensatory area for the fluid. If pressure were applied to the stapes in the preparation, the membrane bulged outwards. MACH and KESSEL (2) were able to follow stroboscopically the movements of the membrane, and demonstrated further that these were always in opposite phase to the movements of the stapes. In the laboratory of Helmholtz BUCK and BURNETT measured these excursions with the aid of an ocular micrometer. Although these researches were done in the same Institute, their results were not quite the same. Whereas Buck established that the movements of the round window membrane were greater than those of the stapes, Burnett was not able to show any difference. Weber-Liel used a 40 × magnification, and confirmed the observation that when the air in the outer auditory canal is compressed, the membrane bulges outwards. He further found that the excursions of the membrane were greater than those of the stapes. In all these investigations, however, it must be borne in mind that comparatively large mechanical movements of the air were used, and not the microscopical, or even ultra-microscopical amplitudes as occur under physiological conditions.

Link repeated these experiments, with an improved technique, on a large number of human temporal bones. Besides evaluating the influence of a change of elasticity and the elimination of muscular activity in the dead material, Link attached great importance to the maintenance of the intra-labyrinthine pressure. It was shown that a change of this pressure highly influenced the vibration amplitude of the fluid and the membranes. By selecting fresh preparations, in which the aqueducts were not destroyed and the whole preparation covered with paraffin to prevent the perilymph flowing away, he endeavoured to keep this pressure as constant as possible.

In Link's experiments the middle ear was carefully exposed, the edges of the round window filed off and a tiny mirror of minute dimensions (0,5 × 1,5 and 0,5 mm thick) attached to the membrane. The excursions of this little mirror were registered optically with a lightbeam-lever of 30—50 cm. An audiometer was used as a sound-source and the sound carried to the tympanic membrane by a tube 8 cm long. In order to register the excursions of the other components of the conducting system, tiny mirrors were also attached to tympanic membrane (umbo), head of the malleus, incus and stapes.

By means of this technique, Link was able to demonstrate the following:

The round window membrane reacts to sound impulses in the same manner as the various parts of the ossicular chain, its vibration amplitude being partly smaller, partly larger, than that of the different ossicles. For instance, it is less than the amplitude of the head of the malleus, but greater than that of the stapes. With equal intensity and variable frequency the amplitude shows a certain characteristic response. With low frequencies it appeared to be already fairly large, with increasing frequency the amplitude increased, to reach a maximum between 500 and 900 c/s and then to fall rapidly. Above 2000—3000 c/s, even with the greatest intensity and a highly sensitive method (2 m long lightbeam-lever) no movement could be observed. For the various frequencies the minimum intensity was also determined which was required to cause a just-noticeable vibration of the round window membrane. This intensity appeared to be smallest for the frequencies between 500—900 c/s and the curve obtained by representing graphically the various intensity values for different frequencies showed a certain resemblance to the normal human threshold curve. Thus, a sort of air-conduction audiogram could be made for the cadaver ear. KOBRAK (9), using a similar technique, also demonstrated in a moving picture film how the round window membrane can be used as a "dynamic manometer" of the cochlea. It was further shown that the inward movement was larger than the outward motion.

v. BÉKÉSY (12) endeavoured in an entirely different way to measure the vibration amplitude of the round window membrane. Since the round window has a surface of 2 sq.mm and moreover, is very concave, lying hidden in a deep niche, v. Békésy held the opinion that with the optical methods at our disposal it would not be possible to measure in a direct way the extremely small amplitudes occurring at physiological intensities. v. Békésy measured the volume-displacements caused by a vibration of the membrane with an indirect or "nul" method. For this purpose the middle ear of a freshly prepared temporal bone was opened from below, and a short T-piece cemented upon the niche of the round window. A small loud-speaker was attached to one end while the other was connected to a hearing tube. The opening in the middle ear was again closed with cement. If the tympanic membrane sinusoidal preparation was supplied with sinusoidal pressure-variations, the round window membrane also carried out sinusoidal volume-displacements. The sound produced in this manner could be listened to via the hearing tube. This sound could be compensated with a compensation loud-speaker by a current of the same frequency, but of opposite phase.

By gauging, the volume-displacement of the loud-speaker membrane and that of the round window membrane could also be determined. By this method v. Békésy found that the amplitude of vibration of the round window membrane, in response to a constant sound-pressure at the tympanic membrane, is almost independent of frequency, so that in his opinion the peculiar form of the hearing threshold curve must be ascribed to the sense organ itself.

Practically all the investigators who have studied the movements of the round window membrane have observed that the amplitude of the stapes is smaller than that of the round window membrane. According to Link this can be explained by taking into account that the area of the stapedial footplate is about twice as large as that of the round window membrane (resp. 3.2 and 2 sq.mm). If the latter was the only way of escape for the fluid then its amplitude would have to be also twice as great as that of the stapes. The ratio between the amplitudes of stapes and round window membrane, however, depends largely upon the intra-labyrinthine pressure. If this pressure be reduced by allowing the fluid to flow away, the amplitude of the stapes increases, and contrarily that of the round window membrane decreases rapidly. This is probably the reason why the results of the different investigators do not entirely agree. Increase of pressure will

have exactly the reverse effect. With bone-conduction Link could not observe any vibrations either of the conducting system or of the round window membrane.

What will be the influence of immobilisation of the round window membrane upon the function of the inner ear?

Various clinical and experimental data indicate that an undisturbed mobility of the membrane is not essential to a normal hearing function. Oppikofer described the presence of fat in the round window niche (16 % of 234 cases) without the hearing function being affected to any degree, even when the fat filled up the whole niche. Hallpike and Scott described one case in which a hearing test made shortly before death had revealed no abnormalities, and the pathological-anatomical investigation showed an almost total calcification of the round window. In animal experiments attempts have repeatedly been made to ascertain the effect of blocking the niche upon the hearing function. As a test for the cochlear function Hughson and Crowe (1) utilized the cochlear response derived from an electrode on or near the auditory nerve. No change in the responses was noted as a result of blocking the window with wax or plaster, but an enhancement (ranging from 10—30 db) was reported when pressure was exerted on the window with plugs of moist cottonwool. Since the potential fluctuations occurring in the cochlea spread via the round window in all directions over the mucous membrane of the middle ear, it is not precluded that the moist pledgets improved the conduction of the potentials from the round window to the electrode lying in the vicinity of this window.

Culler, Finch and Girden repeating these experiments, and utilizing the conditioned response method in dogs, found the cochlear function invariably impaired after plugging of the niche. The average reduction of responses was about 10 db. After removal of the plug, this function was immediately restored to normal.

Hallpike and Scott, using the action-currents of the contralateral auditory tract, failed to notice any significant alteration in the cochlear function after a very effective closure of the niche with plaster of Paris.

These contradictory results led WEVER and LAWRENCE to another study of this problem. With various forms of blocking it was shown that only minor alterations of cochlear sensitivity were caused. The reduction of responses rarely exceeded 10 db and was usually of the order of 5 db. With the middle ear intact the high frequencies were more affected than the low frequencies whereas after removal of the middle-ear structures the blocking of the round window mainly reduced the responses to low tones.

The experimental results obtained by Hughson and Crowe led HUGHSON (1, 2) to attempt to improve the hearing of patients suffering from a hearing loss by closing the round window with a tissue-graft. According to him, in most cases an improvement in hearing was noticed. It was suggested that the membrane would absorb much of the energy of the sound-vibrations, and that this loss of energy under normal conditions will be even detrimental to the auditory perception. Conforming to this conception the round window membrane functions as a sort of safety valve for sounds of high intensity.

VAN EUNEN, after closure of the round window niche in the pigeon found practically no difference in the reaction of Tullio.

MILLSTEIN used as a test the degree of impairment of the inner ear caused by exposure to loud tones. If the round window were closed off on one side, a sound trauma occurred only on the non-operated side. From this Millstein deduced that closing of the round window niche has a protective effect upon the cochlea. LINK, also studied the influence of a closure of the round window niche upon the fluid-displacement in the cochlea. At a distance of 4—6 mm from the round window an opening was made in the basal turn of the cochlea, till the membranous wall was exposed. Upon this "membrane" a tiny mirror was placed, and its excursions registered optically. When the niche was closed with paraffin the amplitude of the fluid remained the same. If any pressure were applied to the membrane, however, the vibration amplitude of the membranous labyrinth showed a decided increase in the tonal range up to 3000 c/s. If this increase corresponds to a better perception of the sound then the conclusion might be drawn that closure of the niche alone is not sufficient to influence the hearing. If, however, pressure be applied to the membrane a slight improvement in hearing might result.

At the present state of our knowledge it is still impossible to give a satisfactory explanation of the function of the round window membrane. It has been conclusively shown, that under normal conditions the round window has no important bearing upon the conduction of sound to the inner ear and since obstruction of the membrane impairs the cochlear function only to a minor degree, the round window cannot be regarded as the only significant low-resistance pathway.

As an alternative explanation it has been suggested that the round window membrane operates as a pressure-stabilizing device in response to slow displacements of the stapedial footplate (POHLMAN). To this assumption HALLPIKE and SCOTT add the possibility of a connection between the movements of the membrane and the flow of perilymph. If no distensible vent in the wall of the bony labyrinth, such as the round window would be present, the bulk modulus of the labyrinth would attain very high proportions approximating to that of water itself; and the circulation of cerebrospinal fluid through the cochlear aqueduct in response to pressure changes in the subarachnoid space would thus be brought to a standstill.

VII. The round window forms the only compensatory area for the pressure exerted upon the fluid.

Theoretically besides the round window there are other ways of escape for the pressure-variations in the labyrinth. HERMANN, in his handbook, names the following possibilities:

1. The aquaeductus vestibuli — in this case the fluid will flow along the otoliths and set the fluid in the sacculus in motion (fig. 5).
2. The aquaeductus cochleae — a capillary tube, by which the perilymphatic space communicates with the cerebrospinal space.
   KOBRAK (3) has studied in how far the differences in pressure between the labyrinth and the cerebrospinal space can be equalised, and arrived at the following results:

The static pressure-variations (as with a contraction of the intra-tympanic muscles) are entirely equalised. The dynamic pressure-variations (as in periodic sound impulses) are only equalised at very slow movements of the stapes.

Since the sinusoidal pressure-variations in a capillary decrease proportionally with the frequency, the labyrinthine fluid, in rapid movements of the stapes, can no longer escape towards the cranial cavity, so that this way of escape for the rapid sound-vibrations may be disregarded.

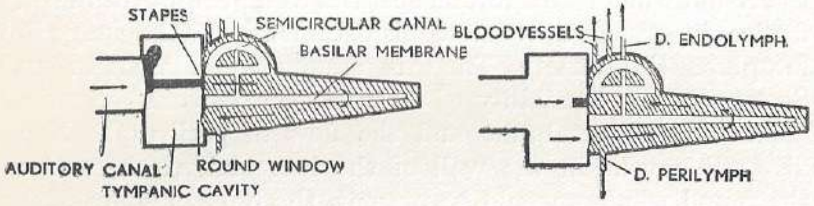

Fig. 15. Release of pressure in the cochlea in the case of a normal middle-ear system (left) and in a case where the tympanic membrane and the outer ossicles are missing, according to v. Békésy (7).

3. The blood- and lymphvessels of the labyrinth — the very abundant blood- and lymph supply of the inner ear indeed afford the fluid a certain opportunity of pressure-escape (Pohlman (3)). This factor is extremely difficult to determine experimentally. Considering the mechanics of the internal ear in cases where the tympanic membrane and ossicles are lacking, v. Békésy (7) attached great importance to the possibilities mentioned above (see fig. 15).

   Where the tympanic membrane is missing the sound-pressure thrusts the round window membrane inward, whereas the stapes is regarded as fixed. Under these conditions the vents become operative. According to v. Békésy the upper system of vents connected with the scala vestibuli is more effective than the single vent (ductus perilymphaticus) connected with the scala tympani. Accordingly the fluid-displacement would take place toward the upper system of vents and the basilar membrane would respond in a phase opposite to that of the normal (see page 51).

VIII. The fluid of the labyrinth is incompressible.

From the physicist's point of view a liquid cannot be considered as being incompressible. For every material has a certain compression modulus, and although this for most fluids and solids is great, there are an immense number of substances which are capable of propagating sound-waves in the form of compression-waves.

Waetzmann (1) has written on this question:

"We must, however, understand clearly that in so far as a detailed consideration is concerned, the liquid cannot be regarded as a completely incompressible medium, because otherwise variations in density would be impossible, and the rapidity with which a pressure applied to one area could be conducted would be infinitely great". A liquid, however, enclosed in a very elastic surrounding may be regarded as being practically incompressible with respect to pressure-variations affecting such a system. We may therefore assume that the elasticity of the inner-ear system is set up by the compensatory areas and not by the compressibility of the fluid.

IX. The labyrinth capsule is to be regarded as a non-elastic container of the fluid.

v. Békésy's (3) investigations have rendered it probable that sound-vibrations which reach the cochlea by means of bone-conduction partly set the fluid of the internal ear directly in motion, by means of compression of the labyrinthine fluid.

Now Pohlman (2) postulated that if the bone-conducted vibrations are directly transmitted to the fluid, then the air-borne vibrations can also be transmitted from the fluid to the osseous capsule of the labyrinth. Thus he assumes that a relatively free transfer of acoustic energy through the bony wall of the labyrinth is possible.

In connection with their experiments concerning the blocking of the round window niche, HALLPIKE and SCOTT examined physically this possibility. They proceeded from the formula for the transfer of acoustic energy from a fluid to a solid medium: $\eta = \frac{4\,r}{(r + 1)^2}$ in which η is the ratio between the acoustic energy of transmitted and incident wave and r is the ratio of the acoustic resistances in fluid and solid media. If the value of the acoustic resistance for water is taken as $14.\,10^4$ and the same physical constant of the living labyrinth capsule is estimated at 22.10^4 (which represents the value for certain hard woods- e.g. beechwood), then the probable value for η on the boundary between fluid and bone in the ear, would be 0.95.

Hallpike and Scott, however, held the opinion that "a considerable difficulty in assuming any free transmission of sound through the bony labyrinth wall lies in the extreme attenuation of sound, air-conducted to one cochlea, in its transmission through the skull to the opposite cochlea. The figure given by Fletcher (1923) for this attenuation is 60 db. According to Pohlman's hypothesis, the first cochlea, might be regarded as a point source transmitting to a point receiver in the opposite cochlea. In these circumstances the resulting attenuation would follow the law of inverse squares. If the source be taken as the stapes footplate, then the approximate distances to the nearest points of the cochlear spirals in the same and opposite ears are 2.8 and 80 mm respectively, giving an extreme attenuation of some 30 db. For these reasons it would appear to be impossible to accept Pohlman's hypothesis."

CHAPTER V

THEORIES AND EXPERIMENTS CONCERNING FREQUENCY-ANALYSIS IN THE EAR

In 1863, more than 100 years after the publication of Cotugno's dissertation, HELMHOLTZ published his famous book "Die Lehre von den Tonempfindungen", which may be regarded as the foundation of physical and physiological acoustics.

In the first part of this work Helmholtz, in a detailed description of the composition and analysis of the various sounds, gives a possible explanation for the sound-analysing function of the ear. Although he neither refers to earlier opinions about the existence of a resonance-system in the ear, nor mentions the conceptions of Cotugno, it is undeniably to his great merit that he furnished a better and more scientific foundation to the resonance-theory and that he gave it a physico-mathematical treatment.

Sound-Analysis by way of mathematics and of physics.

In a simple harmonic vibration the air-particles execute a periodic movement, the motion curve of which can be represented graphically by a single sinusoidal wave, whereby the amplitude corresponds with the intensity, and the periodicity with the frequency of the vibration. Now, a complex sound is composed of a number of such periodical vibrations, each component having a particular frequency. If the movements of the air-particles in a complex sound-wave are represented graphically the curve obtained is generally neither sinusoidal nor even periodical. If we restrict ourselves to the complex sound showing a periodic motion curve, such a curve is obtained by the superposition of a number of sinusoidal vibrations, each component having a particular frequency. The form of such a motion curve depends upon the frequency- and the intensity-, as well as upon the phase-relations of the partials.

Mathematically, a sound can be analysed according to the theorem of Fourier, which states that any periodic motion can be analysed, and only in one way, into a number of single sinusoidal waves of various amplitudes and periods.

By a physical method Helmholtz succeeded in analysing the various sounds of musical instruments and the vowels of the human voice into their single components. For this purpose he made use of the physical principle of resonance. By means of glass or metal globes of various diameter and provided with an opening at each side (the so-called resonators of Helmholtz) this analysis could be carried out in a simple way.

One opening of the resonator, furnished with a neck, was inserted into the outer ear canal, while the other opening was turned towards the sound-source.

By resonance, that tone, whose frequency corresponds to the natural frequency of the vibrating air-column in the resonator, is reproduced more strongly than the other components of the complex sound.

Sound-analysis by the ear.

Even without making use of the resonator a suitably trained ear is also capable of performing a sound-analysis. This fact, so important in the physiology of hearing, was established by G. S. OHM in 1843, in a law, the so-called acoustic law of Ohm, which states: that sinusoidal vibrations are perceived as a pure tone, that a complex sound is analysed by the ear into its different sinusoidal components, and that these components will be perceived as pure tones having a pitch determined by the respective frequencies. This law was again tested and confirmed by Helmholtz, who demonstrated at the same time that the phase-relations between the various sinusoidal components have no influence upon the sensation of a complex sound. The ear, thus performs in a way, an analysis of sound in accordance to the theorem of Fourier. These two fundamental characteristics of the ear were for Helmholtz the basic principles for formulating his auditory theory with the, now classic, resonance-hypothesis. Since no physical method of sound-analysis was known to him other than that by resonance, he tried to explain the subjective sound-analysis

by the ear by means of resonance-phenomena in the auditory organ. When looking for a structure, which might be responsible for the resonance-phenomena in the ear, Helmholtz made use of the anatomical data which had been published a decade earlier by the Italian anatomist Alphonse Corti. At first the vibrating function was ascribed to the rods of Corti formed by the supporting cells, but when HASSE demonstrated that these rods were lacking in birds and amphibians, Helmholtz followed the conception of HENSEN, who had already expressed the view that the basilar membrane might be taken as the resonant system. For this membrane has a structure which, as regards the width at least, exhibits a certain progressive differentiation from base to apex, while also the nerve-terminals that finally conduct the stimulus to the brain terminate in the organ of Corti. The task of conveying the vibrating energy of the basilar membrane to the auditory cells was left to the apparatus of the pillar cells. Helmholtz thus regarded the basilar membrane as a set of resonant elements, each possessing a certain natural frequency and each capable of vibrating with a particular tone in the auditory scale. Helmholtz tried to make this acceptable by a mathematical treatment of a membrane with the characteristics of the basilar membrane. The difference in tension in radial and longitudinal direction was considered to be one of the most important features of the basilar membrane. From the fact that the radial fibres possess a high degree of tenacity, but may be easily separated from each other, Helmholtz concluded that the basilar membrane displayed a certain tension in radial direction, but not in a direction longitudinal to the membrane. Now, a membrane stretched only in one direction behaves quite differently from one tensed equally in all directions. Whereas the latter possesses a very particular natural frequency dependent on the size, tension and other qualities of the material, Helmholtz came, by way of a complicated mathematical analysis, to the conclusion that a membrane with the characteristics of the basilar membrane, when activated by a periodic force, may approximately be regarded as a system of parallel stretched chords. Such a membrane possesses numerous natural periods, and when it is activated by a simple harmonic vibration, that part of the membrane whose natural period corresponds with the frequency of the vibration will be set into strong oscillatory movement. The adjacent resonance-areas, whose natural periods are not entirely in concordance with the frequency of the forcing vibration will also be moved more or less, their rate of movement depending upon the degree of damping of the membrane (fig. 16).

Thus Helmholtz in fact assumed a vibration of a radial *segment* of the basilar membrane with maximal displacement in the centre, and not a selective vibration of mutually independent fibres, as may be seen from what Helmholtz wrote in the third edition of his work:

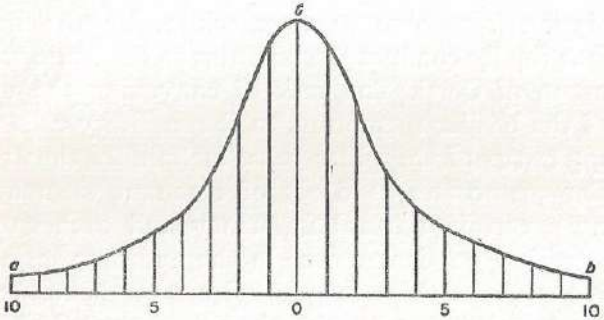

Fig. 16. The fibre oc is set into strong vibration to a given tone. The fibres on either side of this resonance-area are also activated but to a much smaller degree.

"But if the tension in the direction of its length is infinitesimally small in comparison with the tension in direction of the width, then the radial fibres of the basilar membrane may be approximately regarded as forming a system of stretched strings and the membranous connection serving only to give a fulcrum to the pressure of the fluid against these strings. In that case the laws of their motion would be the same as though every individual string moved independently of all others, and obeyed, by itself, the influence of the periodically alternating pressure of the fluid of the labyrinth contained in the vestibule gallery. Consequently any exciting tone would set that part of the membrane into sympathetic vibration, for which the proper tone of one of its radial fibres which are stretched and loaded with the various appendages already described, corresponds most nearly to the exciting tone; and thence the vibrations will extend with rapidly diminishing strength on to the adjacent parts of the membrane."

Whereas Helmholtz deduced the characteristics of the basilar membrane theoretically, WAGNER succeeded in constructing model membranes with the above properties, the so-called "polyphonic membranes" of Wagner. If, in a metal plate, a fenestra be cut along two short parallel and two long exponentially running lines, and over this fenestra a membrane be fastened in such a way that it is attached only on the sides of the exponential lines and ends freely towards the parallel sides, then such a membrane will have tension in the transverse direction, but no tension in the direction of its length (fig. 17).

If, now, a vibrating tuning-fork be moved backwards and forwards above the membrane a very particular part of the membrane will be set in resonant vibration. The position of this part, characterised by a vibrating segment, is governed by the forcing frequency in such a way that low tones set into vibration the wide part and high tones the narrow portion of the membrane. A complex sound is analysed by such a membrane into its components, so that differently localised maxima of vibration occur for the different tones.

These experimental data may not, however, be applied unreservedly to the basilar membrane, as the model membrane of Wagner and the basilar membrane do not vibrate under the same conditions. Whereas the former can vibrate freely in the air, the basilar membrane lies enclosed in a small space filled with fluid, and the physical properties of the latter may greatly influence the mode of vibration of the basilar membrane.

Under the conditions assumed by Helmholtz the parts of the membrane resonating with the low tones will be found at the apex of the cochlea, while the high tones will set into vibration the parts of the membrane situated at the base of the cochlea. This conception was thus in agreement with the opinion expressed by Cotugno 100 years previously, while Hensen also arrived at a similar conception. (For a further study of these early theories of hearing the reader may be referred to the article of Bast and Shover, in which the various stages in the development of Helmholtz's resonance-theory are elaborately discussed).

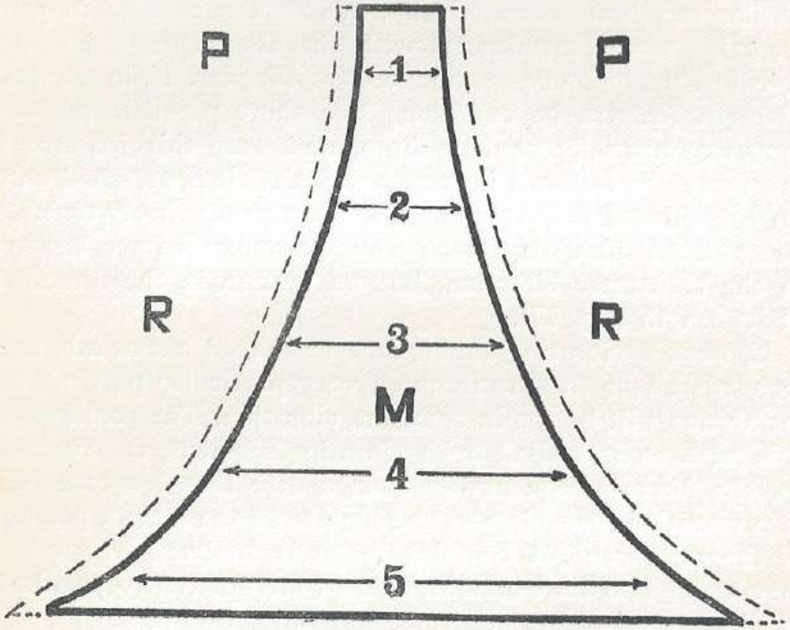

Fig. 17. 'Polyphonic membrane' after WAGNER.
M — membrane.
R — margins where the membrane is attached to the metal plate P.
The position of maximal vibration shifts from 1 towards 5 with lowering frequency of stimulation.

The theory of Helmholtz may in fact be considered as being built up of different parts, namely:

1. the analysis of a complex sound by the ear is performed in a physical manner, by resonance of the radial fibres or segments of the basilar membrane (*resonance hypothesis*).
2. every tone sets into vibration a particular part of the membrane, in such a way that the high tones are localized in the narrow portion, i.e. near the round window and the low tones at the apex, on the wide portion of the membrane (*localization hypothesis*).
3. each hair-cell or group of hair-cells will, when stimulated, produce invariably the same pitch-sensation. This is the so-called principle of "specific energy" of JOH. MÜLLER, which implies that a nerve-fibre, no matter how it is stimulated, produces a specific sensation, differing for each nerve-fibre. Thus, stimulating the terminal organ of a certain auditory nerve-fibre invariably produces the same pitch-sensation. This principle deprives the nerve-impulse of any qualitative character.

Although the theory furnished a simple explanation for several facts, e.g. the capacity of sound-analysis, the combination-tones and the beats, some facts remained difficult to explain and a number of theoretical objections against this theory were soon advanced.

These arguments were mainly directed against the resonance-hypothesis and were of an anatomical as well as a physical nature.

They are chiefly:

1. That it is difficult to understand that an organic fibre, only $^1/_{10}$ mm in length which is part of a membrane, will respond in the same way as a stretched string one meter in length. Helmholtz has already attempted to meet this objection by pointing to the investigations of HENSEN, who demonstrated that tiny hairs of this length on the tail of the opossum shrimp were set into sympathetic vibration, so that different groups of hairs were activated by different tones.

At the same time he advanced that the fluid of the inner ear and the solid structures of the organ of Corti may be considered as loading the basilar membrane, whereby the natural period of a certain area of the membrane will be lowered:

"That such short strings should be capable of corresponding with such deep tones, must be explained by their being loaded in the basilar membrane with all kinds of solid formations; the fluid of both galleries in the cochlea must also be considered as weighting the membrane, because it cannot move without a kind of wave-motion in that fluid".

This weight, however, exercises a great damping effect upon the system, so that the process can have little in common with resonance in the physical sense. For, according to Helmholtz's computation, a sharply demarcated radial zone of the membrane will vibrate only when the damping is small enough.

2. The anatomical structure of the basilar membrane makes an independent vibration of individual segments very unlikely. The investigations of Hardesty (1) had already revealed that the various elements of the membrane, and the supporting apparatus of the organ of Corti, are so interlocked as to make individual movement impossible. In various animals, especially in birds, the basilar membrane is a dense membrane with the fibres running in several directions, which apparently makes it unsuitable as a selective response-mechanism.

When a tone sets into vibration a particular part of the basilar membrane the areas on either side will also vibrate but to a much lesser degree. Not only the nerve-fibre belonging to that particular "resonator" will be stimulated, but also the adjacent fibres. While we adhere to the principle of specific energy of senses, however, we shall have to accept auxiliary hypotheses in order to explain why no more tones are heard. Such a hypothesis was first formulated by Gray, who assumed that only the nerve-fibre which is maximally stimulated will transmit the impulse to the brain ("principle of maximal stimulation"). Even if we accept this hypothesis we are still lacking a satisfactory explanation.

From the work of Galambos and Davis (1, 2) on the electrical activity of single nerve-fibres we now know that a given tone at threshold stimulates a localized area of the organ of Corti. With increasing intensity of this pure tone a greater part of the adjacent structures is stimulated. This spread of response is not symmetrical, but mainly towards the higher frequency side, so that at 100 db a 300 cycle tone stimulates the whole region between the response-areas of the 250 and the 2500 cycle tone.

3. It is difficult to understand that the resonating elements of the ear may respond to a range of 10—11 octaves. In order to explain this fact, it will have to be made acceptable that

the physical properties of the membrane show a large degree of progressive differentiation from base to apex. The natural frequency of a stretched string is determined by three factors, viz. length, tension and mass per unit length, and that according to the formula:

$$n = \frac{1}{2\,L}\sqrt{\frac{E}{m}} \text{ or } n = \frac{1}{2 \times \text{length}}\sqrt{\frac{\text{tension}}{\text{mass per unit length}}}$$

The frequency is thus inversely proportional to the length and the square root of the mass per unit length, and directly proportional to the square root of the tension of the string.

Does the basilar membrane possess these necessary requisites of length, tension and mass to justify the application of this formula to the cochlear structures?

The only factor which Helmholtz was able to determine was the difference in width of the basilar membrane between base and apex (and therefore the difference in length of the resonating "chords" or membrane segments), but he indicated also that the load or mass from base to apex will vary. In spite of the fact that the mechanical continuity is preserved in all directions, we may regard a membrane stretched in *one* direction as a series of parallel tensed strings (Wagner) and apply to it the formula for the stretched string.

Hartridge, as well as Wilkinson and Gray especially have attempted to show that the physical properties of the membrane allow for a progressive differentiation of the three factors along the length of the basilar membrane.

a. length of the 'fibres' — The accounts of the ratio of the length of the 'fibres' at base and apex differ widely with various authors. Whereas Helmholtz proceeded from the measurements of Hensen, who found the ratio to be 1 : 12, later investigators demonstrated that great individual differences occur and that the increase in length may be very irregular (see Chapter II).

If we assume an average ratio of 1 : 6, this would only account for an acoustic spectrum of 2½ octaves at the most.

The prime importance of the difference in length of the radial fibres as the underlying mechanism for the sound-analysis was already questioned by Denker on account of his investigations of the auditory apparatus in the parrot. This bird has a basilar membrane of relatively even width throughout, its total length not being more than 2.6—2.7 mm. The parrot, however, has not a very limited frequency-range and frequency-analysis seems to be quite good. The number of radial fibres was estimated at 1200.

b. tension of the 'fibres' — The computations of Helmholtz had led him to the conclusion that well-defined segments of an elongated triangular membrane could only be brought into vibration when the tension in transverse direction considerably exceeded the tension in the direction of its length. Helmholtz made no mention, however, of any difference in tension between base and apex. Gray's anatomical investigations, which demonstrated that the thickness of the spiral ligament increases very considerably from apex to base, led him to the conclusion that the tension exerted by this ligament would increase correspondingly. The short 'fibres' at the base would thus have a much greater tension than the long 'fibres' at the apex.

With regard to the actual tension of the basilar membrane we possess very few experimental data. BERENDES determined the tension in a fresh cadaver ear to be a few dyn/cm^2 in the second turn from the base. v. BÉKÉSY (11) demonstrated that the basilar membrane displays no tension, and may be compared with a gelatinous layer. With a thin glass rod the basilar membrane at the apex was gently impressed, the deformation being practically the same in every direction, whereas with a difference of tension in two directions a more oval indentation might have been expected. v. Békésy thus concluded that the tension in transverse direction cannot exceed that in longitudinal direction. These experiments make one of the basic principles of the resonance-theory valueless, and in this light the theory becomes scarcely tenable.

c. mass of the 'fibres' — While Helmholtz had already assumed that the fluid of the inner ear may be considered as loading the basilar membrane, WILKINSON (2) attempted to demonstrate that the mass of the fluid loading the 'fibres' must be greater at the apex than at the base. A vibrating segment of the basilar membrane would have to displace a double column of fluid. This column stretches on one side from the oval window to the vibrating segment, and on the side of the scala tympani from here to the round window. A segment at the apex of the cochlea would thus be loaded by a longer fluid column than a segment near the oval window. The factor m in the formula would thus acquire a greater value.

4. If the analysis of the sound is achieved by resonance-phenomena in the cochlea, the characteristics of the auditory organ must correspond with the physical behaviour of resonance-systems. Under the influence of a forcing frequency a system capable of vibration, e.g. a series of resonators, will be set into forced vibration. Owing to resonance, that part of the system whose natural frequency corresponds with the forcing frequency, will be set into vigorous motion and will respond to a higher degree than when the same force is applied statically. The greater the difference between resonant and forcing frequency the smaller will be the forced vibrations. The displacement amplitude of the resonator, whose natural frequency equals the forcing frequency is dependent upon the damping of the system. When the damping is increased this amplitude decreases, so that at critical damping no magnification of amplitude due to resonance is present, and all resonators respond equally to all vibrations (fig. 18).

The system loses its analysing function. We may thus conclude, that in any resonance-system selectivity (i.e. magnification due to resonance) and damping are closely related to each other. A highly selective system will show small damping and a highly damped system will have poor selectivity. With small damping and its accompanying high degree of selectivity, time is required for a resonance-system to come to a steady state in response to an applied force and a relatively long time is required for the system to return to the quiescent state after cessation of the driving force.

We will now examine whether the characteristics of the ear correspond with these properties of physical frequency-analysers. Should we accept a resonance-mechanism, acting as a harmonic sound-analyser, to exist in the human ear, it must possess a high degree of selectivity. For the ear, especially in musical persons, is capable of distinguishing very slight differences in pitch. It was shown that at 80 db a 1000 cycle tone is different in pitch from an equally intense stimulus of 1003 cycles (Shower and Biddulph). On the other hand the system must be highly damped for the subjective persistence of a discontinued sound is of very short duration, which enables us e.g. to distinguish clearly the slightly different tones of a rapid trill (up to 10 times a second).

The experiments designed by Hartridge in which a test-person noticed at a sudden phase-reversal of a steady tone a momentary period of silence (the "phase-change" beat), were taken as evidence of the transient arrest of some tuned resonant structure in the inner ear with less than critical damping. Many efforts were made to determine the damping factor of this resonant structure, but the values obtained do not represent the damping of the resonance-mechanism in the inner ear solely, because they concern the damping of the overall auditory mechanism, in which the physical characteristics of the whole sound-conducting apparatus, and the

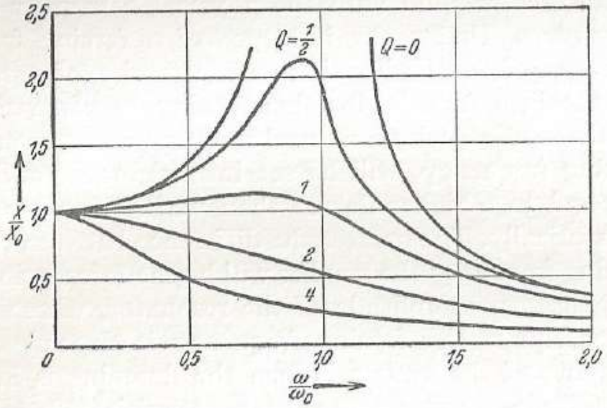

Fig. 18. Graph showing the amplified vibrations due to resonance. The amplitude is plotted against the frequency. The maximum displacement amplitude, which occurs at resonance, becomes less pronounced as the damping is increased (indicated by smaller values of the parameter Q). At critical damping amplification due to resonance is completely annulled. (After Trendelenburg).

behaviour of the central nervous system also play an important rôle.

Objective evidence of the phenomenon described by Hartridge was sought by means of the Wever and Bray technique (Hallpike, Hartridge and Rawdon-Smith (1)). It was shown that:

a. the cochlear response followed the phase-change accurately without any "silent period" — the mechanism in which these potentials are generated must therefore possess critical damping.

b. the action-potentials, however, showed some faltering in the response, comparable with the periods of silence reported in the subjective tests. From these experiments the authors concluded that the auditory action-potentials are generated by a structure possessing definite resonance — namely the basilar membrane (or rather the hair-cells on this membrane), whereas the cochlear microphonics arise in a structure possessing little mass and no resonance. Reissner's membrane, as a polarized membrane, was proposed as the most likely source. Stevens and Davis (1), however, adhering to the theory that the cochlear potentials are generated by the hair-cells of the organ of Corti maintain that this structure and the underlying basilar membrane are critically damped, and provide an alternative explanation of the "silent period" of the action-potentials.

Whether the damping of the resonance-mechanism is critical (as maintained by the American school) or not (as accepted by the English school) we are still facing the problem of a possible resonance-mechanism exhibiting apparently two incompatible properties, i.e. high selectivity and heavy or almost critical damping. A resonating system, however, if critically damped, loses its characteristic frequency and a set of such systems, if critically damped, can no longer act as a harmonic analyser (Tumarkin (1)).

Only two ways may lead out of this dilemma. We must either abandon the resonance-hypothesis (as is suggested by Stevens and Davis and others) or introduce alternative explanations. Ever since Max Wien in 1905 pointed to the paradox, attempts have been made to reconcile the heavy damping with the high selectivity of the ear.

Jung demonstrated that the combination of high selectivity and large damping may be realised in an electrical system. Recently TUMARKIN (1) argued that the heavy damping may not be solely due to frictional losses. Any other process which can irreversibly extract energy from a vibrating system will damp it. Tumarkin suggested that the greater part of the sound-energy dissipates by way of reverse radiation. The same impedance-matching function of the middle ear, which enables the ear to absorb energy so readily from the air, equally enables it to radiate energy back into the air. Thus even in the extreme case of a completely frictionless inner ear, giving ideal selectivity, the residual energy is expected to be so rapidly dissipated as to approach critical damping.

Another study dedicated to this problem was presented by GOLD and PUMPHREY. After discussing elaborately the physical properties of a system of mutually independent resonators, experimental evidence was submitted that the degree of resonance of the various receiving elements of the basilar membrane must be high. In the frequency-range from 1000 to 10.000 c/s the values found for the parameter Q, defining the quality of a resonant system, varied from 60 to 250. These values were taken as proof of a comparatively high degree of resonance of the receiving elements of the basilar membrane.

The authors strongly argue against the prevailing opinion of nearly critical damping of the basilar membrane, and the experimental data which have been supposed to be evidence of high damping of the cochlear structures were found to be irrelevant. It is stated that only the resonance-hypothesis of Helmholtz is consistent with the observations made and that the cochlea contains an array of linear resonant elements ranged in serial order of resonant frequency, and that these elements are the agents which individually excite those hair-cells of the organ of Corti which are in apposition to them.

In a subsequent paper GOLD dealt with the physical arguments against the resonance-hypothesis. If the cochlea is regarded as a 'passive' mechanism, whose elements are brought into mechanical oscillation by means of the incident sound-waves, the high viscous damping of the basilar membrane indeed presents an important physical argument against resonance of sufficiently high peak-values in such a small fluid-filled space.

If, however, this resistance may be counteracted by a supply of energy from another source (negative resistance), then oscillations with a high resonance peak-value again become possible. This is a well-known principle in radio-engineering, in which receivers employing it are called 'regenerative receivers'.

A similar 'regeneration'-mechanism is suggested by Gold to exist in the inner ear, the 'regenerating' forces being derived from the cochlear microphonic potential, which has hitherto been regarded as an unexplained by-product of cochlear activity. This supply of electrical energy may then be regarded as counteracting the high damping caused by the physical qualities of the basilar membrane and the fluid.

5. One of the basic principles on which the resonance-hypothesis was formulated, is the capacity of the ear to resolve a complex sound into its composing elements. Apart from the fact that many persons are unable to perform such an analysis, several observations have revealed that this analysing function is limited. The loudness of a tone of constant intensity and frequency may be considerably influenced by the presence of other tones. High-frequency tones are effectively masked by low-frequency tones, whereas conversely the low tones are but little influenced by the high ones. The loudness of the partials of a complex sound will thus be less than when they were sounded separately with equal intensity.

The investigations of SCHOUTEN, which confirmed the observations made by SEEBECK more than a century ago, have shown that for the subjective sound-analysis Ohm's law has but a limited validity, and that some extension is necessary to explain the phenomena first described by Seebeck and later again by Schouten. Should a periodic sound containing a great number of higher harmonics be presented to the untrained ear a sound of a sharp tone quality with a pitch equal to that of the fundamental tone is perceived. Now a suitably trained ear is able to perceive the lowest dozen harmonics separately in the sound. The higher harmonics, however, cannot be perceived separately but are perceived collectively as one component (which was called the 'residue') with a pitch determined by the periodicity of the collective waveform, which is equal to that of the fundamental tone. Schouten suggests Ohm's law of subjective sound-analysis to be extended as follows:

1. the ear analyses a complex sound into a number of components each of which is separately perceptible.

2. a number of these components corresponds with the sinusoidal oscillations present in the inner-ear sound-field. These components have a pure tone quality.

3. Moreover, one or more components may be perceived which do not correspond with any individual sinusoidal oscillation, but which are a collective manifestation of some of those oscillations which are not, or are scarcely, individually perceptible. These components (residues) have a sharp, impure tone-quality.

While numerous theoretical objections have been advanced against the resonance-hypothesis, clinical and experimental evidence is strongly favouring the conception of tonal localization in the cochlea (place-theory of frequency-reception). As evidence of such a spatial arrangement of the various tone-receptors in the cochlea may be mentioned:

1. *Embryologic evidence* — in the developing opossum LARSELL and co-workers found the appearance of the cochlear response to be closely correlated with the differentiation of the organ of Corti to an apparently functional stage. In this animal the development of this structure is not a simultaneous process. It was found that the organ of Corti reaches maturity first in the upper part of the basal coil of the cochlea. During the period in which the opossum continues to develop the differentiation of the organ of Corti extends both apically and basally from this initial zone. Functional activity of the cochlea was found to be closely related to the development of this sensory mechanism. The cochlear response begins on the fifteenth day and is at first limited to one frequency of approximately 1300 c/s. A spread of this response in both directions was noted on completion of differentiation of the organ of Corti.

2. *Histo-pathologic evidence* — by histologic study of a great number of human temporal bones CROWE, GUILD and POLVOGT were able to demonstrate that the lesions in the human ear, responsible for abrupt high-tone deafness, may be located in the basal turn of the cochlea.

3. *Evidence from prolonged stimulation with loud tones* — the observation of HABERMANN, who in a case of professional deafness found destruction of the organ of Corti, led to a great number of experiments, in which a more or less local destruction of the organ of Corti was obtained after long exposure to intense tones (WITTMAACK (1)). Mild degrees of damage are localized, but abnormally loud stimuli produce widespread damage. This damage tends to be located nearer to the helicotrema when caused by low tones, and nearer to the round window when caused by high tones. (Summaries of these experiments may be found with STEVENS-DAVIS and WERNER).

4. *Evidence from cochlear microphonics* — experiments made by various investigators (HALLPIKE and RAWDON-SMITH (2), CULLER, KEMP and JOHNSON) have demonstrated that each frequency is characterized by a focus of maximal electrical activity in the cochlea. Relatively greater potentials were obtained from the round window in response to high tones, and to low tones from the apex. CULLER in plotting the positions of optimal response for various frequencies was thus able to construct a map of the cochlea (fig. 19). Application of certain chemical substances to the round window resulted in an impairment of the response to high tones and a local destruction of the hair-cells in the basal turn of the cochlea (FOWLER and FORBES).

5. *Evidence from surgical lesions* — various attempts have been made to obtain impairment of cochlear function for particular tones by destruction of localized regions of the organ of Corti. The first experiments date from 1883, when BAGINSKY observed that removal of the apical turn of the cochlea in the dog resulted in the loss of response to low tones. HELD and KLEINKNECHT made little holes in the bony capsule over the spiral ligament, and by depressing this structure tried to distend locally the basilar membrane. In using Preyer's

reflex as an indicator of cochlear function they found a loss of response for certain tonal areas. These experiments were taken as confirmatory evidence for the resonance-theory of Helmholtz, as it was assumed that a local distension of the fibres of the basilar membrane was responsible for these tonal losses.

Similar experiments were performed by Walzl and Bordley in which small localized lesions were made in the cat's organ of Corti by drilling away the bony capsule over the spiral ligament without opening the endolymphatic space. Lesions in the basal coil caused high-tone loss, and lesions toward the apex caused low-tone loss. It was found that at threshold there is sharp localization of tones along the spiral organ, but that as the intensity is raised, there is spread of response to adjacent areas. In none of the experiments, however, was there a complete loss for any tone, though subsequent histological examination showed that the organ of Corti was completely destroyed at the site of operation.

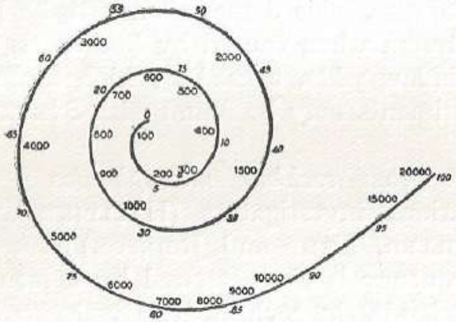

Fig. 19. Map of the cochlea indicating the position of maximum response to pure tones (from Fletcher).

The regions of optimal response for successive octaves were found spaced at equal distances along the organ of Corti. The results of these experiments are slightly at variance with the results of Culler's experiments, which indicated that the low octaves were relatively more and more compressed toward the helicotrema.

Additional evidence was obtained from psychophysical measurements, which led to the construction of maps almost identical to those derived from the physiological experiments (Fletcher (2), Stevens and Volkman).

On the basis of these independent supporting data it is now possible to accept with confidence the pitch maps of the cochlea. With the aid of these maps Fletcher has calculated the "auditory patterns" produced by various types of sound (fig. 20).

These experimental data, are thus all in favour of a fixed pattern of pitch-localization along the basilar membrane. A reservation must, however, be made as to the localization of very low tones (Symposium: "Is there localization in the cochlea for low tones?". Ann. Otol. 44, 1935). Whether this pattern is a vibratory pattern or a pressure-gradient pattern will be discussed in the following chapter.

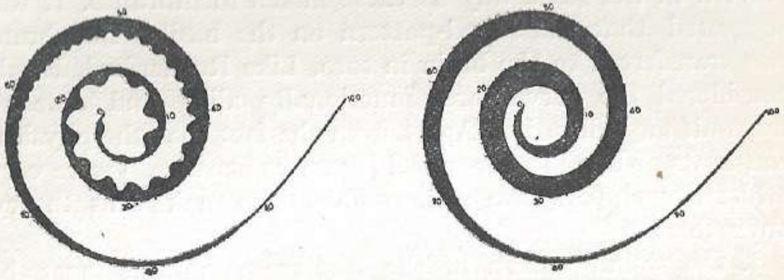

Fig. 20. Auditory patterns of steamboat whistle (left) and street noise (right) (from Fletcher).

The various objections raised against the resonance-theory led to the construction of other theories of hearing. The "telephone-theory" of Rutherford, first presented in 1886, assumed that the sound-pattern was transmitted directly to the auditory cortex, without being analysed by the cochlea. The overwhelming evidence in favour of localized pitch-perception in the cochlea makes this theory of historical interest only.

An experimental approach to the problem was made by Ewald (1) in 1899. A loosely stretched rubber membrane submerged in water was set into motion by means of tuning forks. Though the membrane had a longitudinal form and their dimensions were chosen as far as possible in accordance with those of the basilar membrane, Ewald failed to observe a local vibration-maximum as was suggested by Helmholtz. Instead, under the influence of a tone, numerous zones of maximal vibration were noted. Every tone was characterized by a resulting vibration-pattern of standing waves on these membranes. ("Schallbilder" or sound-patterns). With low tones the nodes of these waves lay farther apart than with high tones.

Ewald postulated that in the ear the basilar membrane reacted in the same way as these model membranes. It was suggested that the sound-pattern on the basilar membrane was transferred to the brain in toto. Like Rutherford, Ewald considered the nerve-fibres functionally alike and able to transmit any vibration. Apart from the fact that the physical constants of Ewald's ear-model ("camera acustica") were very arbitrarily chosen, two serious objections make this theory untenable:

1. the sound-pattern of the basilar membrane must be dependent upon the phase-relations of the component frequencies in a complex sound. A phase-shift of one of these components would cause a change in the pattern of vibration of the membrane and a consequent change in the sound-perception. This is not borne out by the experiments, which have demonstrated that the sound-sensation is independent of the phase-relations of the composing elements of a complex sound.
2. the various experiments respecting the localized pitch-perception in the cochlea are not in conformity, neither with Rutherford's nor with Ewald's theory.

Both the theory of Helmholtz and that of Ewald, formulated to explain the characteristics of the auditory organ, are based upon a particular mode of vibration of the basilar membrane. Whereas Helmholtz deduced this vibration-form by a physico-mathematical analysis, Ewald arrived empirically at an entirely different conception. Although Ewald endeavoured to deduce the vibration-form of his model membrane analytically, he does not seem to have succeeded in doing so. Koch, in a physico-mathematical treatment of Ewald's membrane, has tried to find out the reasons for the different mode of vibration in both theories. Helmholtz, in his calculations, proceeded from an elongated triangular membrane of constant mass and constant damping with no longitudinal tension, activated by a sinusoidal force, which affected the whole membrane equally. Only if the damping was small enough could a particular tone set into vibration a localized area of the membrane and only when these conditions are fulfilled will the membrane be able to react as a series of independent, parallel stretched chords (as the model membranes of Wagner have demonstrated). Should the physical constants be modified, however, the mode of vibration will also be different.

In the camera acustica of Ewald the periodic force acted perpendicularly upon the membrane, while the mass and damping could be regarded as constant. Only the tensions in radial and longitudinal directions probably differed little from each other. The vibration-form of the membrane now becomes totally different and it is clear that slight differences in the physical constants may entirely modify the result.

Koch, in his computation proceeded from a rectangular membrane with constant mass and damping, acted upon by a periodic external force. The longitudinal tension was taken as being very small compared with that of the radial tension. Koch, by applying the computations of Helmholtz along a boundary transition, showed that the difference between the two theories could not be due to a different form of the membrane.

According to him the different behaviour of the membrane in the two theories may be explained by taking into consideration the fact that Helmholtz used the natural periods of the different zones of the basilar membrane to explain its vibration-form, whereas in Ewald's experiments the lowest natural period of the membrane was higher than the frequency of the forcing vibration. According to the theory a standing wave-pattern may be formed on such a membrane, the vibration amplitudes of the waves being smaller towards the middle of the membrane, a fact which had already been observed by Ewald in his models. The physical properties, which the membrane had to possess, to allow the entire range of audiofrequencies to come to lie below the natural period of the membrane, were determined by Koch.

Whereas Ewald himself stated that the basilar membrane in the 'sound pattern'-theory is set into vibration by 'resonance' (in which no distinction was made between the forced vibrations in general, and the resonance-vibrations as a particular form of these vibrations), Koch renounced completely the conception of resonance-phenomena in the cochlea in response to tone-stimulation.

Though Koch's work must be regarded as an important contribution to membrane-vibrations in general, the various physical conditions in the cochlea were not fully recognised (e.g. the characteristics of a membrane vibrating in a fluid were not adequately examined) and the same objections as were raised against the theory of Ewald may be advanced against his views. The argument of a spatial distribution of tone-perception in the cochlea was met by GILDEMEISTER and KOCH by assuming that under certain conditions the greater part of the standing waves may be suppressed. These conditions are:

1. the membrane, on one short side, must end with a free edge.
2. the driving force must not act equally on the entire membrane, but only in the proximity of one of the short sides.
3. the damping must increase from one side to the other.

Whereas the first two conditions are satisfied by the anatomical structure of the cochlea, Gildemeister assumed that the damping increased rapidly in the direction of the helicotrema. It was held that under these conditions a series of standing waves will be formed along the basilar membrane, with rapidly decreasing amplitude towards the helicotrema. This decrease in amplitude will entirely depend upon the damping of the system, which is determined by the viscosity of the fluids, the mass of the membranes and fluid as well as by the tension of the basilar membrane. This damping was regarded as being so high that in all probability only one, or at the most two vibration-maxima are found.

Since the distance of the nodes of these waves is inversely proportional to the frequency, the lower the forcing frequency is, the further will the first, and practically the only, maximum of vibration be located from the oval window.

In this way the theory, like that of Helmholtz, may furnish an explanation of the sound-analysis, the phase-independence of the sound-sensation and the tonal localization, based upon the theory of forced vibrations, without making use of the special case of resonance-vibrations.

This theory forms a gradual transition towards the group of hydrodynamic theories, which will be discussed in the next chapter.

CHAPTER VI

HYDRODYNAMIC THEORIES RESPECTING FREQUENCY-ANALYSIS IN THE EAR

Helmholtz as well as Ewald assumed that a particular mode of vibration of the basilar membrane was responsible for the sound-analysis in the inner ear. In their statements they almost entirely ignored the movements of the cochlear fluid. Helmholtz merely wrote: "the fluid of both cochlear galleries must also be considered as weighting the membrane, because it cannot move without a kind of wave-motion in that fluid", but Helmholtz does not mention either the true nature of this wave-motion, or the way in which the different parts of the membrane are set into vibration by a displacement of the fluid. Though Ewald's membrane was made to vibrate under water, the way in which the membrane was set into motion by a periodic force was not indicated by him. If, however, the sound-vibrations set the basilar membrane in motion, this is only possible through a movement of the fluid, as both the basilar membrane and the fluid are to be considered as a coupled system. When a vibrating system is coupled to another system the motion of the first system is communicated to the second, and the second system is said to execute a forced vibration. A study of the movements of the basilar membrane will thus be impossible without considering in detail the movements of the inner-ear fluid.

Hydrodynamic- or "Wave"-theories:

Four theories, which originated almost at the same time at the end of the last century, constituted the first attempts to deduce the motion-form of the basilar membrane from the movements of the cochlear fluid (Hurst, ter Kuile (1, 2), Bonnier, Meyer). These theories are similar in that they attempt to analyse the possible movements of the basilar membrane resulting from a wave-front initiating at the stapes.

If the stapes is pressed deeper into the oval window by a positive pressure in the external auditory canal, it will tend to compress the perilymph in the scala vestibuli. The fluid will then try to escape by virtue of its relative incompressibility. For slow movements the fluid may find a way of escape through the helicotrema, but with rapid vibrations of the stapes the frictional resistance in the narrow part of the cochlea and the inertia of the mass of fluid in the apical turns make an alternative pathway necessary. Since it is held that the walls of the cochlea are rigid the pressure can only be relieved by bulging the basilar membrane into the scala tympani, whilst the pressure in the scala tympani is relieved by a yielding of the round window membrane into the middle-ear cavity. The elastic qualities of the basilar membrane will tend to counteract this bulge by bringing pressure to bear on a contiguous part of the membrane. On account of the increasing width of the basilar membrane, and its accompanying decrease in elasticity, a travelling wave is thus generated along the membrane (like a pulse-wave is propagated along the arterial wall). The different writers, however, diverged in their opinion about the progress of this wave and the way in which the frequency-analysis was effected (summaries: Waetzmann (1) and Bast-Shover). Although these theories refuted the conception of a frequency-analysis in the ear by resonance, they were little more than theoretical attempts to take into account the existence of a wave-motion in the perilymph ("wave theories" or "hydrodynamic theories"). No physico-mathematical treatment or experimental evidence, however, supported these theories.

Only when all physical constants having influence on the movements of the fluid and membranes in the cochlea are known, will we be able to form a clear concept about the hydrodynamic behaviour of the cochlea. The small dimensions and the inaccessability of the cochlear system make an exact determination of these factors as yet extremely difficult and so little is known about their values that in theoretical statements on this subject, rather arbitrary values for these magnitudes were usually introduced.

During recent years, however, many experimental and theoretical attempts have been made to solve the problem of the mechanism of the inner ear by a better evaluation of the various physical constants involved.

In 1928 the Hungarian physicist von Békésy (1) made an experimental approach to the problem with the aid of a simplified model of the inner ear. The considerations which led to the construction of this model were summarized as follows:

"The essential difference between the various theories is that on all occasions different values were accepted for the mechanical properties of the basilar membrane, the elasticity and friction. This made it possible, that for the same size of the membrane and the same way of stimulation all possible vibration-forms of the membrane were represented. Only when the vibration-form of the basilar membrane is known will we be able to accept a particular theory. As the direct observation of the vibrations of this membrane in the cochlea meets with exceptional difficulties, an ear-model is first constructed, which must be adapted by all possible means to the original circumstances, if the results obtained are to be decisive".

Models of the cochlea had been made earlier than this, in order to study the vibration-form of the basilar membrane. In 1899 Ewald was the first to construct a model in which the basilar membrane was represented by a rubber membrane ("camera acustica"). The model of Wilkinson (1), illustrating the resonance-theory of Helmholtz, consisted of a series of separate chords of phosphor bronze, making it possible to vary the tension and consequently the natural period of these chords by loading them with small weights. The various resonators were connected by a gelatinous layer, thus giving a certain resemblance to the basilar membrane.

Various other models were constructed to study the behaviour of the inner-ear fluid, but the physical constants of the inner ear and of the model, however, usually bore such little resemblance to each other, that the true motion-form of the basilar membrane could hardly be inferred from the results obtained.

v. Békésy attempted to circumvent this difficulty by bringing into accordance as far as was possible the physical constants of the model and those of the inner ear.

1. *Geometrical resemblance* between inner ear and model. This demand could not be fully satisfied owing to the small dimensions of the cochlea. An enlargement of the model of 4 to 5 times was necessary. The spirally coiled cochlea was represented in the model as a straight double canal. A further simplification was the omission of Reissner's membrane and consequently of the cochlear duct containing the endolymph. In later models v. Békésy again introduced this membrane, which, however, but little influenced the mode of vibration of the basilar membrane.

2. *Hydrodynamic resemblance* — in order to maintain an accurate correlation between the cochlear fluid and the fluid in the model some of the physical characteristics of the perilymph were determined by v. Békésy (viz. its density and viscosity).

It was found that the density of this fluid is 1,034 grams/c.c. at 37° C and its viscosity 0.0197 cgs. units. According to v. Békésy accurate hydrodynamic correspondence between cochlea and model was obtained if the viscosity of the glycerine solution, used in the models, amounted to approximately 4 times that of water.

3. *Resemblance in elasticity of the membranous partition.* Since the vibration-form of the basilar membrane is mainly determined by its elasticity, its characteristics had to be accurately imitated in the model. We have no information on the tension of the basilar membrane in the living, although Berendes did carry out a few measurements in the basal turn of the cochlea on human cadavers. In some way or another v. Békésy had to bring into alignment the tensions of the model membrane and the basilar membrane. For this purpose he made use of the experiments of Wittmaack (1) and others, in which localized lesions of the basilar membrane and the organ of Corti in animals were caused by exposure to very strong sound-stimuli over a long period of time.

In a similar way circumscribed holes were produced in the model membrane as a result of strong vibrations of the "stapes". The localization of these holes depended upon the frequency of the sound-stimulus and the mass of the membrane. As long as the membranes were thin, irregular holes occurred in the narrow part of the membrane (near the "stapes"). When the membranes were made thicker, the number of holes was limited to one, which with increasing thickness shifted its position in the direction of the helicotrema. With constant thickness of the membrane and constant frequency the hole always occurred at the same place. The thickness of the membrane was selected in such a way that the location of the hole at a certain frequency corresponded with the damaged area in the animal experiments.

Two vibrations of slightly different frequency also produced two holes near together, leading to the conclusion that even considerable irregularities of the membrane do not essentially affect the movement of adjacent areas.

This simplified model in some ways corresponds more accurately to the natural basilar membrane than did Ewald's membrane, which with a small irregularity no longer exhibited good "wave-patterns".

The model of v. Békésy:

The actual model consisted of an oblong brass box sealed on both sides by glassplates. A thin metal partition separated the cavity into two equal parts ("scalae"). In this partition a long wedge-shaped opening was covered with a rubber membrane ("basilar membrane").

The two separate parts communicated by an opening at the end of the membrane ("helicotrema"). On the outside the "scalae" were shut off by rubber membranes ("windows") and a short metal shaft ("stapes") was attached to one of the membranes. The whole cavity was filled with fluid, the viscosity of which was regulated by the addition of glycerine. In this fluid were suspended fine coal-dust and gold-particles in order to visualize its movements.

It was shown that when the stapes was set in motion, the powder suspended in the fluid was brought into violent movement. From a further analysis of this movement v. Békésy inferred that series of waves sweep progressively along the membrane in the direction of the "helicotrema". Since, even with high magnification and sufficiently high frequency, no movement of the fluid was noticed near the "helicotrema", it was assumed that these waves were highly damped.

The motion of the membrane, however, tends to produce small vortices, or eddies, in the fluid at a certain position on either side of the membrane. The diameter of these eddies was always equal in magnitude to the height of the fluid-column above the membrane, whereas their angular velocity appeared to be proportional to the amplitude of movement of the "stapes" (fig. 21).

With a change of the stimulating frequency a shifting of these eddies was noticed, high frequencies tending to produce eddies in the neighbourhood of the stapes and low frequencies in the region of the helicotrema.

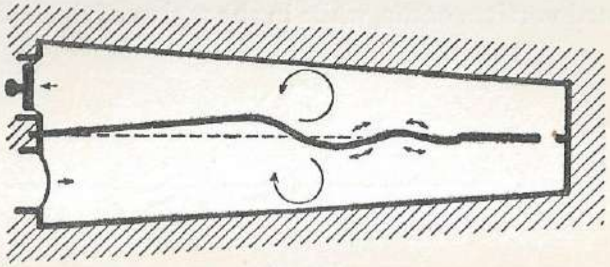

Fig. 21. v. Békésy's model of the inner ear.

A more detailed analysis of the movement of the membrane was made possible by stroboscopic illumination. It was shown that the membrane did not vibrate in standing waves, but that travelling waves spread along the membrane in the direction of the helicotrema.

With a momentary aperiodic outward displacement of the "stapes" the first part of the membrane momentarily bulges up, while the region in the neighbourhood of the helicotrema remains in rest. After the "stapes" has swung back this part also swings back aperiodically to its position of rest, whereas a flat travelling wave is generated spreading towards the helicotrema. This wave is highly damped, and only with very low frequencies is the wave reflected at the helicotrema and are standing waves generated in the apical portion of the membrane.

If the stapes is allowed to make a complete single vibration the first part of the membrane exactly follows the movement of the stapes and moves in almost equal phase. At the region of maximal displacement a phase-shift occurs and from this point two or three highly damped travelling wave-peaks may be observed. If elasticity and damping are well-chosen these waves may even be fully suppressed, which apparently seems to be the case in the cochlea. The velocity of propagation of the travelling wave tends to decrease rapidly in the direction of the helicotrema.

At the position of maximal displacement the abovementioned vortices occur, while in the region of the helicotrema the fluid is only moved to and fro by the highly damped travelling waves (fig. 22).

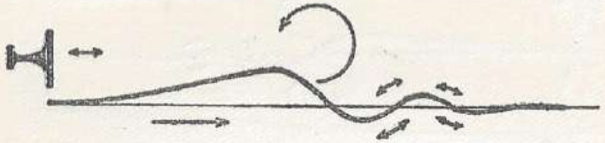

Fig. 22.

v. Békésy subsequently tried to verify this mode of vibration of the basilar membrane in dissected human ears. The apical cochlear turn of freshly prepared human temporal bones was exposed, so that approximately one third of the basilar membrane could be observed, without damaging the delicate structures of the cochlear duct. Fine coal-dust was suspended in the cochlear fluid to visualize the transparent membranes. A small glass tube, provided at one end with a rubber membrane was inserted into the oval window, and the membrane set into motion by the strong vibrations of a 200 c/s tuning fork. With stroboscopic illumination travelling waves were observed, but owing to the high damping only a singular and simultaneous movement of both membranes occurred. At high frequencies the only visible part of the apex of the inner ear remained quiet. The observations on the model were thus confirmed under more natural conditions.

In v. Békésy's model the whole membrane vibrated at not too high a frequency with a high, nearly critical damping, which could be further enlarged when Reissner's membrane was imitated and the space between both membranes ("ductus cochlearis") was filled with a viscid liquid. v. Békésy thus regarded the cochlea as being a frequency-analyser with a very high, almost critical damping and this theory of frequency-analysis was called the '*theory of aperiodic analysis*'.

The position of maximal displacement of the membrane and consequently of the eddies is determined by the stimulating frequency. Both the maximal displacement of the membrane and the angular velocity of the eddies are directly proportional to the stapedial movements. The periodic movements of the stapes are thus transformed into an aperiodic whirlpool movement; or in other words are rectified in the ear.

v. Békésy explained the formation of these eddies by assuming the membrane to consist of a great number of radial sections of constant width, but varying in length along the membrane. The various sections with their corresponding fluid columns were regarded as separate "resonators" with decreasing natural periods in the direction of the helicotrema. As long as these natural periods are higher than the stimulating frequency the membrane moves as a whole. Where this frequency corresponds to the natural period of one of the sections of the membrane, a local vibration maximum occurs. If a sinusoidal force activates such a system of "resonators" their amplitudes of vibration at successive intervals during one complete cycle of a steady tone may be represented by fig. 23.

On outward movement of the stapes the basilar membrane momentarily bulges up to its maximal position, whereas on inward movement of the stapes the membrane bulges into the scala tympani until it again reaches its maximal excursion. From the interjacent curves it appears, that during this movement of the membrane the fluid to the left will be moved in the direction of the arrow. When the membrane moves back the dotted curves show that an equal amount of fluid will be shifted to the right. Thus a constant flow of fluid in the direction of the lower tuned "resonators" will occur at the position of maximal displacement of the membrane. The displaced fluid must flow back at another point, thus giving rise to the whirlpool movement. On the other side of the membrane a similar process occurs only in an inverted direction.

v. Békésy suggested that the pressure exerted by the eddies against the cochlear duct might form the adequate stimulus for the organ of Corti.

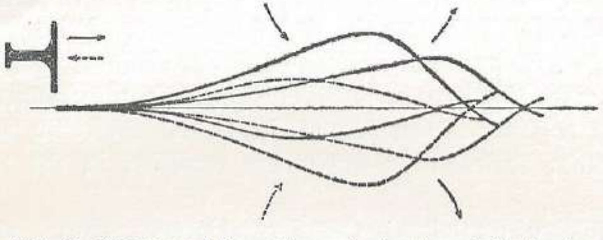

Fig. 23. Diagram of the pattern of vibration of the basilar membrane during one complete cycle of a steady tone (After v. BÉKÉSY).

Mathematical treatments of the hydrodynamics of the inner ear:

Various attempts have also been made to treat the hydrodynamic behaviour of the cochlea from a theoretical point of view.

KUCHARSKI, in a mathematical treatise, computed the wave-propagation in a theoretical model corresponding as far as possible with the original conditions in the cochlea. The variable elasticity of the cochlear partition was taken into account, with the result that travelling waves were found to have a local vibration maximum, the position of which was governed by the frequency.

Travelling waves with maximal displacement at a certain position were also found by FLETCHER (1) in a theoretical study of the mechanics of the inner ear.

Another extensive theoretical study, in which the experimental results of v. Békésy were treated mathematically, was made by RANKE (1, 2).

Ranke proceeded from the assumption that the cochlea may be compared with a hydraulic system contained in a tube with elastic walls. To such a system may be applied the theory of propagated disturbances in fluids constrained by elastic boundaries.

Generally sound-waves in a fluid propagate in the form of compression-waves. As the wave-lengths of these compression-waves, even for the highest frequencies, are large relative to the dimensions of the cochlea, (at 20.000 c/s the wave-length in water is still 7.25 cm) the adherents to the resonance-theory generally assumed that with a sound-vibration the fluid in the cochlea moved as one mass. On that count wave-movements in the cochlear fluid were held to be impossible. Though the theories of ter Kuile, Meyer, Hurst and Bonnier were a first attempt to consider wave-movements (in the form of travelling waves) in the cochlea, they possessed little conclusive power, because they lacked every physico-mathematical foundation. Now Ranke made a definite distinction between compression-waves and "Schlauchwellen", by which the first are propagated on account of the compressibility of the fluid and the second on account of the elasticity of its boundaries.

The cochlea now may be considered as a tube with a partially elastic wall (scala media) so that "Schlauchwellen" may be produced in the inner ear by an oscillatory movement of the stapes. Whereas the wave-lengths of the compression-waves of the acoustic frequencies are large in comparison with the dimensions of the cochlea the wave-lengths of the "Schlauchwellen" can only be computed if the various physical constants of the cochlea viz. its dimensions and shape, the density of the perilymph, and the elasticity of the basilar membrane, are known.

RANKE made use of the computations of FRANK (2) regarding the pulse-wave, which were concerned with the waves occurring under the influence of a periodic force and long wave-lengths in a cylindrical vessel with elastic walls.

In the blood-vessels with practically incompressible content travelling waves also occur, which propagate on account of the elasticity of the wall of the vessel. The conditions in the cochlea, however, differ considerably from the fundamental conditions set by Frank. The cochlea consists of a narrow double-canal with a partially elastic wall, whereas the diameter of the scalae decreases from base to apex and the elastic partition broadens in the same direction, owing to which the physical characteristics of the canal continually vary.

Ranke first proceeded from a double-canal with invariable diameter and constant dimensions of the elastic partition. In considering the membrane as being composed of two parts, of which each layer cooperates with the adjoining fluid in the corresponding canal, the computations of Frank may be applied to the cochlea.

If the anatomical dimensions of the cochlea, such as the diameter of the scalae and the length of the basilar membrane: and the physical characteristics, such as density of the perilymph and the mass and elasticity of the basilar membrane are known, the wave-lengths and speed of propagation of these waves in the cochlea may be computed. Whereas the anatomical dimensions and the density of the fluid are approximately known, information about the tension of the basilar membrane is hard to obtain.

Ranke estimated this tension, by assuming that it could not be more than the breaking strain of the fibres of connective tissue, namely 500 kg/cm^2 (it will probably be considerably less). With an estimation of the tension at a maximum of 500 kg/cm^2 and a minimum of 50 kg/cm^2 the wave-lengths of the acoustic frequencies could be calculated as follows:

frequency	tension 500 kg/cm^2		tension 50 kg/cm^2	
	at base	at apex	at base	at apex
20	2650 cm	20 cm	835 cm	6.3 cm
10.000	5.3 cm	0.04 cm	1.67 cm	0.0126 cm

From this it appears, that the wave-lengths of these waves are generally small, not only with respect to the total length of the cochlea, but also with respect to the diameter of the scalae.

For each frequency the wave-lengths rapidly decrease from base to apex. According to Ranke we may thus expect in the cochlea, for the major part of the tonal range, wave-lengths that are long at the base and short at the apex with respect to the diameter of the scalae. Since the computation of Frank was only valid when the wave-length was long in proportion to the diameter of the canal, Ranke has examined the differences from the theory of Frank that appear when the wave-lengths become short. He arrives at the following conclusion:

The velocity of propagation of "long" waves is for each arbitrary canal with partially elastic walls independent of the frequency. As soon as the wave-length with increasing frequency approaches the value of 2π the diameter of the scale the velocity of propagation diminishes, to decrease rapidly for shorter wave-lengths. The bigger the canal is with respect to the width of the membrane the greater will be the fall in the velocity of propagation. Now Ranke has attempted to explain the behaviour of these "short" waves with the aid of the phenomena of surface-waves.

"Short" waves only set the water in motion superficially, whereas "long" waves effect the water to a greater depth (waves of ship-length are only possible in open sea, whereas in a shallow pond only small wave-lengths occur). Ranke thought to be able to convey these differences, without too many difficulties, to the double-canal of the cochlea. Whereas the "long" waves at the base of the cochlea set in motion the whole fluid content, the fluid movement is entirely limited to the direct neighbourhood of the elastic membrane as soon as the wave-lengths are short with respect to the diameter of the canal. At the point of the canal where the wave-lengths and the 2π diameter of the canal correspond, the lines of flow are forced to curve off in the direction of the membrane (fig. 24). In this transition-area various hydrodynamic forces arise, to the right of this area an over-pressure, and to the left an under-pressure or suction (see arrows). These forces form together a rotation-moment that will set the fluid into a rotatory motion. They always act in the same direction, that is to say they do not change with the phase of the frequency. There arises in this way a rectifying effect in the sense of v. Békésy. The magnitude of these forces, and consequently the angular velocity of the eddy, is dependent upon the amplitude of the stapes, whereas the position of the eddies is determined by the stimulating frequency.

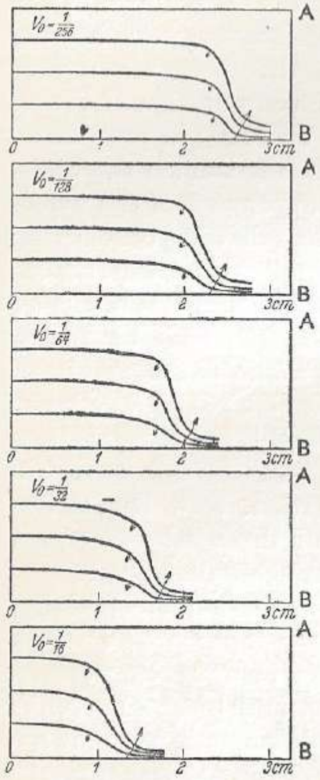

Fig. 24. Diagram of the transition-areas for various frequencies according to Ranke. The arrows indicate the direction of pressure on the fluid (from Ranke).
A — wall of the canal;
B — membrane.

Ranke suggested that a shift of the tectorial membrane in longitudinal direction with respect to the basilar membrane, caused by the pressure-gradient in the transition-area might form the proper stimulus for the sensory cells of the organ of Corti.

The hydrodynamic computations of Ranke made it possible to give a satisfactory explanation of various well-known facts concerning the hearing function, e.g.

1. the frequency of a tone determines by a series of travelling waves the position of the "transition-area" with its over- and under-pressure. Low tones give rise to a "transition-area" at the apex, high tones to one at the vestibulum;
2. the loudness of a tone corresponds with its amplitude of vibration. Over- and under-pressure are directly proportional to this amplitude;
3. the selectivity is almost independent of the damping, as it is only determined by the pressure-gradient in the transition-area; which in turn depends upon the changes in the volume-elasticity coefficient of the membrane and the diameter of the scale. The principal objection of Wien against the resonance-theory thus loses its importance;
4. at least 8 octaves of the audiofrequency range starting with a tone of 20 c/s, produce waves in the cochlea, which have their first vibration maximum on the basilar membrane.

Ranke's computations thus led to a physico-mathematical explanation of the local vibration maximum on the basilar membrane, in response to stimulation by a continuous tone, and the occurrence of eddies in the adjoining fluid, as was found experimentally by v. Békésy. In various aspects, however, the conceptions of these authors are at variance. Whereas v. Békésy still assumed that the localization of pitch-perception in the cochlea was achieved by resonance-phenomena in the basilar membrane, Ranke argued that physical resonance of parts of the basilar membrane in the way that Helmholtz proposed, is impossible. The system does not possess definite natural periods but may vibrate with all frequencies, without one frequency being selected.

According to Ranke the part of the membrane between the stapes and the transition-area vibrates in almost equal phase. In an elastic tube an equal-phase vibration means a standing wave. Since a standing wave is generally attained by reflection of a travelling wave, Ranke considered the region where the waves curve off from the canal wall as the reflection-area. Because reflection at a denser medium increases the pressure-amplitude of the wave at the reflection-area the maximal displacement of the membrane in this area can be readily explained.

In his experiments v. Békésy, however, found no standing wave with a node at the transition-area, as was suggested by Ranke.

Whereas v. Békésy supposed that the eddies, observed in model and cochlea exerted a pressure upon the structures of the cochlear duct, Ranke maintained that these eddies cannot exert a pressure, but must be regarded as the result of pressure-disturbances generating in the cochlea during sound-stimulation. The resulting forces, acting as rotation-moments, are responsible for the formation of the eddies.

The eddies may therefore be regarded as secondary phenomena having no influence upon the various processes of the inner ear.

In his computations Ranke attached great importance to the diameter of the scalae. Later experiments of v. Békésy (12) have, however, shown that the influence of the dimensions of the cochlea is of little importance on the vibration-mechanism of the inner ear.

Another attempt to treat the cochlea as a hydrodynamic system contained in a conical vessel with a partially elastic wall along which a pressure-disturbance is propagated, was made by Reboul (1, 2).

In making reasonable assumptions for the various physical constants of the cochlea Reboul deduced a differential equation relating the displacement of the membrane at any point with the velocity of the wave at that point. For, owing to the variability of the elastic partition and the diameter of the vestibular scale, the speed of propagation of the pressure-pulse in the cochlea may not be regarded as being constant. This speed is greater at the stapes and diminishes steadily in the direction of the helicotrema. It was calculated that points of peak-displacement occur at positions governed by the frequency of the stimulating tone. In addition to the maximal displacement there is a maximal pressure-gradient across the membrane, the location of which is also governed by the frequency. This pressure-gradient will not be in the same phase and at the same position as the displacement of the membrane. Reboul suggested that this pressure-gradient constituted the adequate stimulus for the organ of Corti rather than the displacement of the membrane. It was further shown that at low frequencies the basilar membrane is displaced "like a vibrating reed". The sound-analysis can only be accomplished in this case by the time-pattern in the brain, as was suggested by the telephone-theory of Rutherford. At higher frequencies the membrane shows maximal displacement at a point which moves steadily downwards to the stapes as the frequency rises, thus conforming with the general conception of a distribution of pitch-perception along the basilar membrane.

The various theories considering the acoustic stimulus as a propagated disturbance in an elastic tube, give a different explanation of the movements of the fluid and the basilar membrane. Although these theories generally state that a local vibration maximum occurs in response to a steady tone, they are not in complete conformity with the experimental findings of v. Békésy.

Zwislocki, who recently again dedicated an extensive study to this problem, subjected the existing theories to a critical discussion and concluded that none of these theories can be regarded as adequate. He also considered the propagation of vibrations in the cochlea to be of a predominantly hydrodynamic nature, exhibiting great similarity to that of surface-waves arising at the interface between two liquids. In contrast to an ideal surface, in which only capillary forces with an elastic character are concerned, the surface in the case of the cochlea is represented by the ductus cochlearis, which possesses both mass and damping. In addition, its elasticity is subject to local variations, a fact which is responsible for the specific character of vibrations in the cochlea. Zwislocki deduces a dynamic differential equation containing all the physical factors influencing the propagation of vibrations in the cochlea. This differential equation is independent of the shape of the canal and the course of the vibrations with respect to time.

The factors contained in the equation are:

1. the density and viscosity of the perilymph;
2. the dimensions of the canal;
3. the impedance of the ductus cochlearis — in evaluating the components of this impedance, viz. its mass, damping and elasticity, Zwislocki for the first time gave a detailed description of the dynamic behaviour of the ductus cochlearis.

The damping and elasticity components were taken from the experiments of v. Békésy (13).

This investigator found in human temporal bones a logarithmic damping factor of 1.4 to 1.8 independent of frequency for the vibrations of the basilar membrane. The mass and damping may thus be regarded as constant for the entire length of the canal. The elasticity, however, diminishes rapidly as the distance from the base of the cochlea increases. v. Békésy (14) determined the volume-displacement and accordingly the elasticity of the cochlear partition over its entire length. It was shown that the flexibility of this partition increases from base to apex in a rate of approximately 1 to 100.

An approximate solution of the differential equation of the cochlea shows that the amplitude and wave-length of the waves which are propagated in the cochlea change without discontinuity. A single local vibration maximum is produced. This requires neither resonance nor wave-reflection within the ductus cochlearis. The maximum is caused by the combined effects of the inconstant flexibility of the basilar membrane and its damping. It occurs at a point where the impedance of the ductus cochlearis possesses an elastic character and, on account of the presence of damping, cannot arise at the point of resonance.

The flat local vibration maximum moves down from the apex to the base as the frequency increases, which accounts for a frequency-analysis in the cochlea. This can only be a rough resolution of frequencies and it appears necessary to accept a finer frequency-analysis in the central nervous system, as was already suggested by v. Békésy (2).

This calculation leads to results which are in better agreement with the experimental findings of v. Békésy than former theories.

Zwislocki further demonstrated that the eddies which occur at the place of maximum vibration, as was demonstrated by v. Békésy, have a mathematical foundation.

They are to be attributed to quadratic terms in the hydrodynamic equations, which at the amplitudes occurring in acoustics, represent small magnitudes of the second order. Accordingly, the eddies are to be regarded as a secondary phenomenon having no noteworthy influence upon the other processes.

Zwislocki refutes the possibility of a stimulation of the sensory cells by a pressure exerted by the eddies (v. Békésy), or a displacement of the membranes caused by a pressure-disturbance at the vibration maximum (Ranke), but draws attention to the forces of mass arising in the ductus cochlearis.

As a final conclusion about this group of theories we may quote Stevens and Davis (1, page 445) where they state that: "These theories regarding the dynamics of the cochlea which consider the acoustic stimulus as a propagated disturbance in an elastic tube, rather than as a forced vibration impressed upon a set of resonators, have the additional advantage that they enable us to see how the cochlea can behave as an analyzer in spite of a large damping factor. A simple system which is critically damped will not have a maximum in its resonance-curve and a set of such systems could not, therefore, serve as an analyzer. Hence if we were to treat the cochlea as a set of resonant systems, we should have to assume a damping less than critical. No such restriction is necessary, however, when we treat the cochlea as a hydrodynamic system in an elastic tube, for a maximum of displacement of the basilar membrane can be obtained in spite of a large damping factor. Thus it is possible for the basilar membrane to act as an analyzer, and at the same time show no free vibrations after a stimulus has ceased".

By inserting small manometers into the cochlea of human temporal bones, which made it possible to register the pressure-variations in the scala vestibuli, Schulze attempted to provide experimental evidence of a local increase of pressure, as was suggested by v. Békésy and Ranke to occur in the cochlea during sound-stimulation. At various positions along the cochlear turns drillholes were made, without damaging the middle- and inner-ear structures.

At a distance of 8 mm from the oval window a maximum was found for a tone of 580 c/s, at 12 mm for 270 c/s, whereas a frequency of 140—150 c/s caused a pressure-maximum at a distance of 18—19 mm from the oval window. From these experiments it was inferred that the vibration maxima for the high tones are relatively compressed in the basal coil of the cochlea.

In comparison with the overwhelming evidence in favour of a fairly regular distribution of pitch-perception along the basilar membrane, the experiments of Schulze do not indicate a definite correlation between the pressure-maxima and the various tone-perception areas in the cochlea.

Two-place theories of hearing:

Though the results of various animal and psycho-physical experiments are highly favouring a one-place theory of pitch-perception some psycho-acoustic phenomena are difficult to explain by the acceptance of one local stimulation-mechanism in the inner ear.

Experiments on the fatiguing effect of prolonged tone stimulation led GÖRAN DE MARÉ to the construction of a two-place theory of hearing, which was based on the experimental results of v.Békésy and the theoretical computations of Ranke. It was demonstrated that on pure tone stimulation there is a rapid decrease in the perception of the stimulating tone. The subjective harmonics, however, which attained a considerable loudness, with the intensities employed for the stimulating tone, did not give rise to any "fatigue"-effect.

It was assumed by Göran de Maré that the decrease in loudness of the test-tone was due to the receptive elements being adapted to the pressure of the eddy, whereas the subjective harmonics are not generated by an eddy-pressure but by a so-called phasic stimulation-mechanism, that is, by that part of the organ of Corti that is situated between the stapes and the position of the eddies.

It was further stated, that the structure of the inner ear and the different innervation of inner and outer hair-cells (LORENTE DE Nó (3)) suggests that the former are chiefly stimulated by the eddy-pressure, the latter by the phasic stimulation-mechanism.

v. Békésy had already suggested that with a tone of 125 c/s the eddies occur right down at the helicotrema. For frequencies lower than 125 c/s it was assumed that a movement of the whole fluid and a corresponding movement of the whole basilar membrane would occur, and that the pitch of these tones was determined by the time-pattern in the brain.

In this case only the phasic stimulation-mechanism of de Maré would be active.

On account of their experiments on the effect of stimulation with very intense tones on the hearing function RUEDI and FURRER also described a two-place theory of hearing. It was suggested that pitch-perception only occurs in the inner hair-cells, whereas the sound-intensity was only perceived by the outer hair-cells.

This theory was also based on the difference in innervation of both groups of cells. This distinction in function between inner and outer hair-cells was already suggested in 1936 by LURIE (1), though this author started out from entirely different premises.

CHAPTER VII

BIOPHYSICS OF THE CONDUCTION OF SOUND IN THE EAR

The study of the physiology of the sound-conducting apparatus has furnished many interesting data regarding the way in which the system responds to the air-conducted sound-vibrations.

Since it has been established that the system may be regarded essentially as a complicated mechanical system, capable of vibration, the entire mechanism will now be considered from a physical point of view. After a discussion of the characteristics and the physical behaviour of acoustic receivers in general, the physical properties of the ear, as a special form of acoustic receiver, will be dealt with.

I. Some physical aspects of sound-receivers.

Electrical, mechanical and acoustic impedance.

According to Ohm's law in a direct current circuit the current is determined by the electromotive force (E.M.F.) and the resistance (R): Current = E.M.F./Resistance, i.e. $I = E/R$ or $E = I.R$

Ohm's law can be generalised in order to include alternating current circuits. In this case the maximum values of both current and E.M.F. must be introduced into the formula, since both magnitudes are a function of time (sine-function). The generalised resistance is in this case called the impedance. It is dependent upon the elements composing the circuit, and as a rule upon the frequency. For example in the case of a series connection of a self-inductance, a condenser and an ordinary resistance, the impedance has the formula:

$$Z = \sqrt{R^2 + (\omega L - 1/\omega C)^2} \text{ in which}$$

ω = circular frequency = $2\pi f$,
L = the coefficient of self-inductance,
C = the capacity of the condenser.

For a certain value of ω, ωL and $1/\omega C$ will be equal and for that frequency $Z = R$. The impedance is now a minimum and therefore the current is maximal, if the voltage is kept constant. This is called the phenomenon of resonance.

Where in an alternating current circuit the current is influenced by the impedance, similarly any oscillating mechanical system presents a certain resistance or an impedance to vibratory energy delivered to it (mechanical impedance).

If a steady, non-oscillatory force acts upon an elastically fixed mass (e.g. a mass attached to a steel spring) the displacement is proportional to the applied force (Hooke's law). The displacement in the case of a constant force will depend upon the stiffness of the spring which tends to restore the mass to its original position (stiffness = the restoring force per unit of elongation).

When a periodic force is allowed to act upon this system the displacement will be almost equal to that in the case of the constant force, as long as the period is great in comparison to the natural period of the system. The stiffness is determinative for the displacement of the system, or the system is said to be stiffness-controlled.

If the frequency of this to-and-fro motion is increased beyond the frequency where the system is stiffness-controlled, and the amplitude of the driving force is kept constant, the displacements of the system will become gradually larger. Maximal displacement amplitude occurs when the forcing frequency equals the natural frequency of the system. ($\omega L = 1/\omega C$). In this case another force opposing the vibrations of a mechanical system, i.e. the frictional resistance offered by the medium in which the system is vibrating, constitutes the limiting factor for the vibration amplitude of the system, which is now said to be friction- or resistance-controlled. With increasing frequency of the driving force the mass, which must be accelerated each time, presents a considerable inertia; at sufficiently high frequencies the stiffness forces, as well as the resistance forces, are negligible in comparison with these inertia forces. The system is now said to be mass-controlled (fig. 25). With very high frequency of vibration (frequency ∞) the amplitude of the system will decrease to zero.

Vibrating mechanical systems can be treated mathematically along the same lines as electric systems. If the following transformations are made the equations of vibration of these systems are analogous to the equations of alternating current circuits:

electrical		*mechanical*	
Current	I	Velocity	V
E.M.F.	E	Force	K
Resistance	R	Friction	r
Inductance	L	Mass	m
1/Capacity	1/C	Stiffness	s

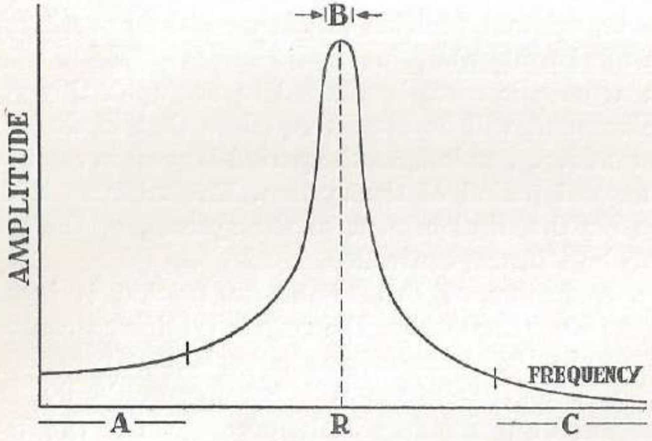

Fig. 25. Diagram of the response of a vibrating system to a periodic force of varying frequency. The amplitude of displacement is plotted against the frequency. R indicates the resonance-frequency of the system. At A the system is stiffness-controlled, at B friction-controlled and at C mass-controlled.

According to Ohm's law the electric impedance is defined as the ratio of the amplitudes of the voltage and the current. In close analogy a mechanical impedance can be defined as the ratio of the amplitudes of the alternating force applied to the system and the velocity resulting from it.

This definition of the mechanical impedance, however, does not completely describe the behaviour of the system, as it only gives the ratio of the maximum values (amplitudes) of force and velocity. Usually these magnitudes do not attain their maximum value at the same time; the quantities that are sinusoidally dependent upon the time are then said to be differing in phase. A complete description of the mechanical impedance must therefore take into account this difference in phase between force and velocity. Its magnitude may be given by the phase-angle Φ, which is defined by the equation

$\Phi = 360° . \frac{\Delta t}{T}$; in which Δt is the time interval between the moments that both quantities attain their maximum value and T is the period of the vibration.

If $\hat{K}$ and $\hat{V}$ represent the maximum values or amplitudes of force and velocity the momentary values of these quantities are given by the equations $K = \hat{K} \cos \omega t$ and $V = \hat{V} \cos (\omega t - \varphi)$ respectively.

The use of these trigonometric magnitudes may, however, lead to complicated computations and the introduction of the so-called complex quantities into the formulas facilitates these computations considerably.

Complex figures are obtained by addition of real and imaginary figures. The unit of imaginary figures is $j = \sqrt{-1}$. These complex figures may be represented graphically, in which the real figures are plotted against the axis of abscissae and the imaginary figures on the ordinate. In the figure 26A a point P represents the complex figure:

$$a' = w + jq = a. (\cos \omega t + j.\sin \omega t)$$

Since $\cos\omega t + j.\sin\omega t = e^{j\omega t}$ or exp $j\omega t$, in which *e* is the base of the natural logarithms, the equation may also be written as:

$$a' = w + jq = a.\exp j\omega t$$

Now both the above-defined mechanical impedance and the phase-angle between the force and velocity may be found easily by using these complex quantities.

If we write $K' = \hat{K} \exp j\omega t$ and $V' = \hat{V} \exp j (\omega t - \varphi)$, and consequently the complex impedance is defined as the ratio of the *complex momentary* values of force and velocity, then:

$$Z' = \frac{\hat{K} \exp j\omega t}{\hat{V} \exp j(\omega t - \varphi)}$$

Since exp j (ωt — φ) = exp jωt . exp (— jφ), Z′ may be written as:

$$Z' = \frac{\hat{K} \exp j\varphi}{\hat{V}} \text{ or } Z' = \frac{\hat{K}}{\hat{V}} e^{j\varphi}$$

The use of complex quantities in vibration problems has several advantages. In the equation of motion and continuity momentary values are used. If real quantities are used difficulties are encountered in the calculations of the ratios of these quantities, since the ratios of two momentary values are generally functions of the time and do not bear a simple relation to the ratio of the amplitudes. Hence if we are interested in the ratios of the amplitudes and the quantities are considered to be real we are compelled first to determine the amplitudes of the quantities under consideration. Where the quantities are taken as complex quantities any ratio of momentary complex values will be independent of time and bears a simple relation to the ratio of amplitudes of the quantities, without having recourse to amplitudes themselves. In the case of the complex impedance as defined above, the phase-angle may be seen directly from the formula

$$Z' = \frac{\hat{K}}{\hat{V}} . \exp j\varphi$$

Another advantage of the use of exponentials instead of circular functions is that differentiation and integration of circular functions is much more complicated than that of exponentials.

The usefulness of the complex impedance for the special case of a vibrating mechanical system consisting of a mass attached to a spring and opposed by a frictional resistance *r* will be demonstrated in the following calculation.

If K is the force acting upon the mass, the total of forces opposing this force is given by the equation

$$K = sx + r\dot{x} + m\ddot{x}$$

If the displacement *x* is substituted by the velocity *v*, we find

$$K = s\int vdt + rv + m\dot{v}$$

If *v* depends sinusoidally upon the time ($v = \hat{v} \exp j\omega t$), substitution gives

$$K = \frac{s}{j\omega} . v + rv + j\omega mv$$

According to the definition $Z = \frac{K}{v}$ or $Z = \frac{s}{j\omega} + r + j\omega m$

If this expression is represented in the complex plane (figure 25B) it may be seen that the length of the arrow (the magnitude of the impedance, its module or its numerical value $|Z|$) is given by

$$|Z| = \sqrt{r^2 + \left(\omega m - \frac{s}{\omega}\right)^2} \quad . \quad . \quad . \quad . \quad (1)$$

The phase-angle between force and velocity, which is called the argument, apparently follows from the relation

$$\operatorname{tg} \varphi = \frac{\omega m - s/\omega}{r}$$

The unit of mechanical impedance is the mechanical ohm, which is the impedance of an oscillating, mechanical system which vibrates with a velocity amplitude of 1 cm/sec under the influence of a force of 1 dyne (1 mech. ohm = 1 dyne sec/cm).

Like the vibration-form of an oscillating mechanical system is governed by the mechanical impedance, a sound-wave travelling in a medium will find a certain resistance opposing its progression. In analogy to the mechanical impedance this is called the acoustic impedance. In acoustical problems a distinction is made between the *acoustic impedance*, and the *specific acoustic impedance*. These concepts will be elucidated with a system consisting of a number of plane parallel layers of different materials. The system will be supposed to be acted upon by a periodical pressure p at the beginning. At the same site a velocity v will be found, the amplitude of which ($\hat{v}$) will be proportional to that of the pressure ($\hat{p}$). As a rule v will not be in phase with p. Taking v and p as complex quantities the specific acoustic impedance is defined as: $z = p/v$.

Obviously a system has the unit of specific acoustic impedance (the specific acoustic ohm), if it responds with a velocity-amplitude of 1 cm/sec to a pressure-amplitude of 1 dyn/cm².

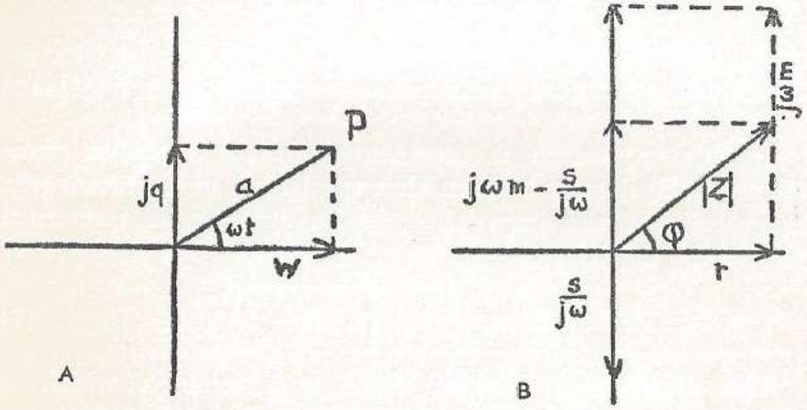

Fig. 26.

The ratio p/v, i.e. the specific acoustic impedance will differ at different points of the system mentioned above i.e. the specific acoustic impedance will, as a rule, be a function of the site. It depends upon the system in front of the site under consideration and describes the behaviour of the system at that site in acoustical respect. Should the system under consideration be a semi-infinite medium, z will obviously be independent of the site, since we then have at any site an infinite layer of the same medium in front of us. Now the ratio p/v only depends upon the medium. This very important specific acoustic impedance is called the wave impedance of the medium. Calculations show that it is equal to $\rho\,c$, where ρ = density and c = sound-velocity. For atmospheric air $\rho\,c$ equals about 42 cgs units. In materials with internal friction damping of the progressive wave occurs, which can be accounted for by taking the velocity of propagation complex. The wave impedance p/v remains equal to $\rho\,c$, which is now a complex quantity, i.e. pressure and velocity are no longer in phase in such materials.

It should be clearly understood that the wave impedance is the ratio p/v for one single plane progressive sound-wave through the medium. If e.g. two identical waves are considered in opposite direction the velocities will extinguish each other at certain places. At these places the sound-pressures will be added and the specific acoustic impedance will be zero. The concept of the acoustic impedance is useful e.g. in cases of the wave propagation in tubes. We are then only interested in the wave propagation across the cross-section of the tubes and the ratio

$$Z = \frac{\text{sound-pressure}}{\text{velocity} \times \text{cross section}} = \frac{\mathrm{p}}{\mathrm{v.S}} = \frac{\mathrm{p}}{\mathrm{V}} = \text{acoustic im-}$$

pedance is very practical. It is merely S times smaller than the specific acoustic impedance. Like z, Z will be as a rule a function of the site in the tube.

For a system consisting of mass, stiffness and resistance the numerical value of the acoustic impedance may be represented by the formula:

$$|Z| = \sqrt{\mathrm{r}^2 + \left(\omega\,\mathrm{m} - \frac{\mathrm{s}}{\omega}\right)^2}$$

In this formula r is called the acoustic resistance and (ωm — s/ω) is designated as the acoustic reactance, consisting of a mass reactance and an elastic reactance.

Damping.

If the periodic force acting upon a vibrating system is suddenly removed, the system will come to rest after a certain lapse of time. The vibration dies out or is damped. Its energy will gradually dissipate. This loss of energy is entirely due to the mechanical resistance, and the total energy of the system is entirely transferred into heat by the resistance in the case under consideration.

The amount of resistance or damping determines the time and the way in which the mass of the system will return to rest after being displaced.

If the resistance to the motion is high the damping will also be high and the system comes to rest sooner. The resistance may become so high that the system, coming back from its displaced position, just reaches its equilibrium position without passing this position. In this case the damping is said to be critical.

Correlation between impedance, reflexion-coefficient and phase-change.

When a plane travelling sound-wave passes from one medium to another the transmission of energy will depend upon the difference of the physical properties of the media. The ratio of the incident energy to the transmitted energy is dependent upon the ratio of the wave impedances of the media. Should the stiffness and density of the second system be greater than those of the first system its acoustic impedance will also be greater. In this case only part of the incident energy will be transmitted into the second medium, while part is reflected back on its course. Simultaneously a phase-shift may take place between the sound-pressure of the reflected, and the pressure of the incident wave.

Where a system is activated by an external periodic force no noteworthy phase-difference exists between the driving force and the velocity of the forced system, as long as the forcing frequency is far below the resonance-frequency of the system. ($\omega << \omega_0$). At resonance ($\omega = \omega_0$) the forced vibration lags 90°, and at very high frequency ($\omega >> \omega_0$) even to 180° behind the phase of the driving force.

Now the acoustic impedance of a sound-receiving system is completely determined by the energy-reflexion-coefficient R (i.e. the ratio between the intensity of the reflected sound-wave and the intensity of the incident wave) and the phase-difference α between the reflected and the incident wave. When $\sqrt{R}$, the amplitude-reflexion-coefficient, is the corresponding ratio between the sound-pressure amplitude of the reflected and the incident wave the correlation between $\sqrt{R}$. and α is given by the equation:

$$\sqrt{R}.\ e^{j\alpha} = \frac{Z_B - Z_A}{Z_B + Z_A}$$

where Z_B is the impedance of the receiver and Z_A the wave impedance of the medium in front of it.

When Z_A, $\sqrt{R}$ and α are known Z_B may be calculated from this formula.

From the impedance-formula the argument φ of Z_B may be determined.

In the case of a system consisting of a mass, stiffness and resistance the phase-lag between pressure and velocity is given by the equation

$$tg\varphi = \frac{\omega m - s/\omega}{r}$$

the magnitudes of resistance and reactance ($\omega m - s/\omega$) are thus determined.

From the energy-reflexion-coefficient the energy-absorption-coefficient may be calculated, as $a = 1 - R$.

Response of vibrating systems to various frequencies.

The equation of motion of a system consisting of an elastically fixed mass, the movements of which are counteracted by a frictional resistance, is represented by the formula:

$$K\sim\ = sx\sim + r\dot{x}\sim + m\ddot{x}\sim \quad . \quad . \quad . \quad . \quad . \quad (2)$$

in which $K\sim$ is the sinusoidal external force, $x\sim$ the elongation, $\dot{x}\sim$ the velocity and $\ddot{x}\sim$ the acceleration of the system and *s*, *m* and *r* the stiffness, the mass and the resistance of the system respectively.

The reactions of the system to the external force will depend upon the frequency of this force. At a certain value of this frequency the factors ωm and s/ω in formula (1) are equal.

Since in this case $Z = r$ the system is said to be friction-controlled and the formula (2) may be reduced to $K\sim\ = r\dot{x}$.

This is the condition of resonance, which occurs if the forcing frequency equals the resonance-frequency of the system

$$f = \frac{1}{2\pi}\sqrt{\frac{s}{m}}\,.$$

At this frequency the greatest elongations of the system occur, since the impedance will be minimal. The transmission of energy will thus be maximal, if the external force is kept constant.

The way in which the amplitude of the system varies with the frequency depends upon the period of the forcing frequency. For on either side of the resonance-frequency the impedance will be larger and the transfer of energy less. For frequencies far below the resonance-frequency the term $m\ddot{x}$ in the equation (2) becomes predominant, whereas for higher frequencies the term $s\dot{x}$ is dominant. The following approximations may thus be made:

$$\omega \ll \omega_0 : m\ddot{x} \sim = K \sim (3)$$
$$\omega = \omega_0 : \; r\dot{x} \sim = K \sim (4)$$
$$\omega \gg \omega_0 : \; sx \sim = K \sim (5)$$

In the case of sound-waves impinging on some material capable of vibration, the amount of sound-absorption will therefore depend upon the correlation between the frequency of the incident sound-wave and the resonance-frequency of the material.

When the values of sound-absorption by a sound-receiver are plotted against the frequency there originates what might be called a frequency-characteristic of the material. In this curve may occur several peaks indicating the various resonance maxima of the system (fig. 27).

Special sound-receivers or microphones are used for the reception and reproduction of sound-vibrations. The periodic movements of the air-particles are converted into movements of a membrane or ribbon, which consequently give rise to an electromotive force in the microphone-circuit:
vibration of air-particles → vibration of membrane → E.M.F.

The electromotive force may be either a frequency-independent function of the elongation, or a frequency-independent function of the velocity of the membrane.

When the electromotive force is a frequency-independent function of the *displacement* of the membrane the same relation must exist between the elongation and the sound-pressure. When the E.M.F. is a frequency-independent function of the *velocity* of the membrane the ratio between the velocity of the membrane and the velocity of the sound-wave must be independent of frequency. This behaviour of the microphone membrane makes it possible to divide the microphones from an acoustical point of view into:

1. *pressure-driven microphones* — if the membrane of a microphone is only exposed on one side to the sound-pressure variations we speak of a pressure-microphone (e.g. coal-, condenser- or crystalmicrophones). From the equations (3), (4) and (5), in which $K \sim$ equals the product of the surface of the membrane and the sound-pressure $K \sim = Op \sim = Op_0 \cos \omega t$, it may be seen that at frequencies lower than the resonance-frequency the ratio elongation/sound-pressure is independent of frequency. In the neighbourhood of the resonance-frequency the ratio velocity/sound-pressure and at higher frequencies the ratio acceleration/sound-pressure becomes independent of frequency.

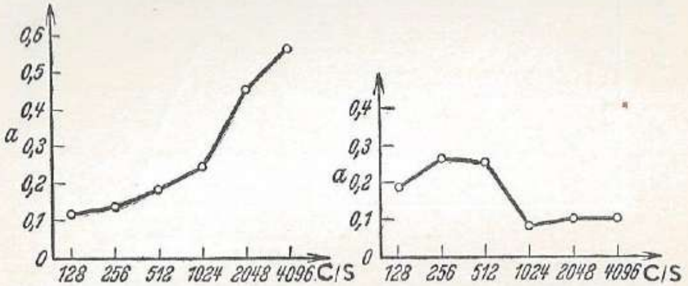

Fig. 27. Frequency-dependence of sound-absorption of various materials. Left porous material, right 3 mM woodlayer. (From Trendelenburg).

In the pressure-microphone the E.M.F. is a frequency-independent function of the elongation. For ideal reproduction the ratio elongation/sound-pressure must be chosen independent of frequency. As was shown above, this condition is fulfilled when the frequencies to be recorded are far below the resonance-frequency of the microphone-membrane ($\omega \ll \omega_0$: $sx \sim = Op_0 \cos \omega t$). The membranes of this type of microphone are usually so constructed that the resonance-maxima lie far beyond the recorded frequency-range. When, however, it is to be used in its resonance-range the damping must be made very high in order to suppress the disturbing resonance, which may occur in this area. Above the resonance-range the sensitivity of a pressure-microphone diminishes rapidly with growing frequency (fig. 28).

2. *velocity-driven microphones* or pressure-gradient microphones (electrodynamic or electromagnetic microphones) — in these microphones the membrane or ribbon is exposed on both sides to the sound-pressure variations. The pressure-difference or pressure-gradient between the sides is proportional to the driving force. They respond to the velocity of the air-particles and reproduce the sound-vibration accurately when the ratio between the velocity of the membrane and the velocity of the sound-wave is independent of frequency, for in these microphones the electromotive force is a frequency-independent function of the velocity of the membrane. These microphones have their resonance-area below the frequencies to be recorded. Whereas a velocity-driven instrument reacts well at a pressure-antinode and badly at a node, the reverse is true for a pressure-driven instrument. In the latter the direction of the wave with regard to the surface of the microphone membrane is of minor importance, whereas the velocity-driven microphones are highly directional.

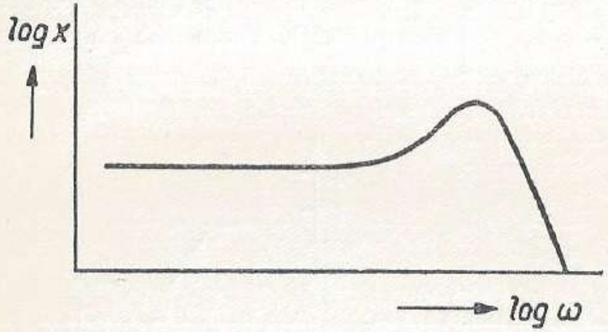

Fig. 28. Response curve of a membrane with only one degree of freedom. The logarithm of elongation is plotted against the logarithm of the frequency. (from Philips Techn. Rev.).

II. The ear as a sound-receiver.

Since it may be assumed that the whole mechanism of the sound-conducting apparatus (tympanic membrane, chain of ossicles and the fluid of the inner ear) is capable of vibration the system may be regarded as a complicated sound-receiver; and the question arises whether some analogy exists between the ear and the acoustic systems constructed for the reception and reproduction of sound (microphones).

Under normal conditions the tympanic membrane is only exposed on one side to the pressure-variations of the atmosphere. The deflections of the membrane in response to these pressure-variations in the outer ear canal are very small. The experiments of Kobrak (11) have revealed that a rotation of the malleus-handle of only 1° takes place at a pressure of 8 cm water. The sound-pressure variations at low frequencies will thus give rise to very small deflections of the tympanic membrane, a fact which was experimentally checked by Wilska.

These small excursions of the membrane at low frequencies are essentially caused by the stiffness of the system, which is mainly established by the cushion of air in the middle-ear cavity (v. Békésy). The tension of the tympanic membrane is in this frequency-region of minor importance. For the low frequency-band the pressure-variations are thus transmitted with minimal displacement, and the ear may in this region (up to 1000 c/s) be regarded as acting as a real pressure-receiver.

As was shown above a faithful reproduction can be achieved in a pressure-microphone when the resonance-area is far above the frequency-band to be recorded.

Various methods have been used to trace this resonance-area in the hearing organ. The natural frequency of the tympanic membrane was determined by v. Békésy (5) as being 1000 c/s and Perlman (3) recorded an over-all resonant frequency of about 750 c/s.

Frank (1) estimated the resonance-frequency of the middle-ear system at 1200 c/s.

In another set of experiments, in which the amplitude of oscillation of the head of the malleus versus frequency was recorded in preparations of dead human ears, PERLMAN (5) showed that at constant sound-pressure there was not uniform amplitude of vibration. The maximum amplitude appeared at about 500 to 600 c/s. The resonance-peak was quite broad suggesting considerable damping.

The vibrating system of the tympanic membrane, ossicles and the inner ear is very complex and it is likely that the system will have several resonance-frequencies. Since there is some evidence that the internal friction of the system is rather high the effect of resonance is, however, not very pronounced.

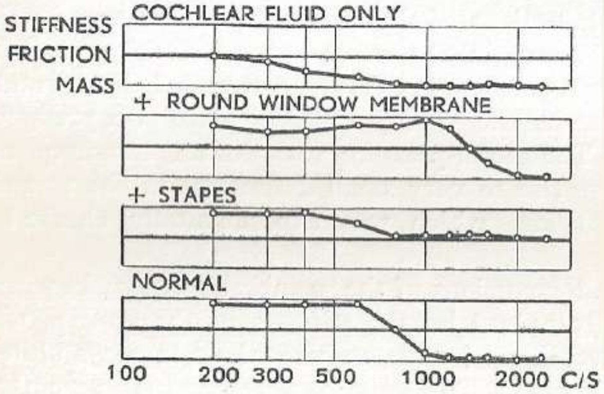

Fig. 29. Graphs showing the response of the component parts of the sound-conducting apparatus to a sound-pressure.

The experiments of v. BÉKÉSY (12) in which the phase-relations existing between the displacements of the sound-conducting apparatus and the sound-pressure at the tympanic membrane were studied, revealed that there was little difference in phase between the sound-pressure and the volume-displacements of the round window membrane at low frequencies. In the frequency-band of 1000 to 3000 c/s there was a phase-difference of 90° and above this frequency-range the phase of the round window membrane lagged more and more behind the phase of the sound-pressure (fig. 29).

These experiments indicate that between 1000 and 3000 c/s the system is friction-controlled and that this area must be regarded as the resonance-area of the ear. Additional evidence for this assumption may be derived from the impedance-measurements of the ear. On the over-all curve for the impedance several resonant points appear as a minimum on this curve in the frequency-band of 800 to 3000 c/s (TRÖGER).

A pressure-microphone with a small damping factor shows an increased sensitivity in its resonance-area. This may cause resonance, which disturbs the faithful reproduction of the sound-vibrations.

Owing to the high rate of damping in the ear practically no increased sensitivity in the resonance-area can be expected, and the ear acting as a pressure-microphone in the low frequency-band remains a pressure-microphone in the mid-tonal region.

TUMARKIN (1) also argues that the middle ear is pressure-driven. His argument is that in a standing wave the antinodes indicate maximal velocity and maximal displacement, whilst pressure changes are zero. At a node the converse is true. Now in a standing wave the human ear detects sounds at a node and not at an antinode, i.e. it is pressure-driven. Moreover the ear is equally sensitive to sounds coming from different directions. Whereas the velocity-microphone is highly directional, the pressure-driven instrument will record equally well at any angle because the pressure changes in a sound-wave are the same in all directions. As the tympanic membrane will act just as efficiently, whatever its angle with the direction of the sound-waves may be, the oblique position of the diaphragm serves as a means to increase its effective area.

Since the ear operates essentially as a pressure-receiver, it is of great importance to know the pressure at the tympanic membrane, as well as the pressure-transformation to the inner ear by the sound-conducting system.

1. the pressure-distribution in the auditory canal :

When the ear is placed into a free progressive sound-field the sound-waves will impinge upon the head and enter the external auditory canal. As the surface of the head and the walls of the canal are to be regarded as entirely rigid the waves are almost completely reflected (v. Békésy, 4). This diffraction of the head causes an increase of sound-pressure at the entrance to the external auditory canal.

Another change of pressure occurring in the outer ear canal

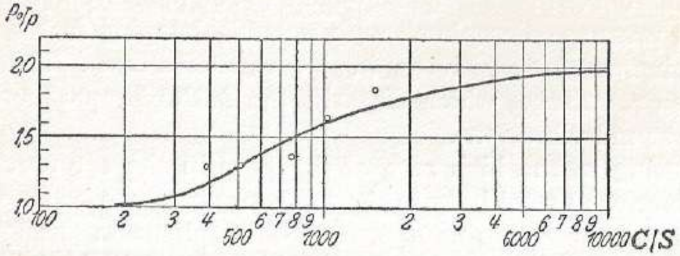

Fig. 30. Increase of pressure at the entrance to the external auditory canal in comparison with the pressure in the undisturbed sound-field as computed by v. Békésy.

is the result of the resonance-activity of this small chamber. v. Békésy (4) computed this pressure-increase, which depends not only upon the dimensions of the canal but also upon the impedance of the tympanic membrane. When this membrane was regarded as completely rigid a sharp pressure-peak was obtained at a frequency of 2800 c/s.

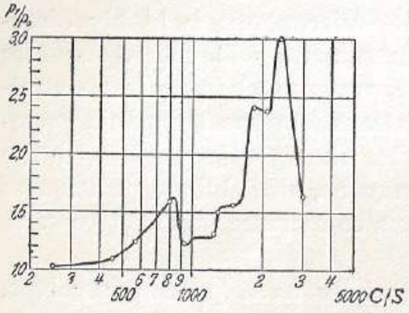

Fig. 31. Pressure increase in the external auditory canal with normal tympanic membrane. (After v. Békésy).

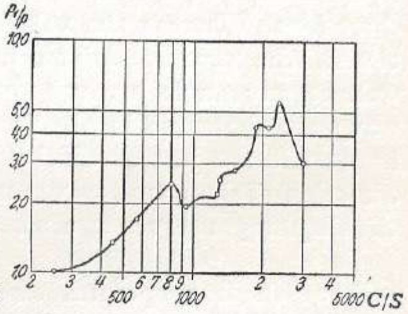

Fig. 32. Total increase of sound-pressure at the tympanic membrane as computed by v. Békésy.

Taking into account the data of the impedance measurements of the ear by Tröger a pressure-curve was calculated as is shown in fig. 31.

The total increase of pressure produced by the head and the external auditory canal is represented by the curve of fig. 32.

The pressure-distribution in the auditory canal was determined experimentally by Kuhl and recently again by Wiener and Ross. These investigators inserted a small, flexible probe at various positions deep into the auditory canal. It was affirmed that over most of the frequency-range the ear canal acts as an acoustic pressure-amplifier, the sound-pressure at the tympanic membrane being greater than that of the free field pressure (fig. 33).

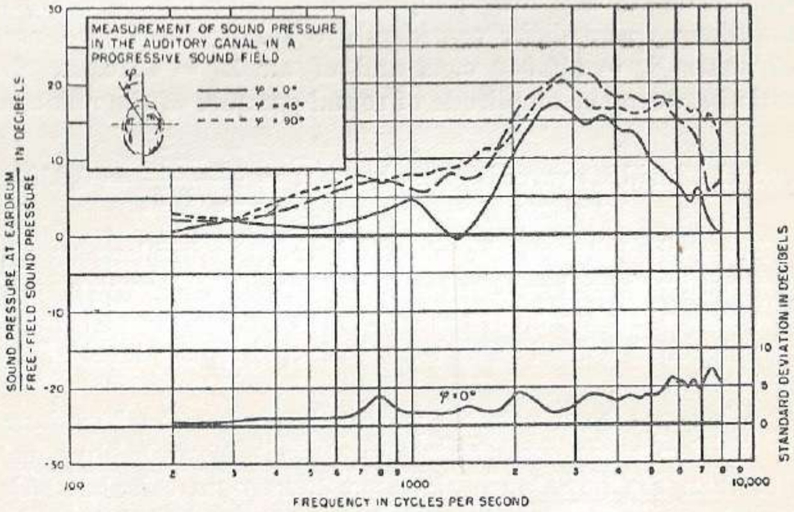

Fig. 33.

Ratio of the sound-pressure at the eardrum to the sound-pressure in the free field at the centre of the observer's head. The average of 6—12 male ears is shown for various azimuths as a function of frequency (From Wiener and Ross).

A maximum gain of 17 to 22 db was found near a frequency of 3000 c/s. Since the average length of the canal is 2.3 cm the peak occurs at a frequency where the length of the canal is approximately equal to one-quarter wave-length. From the above it may be concluded that the impedance of the tympanic membrane, and the associated structures, is of great importance for the pressure-distribution in the auditory canal. Since the acoustic impedance of the over-all auditory mechanism is for the major part of the frequency-range greater than that of air, only part of the tendered sound-energy will be absorbed, another part being reflected. This reflected sound-energy also contributes to the above-mentioned pressure increase at the tympanic membrane.

2. The pressure-transformer action of the middle-ear structures:

Where a sound-wave passes from air to water the amount of energy absorbed by the water depends upon the ratio of the impedances of air and water. Because these media differ widely in density and compressibility the values of their impedances also differ considerably. Taking the impedances of water $Z_w = 145.000$ c.g.s and of air $Z_A = 42$ c.g.s. the ratio between the amplitude of sound-pressure of the reflected and the incident wave is given by $\sqrt{R} = \frac{Z_w - Z_A}{Z_w + Z_A} = 0{,}9994$.

The ratio between the absorbed and the incident energy is given by $a = 1 - R = 1 - (0{,}9994)^2 = 0{,}0012$ or expressed in decibels $10 \log 0{,}0012 = -29$ db: so the sound level of the absorbed wave is about 30 db less than the level of the incident wave.

It has not been possible yet to determine the impedance of the inner ear experimentally, but it is probably much less than the impedance of water. Zwislocki calculated the impedance at the entrance to the cochlea to be of the order of 9.10^3 dyn. sec/cm^3. It was further computed that this impedance was independent of frequency. Introducing this value into the formula it may be calculated that from a sound-wave directly incident on the stapes the sound-energy entering the cochlea will be 18 db less than the intensity of the incident wave. These calculations, however, are based on the assumption of an infinite medium. But the cochlear fluid must be regarded as a finite medium, surrounded by a rigid capsule. The effect of this enclosure is to raise the stiffness which increases the loss accordingly.

It is the primary function of the middle ear to meet this energy-loss and to match the wave resistance in air to the acoustic impedance of the inner ear. To this transformer action of the middle ear two principles may contribute:

1. an increase of pressure on the stapedial footplate

It has already been stated that the concept of Helmholtz, viz.; that the peculiar structure of the tympanic membrane contributed to this pressure-transformation, was not substantiated by the experiments. The main factor in this pressure-transformation will therefore be the difference in area between the tympanic membrane and the footplate of the stapes (transformer ratio). The cross-sectional area of the tympanic membrane in man is approximately 90 sq. mm, that of the stapedial footplate 3.2 sq. mm.

Helmholtz estimated the transformer ratio for man to be between 15 and 20. Wever, Lawrence and Smith determined it in one specimen as 18.2 for the left and 19.1 for the right ear. They pointed out, however, that large variations may exist in the ratio tympanic membrane – stapedial footplate among species and among ears of one species.

Whittle found for the guinea-pig a mean value of 28.1, in the cat a result of 36.5 was obtained.

Since the tympanic membrane is a conical flexible structure fixed at the edges it cannot move as a simple piston, and only part of the whole area of the membrane will actually contribute to the pressure-transformation. This part is called the effective area of the membrane. The very complicated structure of the tympanic membrane only makes an approximate estimation of this effective area possible. Wever and his co-workers estimated it to be about three fourths of the total area, whereas Waetzmann and Keibs give a value of only one third.

The shallow conical form of the tympanic membrane makes the effective area larger than it would be for a flat membrane of the same diameter. In its form it resembles the commercial loudspeaker cones. Contrary to a flat membrane a conical shaped membrane improves the output at high frequencies. At certain frequencies these conical shells exhibit concentric nodal circles. The response characteristics of such a cone may, however, be considerably modified by changing its construction.

The mode of vibration of the tympanic membrane is still a question waiting solution. Since the tympanic membrane is asymmetrical in shape and unsymmetrically loaded by the attached malleus, the loudspeaker is only a very rough approximation of a very complex unsymmetrically loaded membrane, whose response characteristics are still unknown (Stuhlman, 3). The question whether the membrane resembles a diaphragm subjected to partitioning in nodes and antinodes might be solved by further stroboscopic observation of the oscillating membrane. So far the observations of Perlman (2) have revealed that the various parts of the membrane vibrate in equal phase.

v. Békésy (9) has shown experimentally that the central portion of the tympanic membrane involving the manubrium mallei up to a frequency of 2400 c/s, vibrates as a rigid cone.

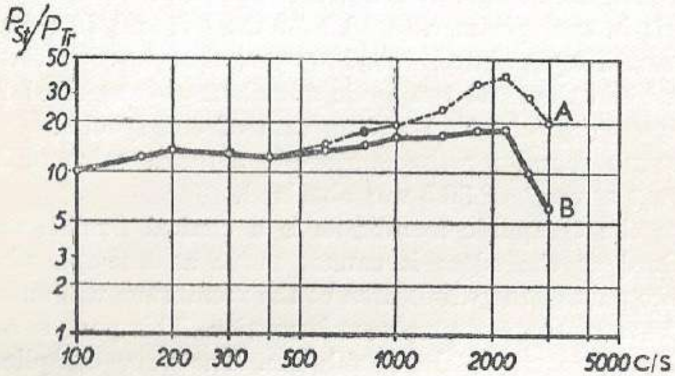

Fig. 34. Graph showing the pressure-transformer action of the middle-ear structures. The broken line represents the pressure-ratio between the entrance to the auditory meatus and the stapedial footplate, whereas the solid line indicates the same ratio between the tympanic membrane and the stapedial footplate. (After v. Békésy).

At the same time this investigator determined the pressure-transformation by the middle-ear structures experimentally. It was shown that for the frequency-range of 100 to 2400 c/s the ratio between the pressure at the stapedial footplate and the constant sound-pressure at the tympanic membrane varied from 10 to 20. If regard was being paid to the pressure increase at the tympanic membrane this factor may even become more than 30 for certain frequencies (fig. 34).

It was indicated that this transformer ratio might be greatly reduced by pathological changes in the sound-conducting apparatus. When the mechanism of the middle ear is intact a 20-fold increase of pressure equals a gain of 26 db.

These findings are in accordance with the experimental results of Wever, Lawrence and Smith, who found the drop in transmission-efficiency following the elimination of the whole middle-ear structure, except the footplate of the stapes to be of the order of 33 db for the mid-tonal range, 24 db for the low and 26 db for the high frequency-range. A loss of 28 db was taken as an over-all figure.

The pressure-ratio therefore seems to be almost sufficient to meet the difference in impedance between the air and the inner ear. An additional increase of force may, however, be provided for by:

2. *The ossicular lever-mechanism.*

Helmholtz suggested that the movements of the stapedial footplate were smaller in amplitude than those of the malleus-handle. A corresponding increase in pressure was assumed to result from this lever-mechanism. From measurements of the lever-arms and estimations as to their axes Helmholtz adopted a lever-ratio of 1.5 to 1, which would only account for a gain of 2.5 db.

In two sets of experiments Wever, Lawrence and Smith have tried to evaluate the significance of this lever-mechanism for the pressure-transformation of the middle ear. Their final conclusion concerning the ossicular lever-problem is that if the lever-action is present at all, it is only of minor importance.

In the foregoing regard has only been paid to the difference in impedance between the air and the inner ear, and it was tacitly assumed that the structures of the middle ear offered no resistance to the sound-waves. In the following a more detailed discussion will be given of:

The impedance of the over-all auditory mechanism.

Between the pressure of the incident and the reflected sound-wave a phase-change usually exists. Since the impedance of a sound-receiver may be calculated from the reflected sound-energy and the phase-difference between the incident and the reflected wave, the impedance of the over-all auditory mechanism may be determined if both these factors are known. The determination of pressure-amplitude and pressure-phase of the reflected wave was made possible by the methods developed by Tröger and Geffcken, the latter using Tröger's method with a slightly modified technique.

More reliable methods were used by Waetzmann (2), Keibs, Thorsen, Menzel and Metz. These investigators adopted the acoustic measuring bridge of Schuster, which was originally constructed to determine the sound-absorbing efficiency of different samples of material.

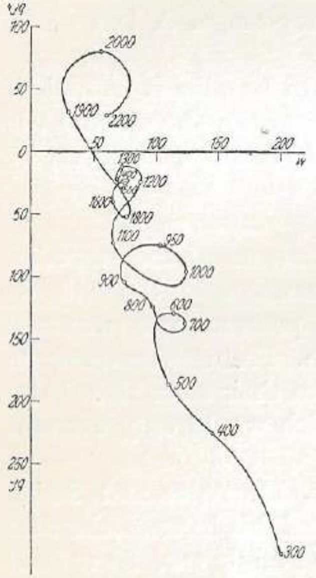

Fig. 35. Impedance-diagram after Geffcken.

From the reflected sound-energy and the phase-change both the reactance and the resistance components of the impedance may be calculated. When these components are plotted in a diagram the abscissa or real axis shows the frictional resistance, while the ordinate or imaginary axis represents the reactance. The positive ordinate indicates the mass reactance and the negative ordinate the elastic reactance. The impedance consists of a real part OX and an "imaginary" part OY representing the difference between the mass and elastic reactances. The impedance value is given by the length of OA. The impedance diagram of fig. 35 was given by Geffcken as the result of measurements on a test person.

From the diagram it may be seen that the impedance for the low frequencies is very great and essentially an elastic reactance. The active mass of the tympanic membrane and the ossicular chain is, at these frequencies, of minor importance. It was already stressed that the impedance of the ear at very low frequencies is mainly determined by the cushion of air in the middle-ear cavity (v. Békésy, 13).

With increasing frequency the elastic component of the reactance decreases. From about 700 c/s the curve has a very complicated, tortuous course, sometimes showing several loops within each other. Between the frequencies of 1800 and 1900 c/s the curve passes the real axis. Theoretically the point where the curve passes this axis indicates the resonance-frequency of the ear. For, at resonance, the mass and elastic reactances cancel and the system is friction-controlled.

It has already been stated that the sound-conducting apparatus does not possess one natural period, but that several resonance-frequencies may occur, owing to the fact that the system has an unlimited number of degrees of freedom. These resonance-points account for the capricious course of the impedance-curve. In the area between the frequencies of approximately 1000 and 3000 c/s, measurements of the ears of various observers may differ considerably from one another, each subject showing various points of resonance. This area may therefore be regarded as the resonance-area of the system, in which the values for the impedance are low, lying in between 40 and 100 c.g.s. The impedance of the over-all auditory mechanism here is closely matched to that of air. The efficiency of energy-transfer must be high, since the air and the ear show almost the same numerical value for their impedances. Metz found agreement between the magnitude of the impedance components previously determined with other methods. The course of the impedance-curve at lower frequencies is essentially the same in normal ears. Owing to unstable experimental results at higher frequencies, impedance-measurements of the ear are only reliable over a limited range of frequencies (the upper limit being approximately 1200 to 1300 c/s).

The structures of the middle and inner ear in their relation to the factors mass, stiffness and friction.

Since the acoustic impedance of a system is determined by the factors mass, stiffness and resistance, it is important to know which structures of the ear contribute to these factors. The whole sound-conducting apparatus is made up of several masses connected by a number of stiffnesses.

mass: in general, the sound-stimuli in air have so little energy that this factor must be as small as possible in order that the system may react to these stimuli. The structures contributing to the mass factor are mainly the tympanic membrane, the ossicles and the intra-labyrinthine fluid.

The particular manner of suspension of the tympanic membrane, malleus and incus tends to reduce the influence of this mass. Its axis of rotation passes through the centre of gravity of this unit and is so placed as to apparently balance out the mass of the membrane and the ossicles. The relatively large mass of the head of the malleus and incus appears to be necessary to bring the centre of this ossicular unit into the axis of rotation. According to E. Bárány, this symmetrical distribution of the mass around the axis of rotation is found in all mammals.

stiffness: this factor is mainly influenced by the tension of the tympanic membrane and the capsular and suspensory ligaments of the ossicles, the air-pressure in the tympanic cavity and the action of the middle-ear muscles. For the inner ear the tension of the basilar membrane and the membrane of the round window must be accounted for.

Perlman (5) states that removal of the elastic, restoring force of the annular ligament allows the stapes to make a much greater amplitude when driven by the intact chain.

frictional resistance: v. Békésy (9) found the amplitude of vibration of the stapedial footplate at constant sound-pressure decreasing proportionally with the frequency up to 2000 c/s. This decrease in amplitude was taken as evidence for the assumption that the movements of the ossicles in response to tones of the mid-tonal region are essentially determined by the frictional resistance of the ossicles, and not by the stiffness of the annular ligament of the stapes, as was previously assumed. The middle-ear structure was regarded as a cone moving with a high frictional resistance, the forces of friction being chiefly caused by the middle-ear muscles. From measurements on fresh human temporal bones a resistance of 1000 c.g.s. was determined for tones of the mid-tonal region.

The response of the various constituent parts of the sound-conducting apparatus to a delivered sound-stimulus were studied by v. Békésy (12) in determining the phase-shift between the volume-displacements of these parts, and the sound-pressure of the stimulus (fig. 29). With both windows removed the cochlear fluid vibrated as a mass-controlled system throughout most of the frequency-range tested. With the round window intact and the oval window removed the vibrations were stiffness-controlled up to a frequency of 1400 c/s. With both stapes and round window intact the system vibrated as a stiffness-controlled system up to a frequency of 800 c/s. Between this frequency and the 2500 c/s the system became friction-controlled. When the entire sound-conducting system with the tympanic membrane, the ossicles and the inner fluid were stimulated, the vibrations of the system were stiffness-controlled in the lower frequency-range, at 800 c/s it was friction-controlled (the resonance-frequency) and for the higher frequencies it resembled a mass-controlled system.

Application of the impedance-formula to the vibrating system of the ear is only possible to a certain extent. The condition for the determination of the impedance from the formula for the various frequencies is that the factors m,s and r are kept constant. The very complicated structure of the middle- and inner-ear system, however, make it very likely that the factors m and s are not constant, and will depend upon the frequency. Only in a very limited frequency-range may we assume these factors to be constant and is it possible to determine the resistance and reactance parts from the formula.

From the impedance-diagram of fig 35 it may be inferred that the factor s mainly influences the impedance for the low frequencies and that the factor m chiefly affects the high frequencies. An increase in stiffness in the middle- or inner-ear structures will therefore result in an increase of the impedance for the low frequencies, whereas an increase in mass will cause greater impedance for the high frequencies. In general, an increase in mass tends to reduce the response for the higher frequencies and lowers the resonance-frequency of the system. The effect of an increase of mass upon hearing was studied experimentally by LÜSCHER (2, 3) and by v. DISHOECK and DE WIT and in the preparation by PERLMAN (5,6). On loading the tympanic membrane with water or mercury the hearing was markedly affected for the high tones (*mass curve*). An increase of stiffness on the other hand, reduces the response for low frequencies and tends to increase the resonance-frequency of the system. In the experiments an over- or underpressure of the air in the tympanic cavity resulted in an impairment of hearing for the low tones (v. DISHOECK—DE WIT and RASMUSSEN)-*stiffness curve*. This relation existing between the impedance-formula and the hearing function obtained under these experimental conditions was further studied by JOHANSEN. Regarding the influence of friction it may be seen that in Geffcken's diagram the frictional resistance drops from 200 to 25 c.g.s. for the frequency-range of 300 to 1900 c/s. It may be noted that these values are much smaller than those determined by v. Békésy for the friction of the middle ear in fresh human temperal bones for tones of the mid-tonal region (1000 c.g.s.), and are in conflict with previous investigations. Whether this difference must be attributed to post-mortem alterations remains uncertain. It is to be concluded therefore that lesions of the sound-conducting apparatus may produce a great variety of auditory threshold curves, depending upon the way in which the masses, the stiffnesses, and the resistances of the component parts are affected.

Correlation between the impedance-curve and the auditory threshold curve.

It may be noted that in the frequency-range where the ear is most sensitive (between 1000 and 3000 c/s.), the values of the over-all impedance of the auditory mechanism show a minimum.

In this area a pressure of only 3×10^{-4} dyn/cm² evokes a hearing sensation.

GEFFCKEN even gives for a certain case a threshold pressure of 5×10^{-5} dyn/cm², which is in the direct neighbourhood of the spontaneous pressure-variations in the air caused by the Brownian molecular movement (10^{-5} dyn/cm²). The amplitude of an air particle at the threshold pressure is approximately 8×10^{-10} cm. Since the diameter of an air-particle is about 4×10^{-8} cm, a hearing sensation may be experienced if the displacements of the air-molecules are smaller than 1/100 times their diameter. The movements of the tympanic membrane at auditory threshold must therefore be of molecular dimensions. Indeed Wilska found the excursions of the tympanic membrane at threshold to be less than 10^{-9} cm at 2000 c/s. In this connection it is clear that the impedance of the auditory mechanism for the just-audible energy must be very small. The minimum-audible energy for high and low tones is, however, much larger.

GEFFCKEN pointed out that these variations in the sensitivity of the ear at different frequencies might be attributed to variations in impedance of the sound-conducting system. TUMARKIN (1) also states that it is quite possible that the different response-areas of the organ of Corti are equally sensitive for a given amount of energy entering the cochlea. The shape of the auditory threshold curve would thus mainly be determined by the characteristics of the sound-conducting apparatus, and not by the sense-organ proper. Experiments of WEVER, LAWRENCE and SMITH, in which after removal of the middle-ear structures the sound was conducted directly to the oval window, seem to support this view. Almost equal responses at constant sound-pressure were obtained over a wide range of frequencies.

Significance of impedance-measurements of the ear.

These measurements may provide information as to three important questions:

1. the minimum audible energy at the tympanic membrane — the determination of auditory threshold may be possible in two ways. Either the amount of energy tendered at the entrance to the outer ear canal, which is partly absorbed and partly reflected at the tympanic membrane, or the amount of energy actually absorbed at the tympanic membrane is taken as a measure for the threshold value. The second method is more accurate because regard is being paid to the pressure-

increase in front of the tympanic membrane (WAETZMANN and KEIBS). The necessary data for the calculations of this auditory threshold curve in an absolute measure are obtained from the results of impedance-measurements.

2. the construction of artificial ears and electrical hearing aids.

3. the vibration-efficiency of the sound-conducting apparatus — direct and objective information about the vibration faculty of the tympanic membrane, and the attached malleus may only be obtained by impedance-measurements of the ear.

It was shown by METZ that a complete fixation of the stapes and the round window, in fresh human temporal bones, only produced a very slight change in the impedance of the tympanic membrane, whereas a fixation of the malleus gave almost a complete absence of sound-absorption. In case of stapes-fixation the greatest amount of the absorbed energy apparently will be lost in differential movement between the ossicles. The influence of a change in the sound-conducting apparatus on the impedance of the tympanic membrane will thus be greater, the nearer this change is situated to the membrane. Factors influencing the vibration faculty of the tympanic membrane and the malleus will then also have an influence upon the impedance. Possible factors may be regarded as being:

1. the pressure in the middle-ear cavity:

Metz demonstrated that even small differences between the pressure in the middle ear and the atmospheric pressure produced distinct and considerable changes of the impedance. At first negative or positive pressure gives rise to a strong increase of the reactance component of the impedance (increasing stiffness). With growing difference in pressure the resistance component decreases and the impedance gradually changes in the direction of a pure reactance. The increase of the impedance and the corresponding hearing-loss seem to be of the same range of magnitude (v. Békésy).

2. the contraction of the intra-tympanic muscles:

It was further shown by Metz that the acoustic reflex-contraction of the intra-tympanic muscles gives rise to a distinct change of the impedance of the tympanic membrane. This change is, however, rather small. With a strong sound-stimulus applied to one ear only a reduction of the absorbed amount of energy of maximal 5 db could be demonstrated in the opposite ear. This reduction will mainly be due to a contraction of the tensor tympani muscle. Whereas the contractions of the stapedius muscle have been studied several times in the human living ear, movements of the tensor tympani have never been observed under these conditions. Even under high magnification and strong sound-stimuli Waar failed to detect any movement of the tympanic membrane.

In persons showing a voluntary contraction of the tensor tympani, however, a distinct inward movement of the membrane may be observed. A corresponding change of the impedance in the same direction, but more pronounced than in the acoustic reflex-contraction was found.

3. pathological changes in the sound-conducting apparatus:

Lesions of the conducting apparatus due to inflammations or its sequelae, give a great reduction of the amount of energy absorbed. A similar reduction was found in otosclerosis. The discrepancy between the change of impedance in the experimental fixation of the stapes and in otosclerosis is explained by a decrease of differential mobility between the ossicles in the case of otosclerosis.

Because of the decrease of the real component, the impedance is nearing the condition of pure reactance, which is mainly due to the increased stiffness of the sound-conducting apparatus.

While the functional diagnosis of a conduction affection is only possible by means of subjective methods (tuning-forks, audiometer) the impedance-measurements may be used as a direct, objective method to demonstrate the vibration faculty of a major part of the sound-conducting apparatus.

III. The ear as a sound-transmitter:

The function of the middle-ear apparatus is to deliver the sound-energy received by the tympanic membrane to the inner ear. The way in which this energy-transfer is effected has already been discussed in detail sub II.

Not the whole amount of energy received by the tympanic membrane is, however, transmitted to the labyrinth. Part of this energy is lost on its way to the sense-organ proper. Possible factors responsible for this absorption or loss of energy may be:

1. the middle-ear cavity and the adjoining air-filled cells of the mastoid process — because of the tenseness of the tympanic membrane and its minimal excursions, this factor is only of minor importance.

2. the pars flaccida of the tympanic membrane — the vibrations of this part of the membrane do not effectively contribute to the energy-transfer to the labyrinth.

3. part of the pars tensa of the tympanic membrane — the effective area of the pars tensa is smaller than the total surface of the membrane.

This effective area was estimated by v. Békésy at 55 sq. mm against a total surface of 85 sq. mm.

The remaining part of the membrane consists mainly of a very mobile fold at the lower border of the membrane, allowing the stiff cone-shaped part to move without noteworthy deformation.

It must be assumed that this mobile part will be able to continue to carry out vibrations and thus absorb sound-energy even after complete fixation under pathological conditions of the malleus, and the cone-shaped part of the tympanic membrane (Metz).

4. frictional resistance of the middle ear — it has already been stated that loss of energy in a vibrating system is entirely due to friction.

5. differential mobility of the ossicles — though at very low intensities of the sound-stimulus the movements of the ossicles have still escaped notice it may be assumed that, under these conditions, the whole chain vibrates as a single unit (Dahmann). The amplitude of the stapedial footplate is, under these conditions, almost a linear function of the displacements of the handle of the malleus.

With increasing intensity a gradual shift from linearity takes place (Stuhlmann, 1). At an intensity of 50 to 60 db the outward movements of the whole sound-conducting apparatus are greater than the inward thrusts (Kobrak, 9, 11), whereas the middle-ear muscles already display their action at this intensity. Apart from influencing the impedance of the system this contraction will affect the transfer of energy to the labyrinth. Though the vibration-mechanism is in this case already complex, the movements of the chain are becoming even more complicated with growing intensity.

Partly through the action of the middle-ear muscles several axes of rotation may develop and even a complete change of axis may occur in the stapes. It is clear that under these conditions the transport of energy to the labyrinth is greatly reduced; this may serve as a means to protect the inner ear from sounds of too high intensity, which tend to produce too great a displacement of the vulnerable structures of the inner ear.

From the above it may be concluded that impedance-measurements may only yield direct information about the sound-absorbing function of the tympanic membrane and part of the ossicular chain, but give no information about the ultimate amount of the absorbed energy reaching the inner ear.

Changes of the impedance may be present without any change of the energy-supply to the labyrinth (i.e. increased stiffness of parts of the tympanic membrane which are not essential for the energy-transfer to the inner ear), whereas changes of the energy-supply may exist without a marked change of the impedance of the tympanic membrane (i.e. stapes-fixation).

CHAPTER VIII

CONCLUSION

The entire process of hearing may be regarded as being built up of three consecutive stages:

1. the conduction of physical energy to the organ of Corti.
2. the transformation of the physical energy into nervous energy.
3. the conduction of the nerve-impulses to the auditory cortex. The second and the third stages are inherent to structures of a true biological nature (the hair-cells of the organ of Corti and the auditory pathways), whose normal activity ceases after the death of the individual. The structures involved in the first stage, however, show few biological aspects and may rather be regarded as forming a complicated mechanical system, which under the influence of a periodic external force is capable of executing forced vibrations. The properties of this system, and hence its activity, remain essentially unaltered after the death of the individual. It is small wonder that these structures, to which the laws appertaining to both mechanics and hydrodynamics may be applied, have several times drawn the attention of physicists. The study of biophysics of this part of the hearing process is now taking its place beside the study of normal physiology of the auditory function. The whole sound-conducting apparatus, which comprises the tympanic membrane with the ossicular chain, the intralabyrinthine fluids and the membranes suspended in these fluids as well as the membrane of the fenestra rotundum, is composed of two systems with an entirely different function.

1. *the middle-ear system,* which includes the tympanic membrane and the chain of ossicles.
2. *the inner-ear system,* which consists of the intralabyrinthine fluids and the various membranes.

The middle-ear system is essentially a mechanical system capable of vibration. The vibrating air-particles in the canal of the outer ear form its source of energy. It has been conclusively demonstrated by various procedures that the tympanic membrane and the chain of ossicles are set into vibration by these air-borne sound-waves. Owing to its complicated, conical structure the mode of vibration of the tympanic membrane in response to various frequencies has not yet been clarified.

According to v. Békésy the central portion of the tympanic membrane up to a frequency of 2400 c/s moves as a rigid cone, rotating round an axis at the upper margin of the membrane. Above this frequency the conical part of the membrane loses its rigidity and the malleus-handle lags behind the movements of the adjacent parts of the membrane.

Also the complex structure of the ossicular chain and its suspension by various ligaments make an accurate determination of the axes of rotation extremely difficult. The study of the vibrating ossicular mechanism by stroboscopic illumination and slow motion picture (Kobrak) has revealed the very complex nature of this oscillating system.

The results of various experiments support the view that the middle-ear system delivers the sound-energy to the fenestra ovalis in preference to the foramen rotundum.

In reptiles, amphibians and birds this energy-transfer is effected by one ossicle, the columella, which connects the tympanic membrane directly with the inner-ear system. The complicated structure of the middle-ear system in mammals can only be looked upon as a protective device for the vulnerable structures of the inner ear. It is not likely that the efficiency of conduction is improved by this structure. For low intensities of stimulation the system operates as a whole, the stapedial movements being almost the same as the movements of the tympanic membrane (Dahmann). With increasing intensity of the sound-stimuli, however, various mechanisms may cooperate in restricting the movements of the ossicles and thus reducing the transmission of dangerously large amplitudes to the inner ear.

These mechanisms are:

the relative mobility between the individual ossicles;

the change of axes of rotation with large amplitudes of vibration; the acoustic reflex-contraction of the intra-tympanic muscles;

The primary function of the middle-ear system is, however, to match the impedance of the inner-ear system to the wave resistance of sound-waves in the air. If two media differ considerably in acoustic impedance, the sound-waves will not readily pass from the medium with low to the medium with high acoustic impedance. In this case the greater part of the sound-energy is reflected back from the boundary between the two media. Owing to this difference in impedance between the air and the inner-ear system a sound-wave directly incident on the stapes would be almost completely reflected and only a very small portion of its energy would actually enter the inner ear (approximately 1/1000).

From the estimated difference in impedance it may be computed that the energy of the transmitted wave will be approximately 30 db less than the energy of the incident wave. Removal of the whole middle-ear system in the animal experiment indeed resulted in a loss of cochlear function of the same order of magnitude (Wever and co-workers).

This impedance-matching function of the middle-ear system is mainly based on the difference in areas of the tympanic membrane and the footplate of the stapes.

If the ratio of these areas (the transformer ratio) is known, the power-transfer may be calculated. Not the whole area of the tympanic membrane, however, contributes to this power-transfer. v. Békésy determined the effective area of the tympanic membrane (55 sq. mm), to be about two thirds of its total area (85 sq. mm).

Since this effective area is the rigid, conical portion of the tympanic membrane the whole pressure-force exerted upon this part of the membrane will be transmitted.

If the total surface of the stapedial footplate is taken at about 3 sq. mm an effective ratio of about 20 may be computed. The pressure per square mm. exerted upon the footplate will thus theoretically be about 20 times greater than upon the tympanic membrane. Indeed v. Békésy found experimentally a 20-fold pressure-transformation between the tympanic membrane and the stapes. This equals a gain of 26 db.

If the pressure-increase effected by the diffraction of the head and the resonance-activity of the external auditory meatus was taken into account, and the pressure-ratio determined of the pressure at the entrance to the canal and the stapedial footplate, this factor would become even more than 30. Both conditions may therefore be regarded as efficiently aiding the pressure-transformation by the middle-ear system.

It is thus clear that the mechanical efficiency of the middle-ear system results mainly from a pressure-transformer action, which almost completely meets the difference in acoustic impedance between the air and the inner-ear system. The lever-mechanism of the ossicular chain, if existing at all, seems to be of very little importance.

Since the main function of the middle-ear system is to receive the acoustic energy from the vibrating air-particles and to transmit this energy to the inner-ear system, it shows a certain resemblance to the acoustic devices constructed for the reception and reproduction of sound-vibrations. In this light the system can best be regarded as a pressure-receiver for the lower and the middle frequency-range. v. Békésy's statement that the pressure-transformation by the middle-ear system is independent of frequency up to 2400 c/s is in accordance with this view. The small displacements of the tympanic membrane in response to sound-vibrations, and its oblique position can readily be explained when the middle-ear system is considered to be pressure-driven. In the area between 1000 and 3000 c/s, the resonance-area of the ear, the acoustic impedance of this receiver is closely matched to that of air, so that a relatively free transfer of acoustic energy from the air to the middle-ear system is made possible.

The inner-ear system is essentially a hydrodynamic system. Since the hearing function is still maintained to a certain extent after total removal of the middle-ear system, it may be considered as an independent system with the stapes as its source of energy. Under abnormal conditions, when the sound-waves have free access to the foramen rotundum niche, it is not impossible that the sound-waves may eventually enter the inner ear by way of the foramen rotundum (Wever, Kobrak).

On account of the small dimensions and the inaccessability of the cochlear system, the study of the hydrodynamic behaviour of the inner-ear system constitutes a problem presenting utmost difficulties.

Since the cochlear fluids must be regarded as incompressibly enclosed in a rigid capsule, the system must have somewhere a low-resistance pathway where the pressure-variations communicated to the fluid by the oscillatory movements of the stapes can be compensated. Ever since Weber the membrane of the foramen rotundum has been regarded as such a compensation-area. Oscillations of the membrane in response to air-conducted sounds have been repeatedly observed.

If this assumption is valid, it is to be expected that immobilisation of this membrane will result in an impairment of the hearing function. Experiments carried out by various observers, however, indicate that blocking of the foramen rotundum membrane does not markedly interfere with the cochlear function. We are thus confronted with the necessity either to accept alternative routes for the pressure release in the inner-ear system, or to abandon the theory that a shuttle-action of the cochlear fluid between the oval window and some low-resistance pathway is necessary to evoke a hearing sensation.

Though a great amount of experimental work has been carried out on the problem of the significance of the foramen rotundum membrane in the process of hearing, its ultimate function has not yet been fully elucidated. In this connection also, may be mentioned the conception of Hughson, who postulated that the membrane may operate as a safety-valve for sharp pressure-pulses occurring in the cochlea. Such a shock-absorbing function, which was also defended by Pohlman, may be regarded as a means to protect the vulnerable structures of the inner ear for shock-pulses of dangerously large amplitude.

In our opinion the hydrodynamic behaviour of the inner-ear system is still open to considerable question, and more experiments will be needed before the problem may be regarded as being completely solved.

Based on the assumption that the pressure-waves initiated at the stapes can be compensated in the inner-ear system, two principally different conceptions about the propagation of a pressure-pulse have been advanced:

1. *mass movement* — the physical basis of this view was provided by the great length of compression-waves in fluid relative to the dimensions of the cochlea. Even for the highest audible frequencies the wave-length in water (at 20.000 c/s still 7.5 cm) is great compared with the length of the fluid column between the fenestra ovalis and the foramen rotundum, via the helicotrema (about 60 mm). The phase-difference between the two windows would thus be less than 1°. Hence every part of the moving fluid column was regarded as being almost in equal phase and the movement of the windows and the intervening fluid was virtually considered to be a mass movement (Weber, Helmholtz).

2. *wave movement* — if the inner ear is treated as a hydrodynamic system contained in a vessel with partly elastic walls, the theory of wave-propagation in media constrained by elastic boundaries may be applied to the system. In such a system travelling waves may occur, whose wave-length and velocity of propagation are much less than the corresponding magnitudes of compression-waves in the same fluid. It may thus be computed that for most of the audiofrequencies these travelling waves have a wave-length which is smaller than the dimensions of the cochlea. (Ranke, Reboul). Though some early theories of hearing suggested the occurrence of travelling waves in the cochlea, experimental evidence supporting this view was first provided by v. Békésy, who observed the movements of the membranous partition in a scale model of the cochlea and in the inner ear of cadavers under stroboscopic illumination. If the various anatomical data, and the physical constants of the inner ear structures, such as the dimensions of the cochlear canal, the density and viscosity of the perilymph, and the variable impedance of the ductus cochlearis are known, it must be possible to deduce the dynamic differential equations describing the wave-movement in the inner-ear system. Such a mathematical

treatment of this wave-propagation has been undertaken respectively by Ranke, Reboul and Zwislocki.

Closely related to the problem of wave-propagation in the cochlea is the question of the sound-analysis function of the ear. Ever since Ohm described this characteristic property of the ear, its explanation has formed a basic principle for any theory of hearing.

The first well-founded theory of hearing propounded by Helmholtz in 1863, attributed this analysis function to the structures of the inner ear, the underlying mechanism being the resonance-activity of selective parts of the basilar membrane in response to tones of varying frequency.

By this mechanism a spatial distribution of pitch-perception along the basilar membrane could be accounted for, the high tones being located at the base and the low tones at the apex of the cochlea.

More than half a century elapsed before experimental confirmation of this theory of localized pitch-perception could be obtained.

The evidence for tone-localization in the cochlea has now become formidable and is quite conclusive for such a place-theory of frequency-reception. At the same time it has been demonstrated that the different responsive areas for the various tones of the auditory range are fairly regularly distributed along the basilar membrane.

Many objections have, however, been raised against Helmholtz's resonance-hypothesis, the most important having always been the inconsistency of a high selectivity of the ear combined with its almost critical damping. No physical resonant system can, however, exhibit both phenomena at the same time and many auxiliary hypotheses appeared to be necessary to regain confidence in the resonance-theory and to explain this damping versus selectivity paradox. (Chapter V).

The travelling wave-theories, which entirely refute the resonance-hypothesis of the basilar membrane, account for the frequency-localization by a local vibration maximum of the basilar membrane resulting from the peculiar physical behaviour of the inner-ear system (Chapter VI).

Although these theories may give a satisfactory explanation of the frequency-discrimination in the cochlea, we have still to face the problem of the stimulating mechanism for the sensory cells of the organ of Corti. Whereas both the resonance-theory and the travelling wave-theories attribute this function to the structures involved in the first phase of the hearing process, Pohlman (4) postulated that the sensory cells of the organ of Corti react directly to the vibrations applied by the cochlear fluid. In this theory the sound-analysis function is referred to the structure involved in the second phase of the hearing process.

Not until more evidence for this assumption, which does not give a plausible explanation of the complicated structure of the inner-ear system is provided, can this theory be accepted.

If, however, the frequency-analysis is effected outside this sensory organ by the cooperation of the various physical constants of the inner-ear system, the stimulating mechanism for the hair-cells must be looked for in the structures in direct contact with these sensory cells. As such our attention is drawn to the tectorial membrane, whose lower surface is in direct contact with the "hairs" protruding from the upper surface of the hair-cells. Either a displacement of this membrane in a longitudinal or radial direction relative to the surface of the sensory cells or a pressure-traction mechanism may constitute the source of hair-cell stimulation.

The first mechanism would be effective if the inner ear operated as an acoustic receiver of the so-called displacement type, whereas the second mechanism presupposes that the inner ear acts more or less as a pressure-receiver.

v. Békésy suggested that the eddies, generated in the cochlear fluid at the local vibration maximum of the basilar membrane, form an adequate pressure-stimulus for the organ of Corti. In Reboul's theory the pressure-gradient in the cochlear fluid resulting from the travelling wave-movement is regarded as the determining factor of hair-cell stimulation.

In this connection mention must be made of the experiments of Davis and his co-workers, which established that the negative phase of the sound-pressure wave constitutes the proper stimulus for the nerve-endings in the cochlea.

In all the theories discussed above the basilar membrane plays a primary rôle in the explanation of the hearing function. Various anatomical objections, such as the variable structure in man (Wever) and in different animals (Shambaugh, Hardesty) may, however, be raised against the basilar membrane holding such a predominant place in most theories of hearing. Moreover, if we accept that sound-waves enter the inner ear by way of the fenestra ovalis, the tectorial membrane lies nearest to the incoming wave-movement and it seems logical to assume that this membrane is first and more easily activated by this movement than the basilar membrane, which is covered by a thick layer of cells. The primacy of the movements of the tectorial membrane as the stimulating factor for the hair-cells was already put forward by Kishi and Shambaugh, both writers ascribing a resonant function to this structure. On account of its anatomical structure, however, Hardesty thought it very improbable that the tectorial membrane was capable of acting as such a sympathetic resonator.

The view that the tectorial membrane may form the principal vibrating element has recently again been advanced by Mygind. Proceeding from the assumption that the cuticular membranes covering the cupula, the otoliths, as well as the organ of Corti operate as pressure-transformers, a theory is developed which accounts for a localized pitch-perception in the cochlea.

The primacy of the movements of the basilar membrane as the sole source of hair-cell stimulation is also questioned by Larsell and co-workers. It was shown that in the developing cochlea of the pouched opossum young the tectorial and the basilar membrane are well differentiated long before cochlear function appears. This applies also to the hair-cells and the nerve-fibres. Not until the pillars of Corti and the remainder of the supporting apparatus which undergo a slower differentiation, have reached adult state was this function established. The supporting apparatus may thus be regarded as a resiliant apparatus between the two membranes, acting as a cushioning and tension mechanism. In such a conception pressure in the perilymph of the scala vestibuli, transmitted through Reissner's membrane and the endolymph, and localized according to the pressure-gradients, as was suggested by Reboul, would impinge on the tectorial membrane and, through it, on the hair-cells. This conception does not deny movements of the basilar membrane in response to vibrations of the perilymph, but it does not assign to the basilar membrane alone the stimulating function.

Whereas the function of the middle-ear system relative to its structure is now fairly well recognized, the functional mechanism of the inner-ear system has not yet been fully elucidated.

If the hair-cells of the organ of Corti are to be considered as the receptive elements for the physical energy of the sound-impulse, any theory of hearing must now provide for a localized stimulation mechanism of these sensory cells. Ever since Helmholtz the basilar membrane has played a dominating rôle in the explanation of such a localized receptivity.

In these theories concerning the movements of the basilar membrane the intricate structure of the organ of Corti has usually been disregarded. But since this structure is capable of receiving the very minute mechanical stimuli occurring at threshold intensity of the audiofrequencies, the prime importance of the basilar membrane in this refined mechanism is open to considerable question. Not until methods are found, which allow of an experimental approach to this delicate structure, can the ultimate function of its different parts be evaluated and the real basis be found for a theoretical approach to the problem of the mechanism of the cochlear system.

SAMENVATTING.

Het is mogelijk het gehele gehoorproces schematisch in drie phasen te verdelen. Door het geluidsgeleidingssysteem wordt de geluidsprikkel naar het eigenlijke zintuigorgaan, het orgaan van Corti, gevoerd (phase I). Hier wordt de physische energie in zenuwenergie omgevormd (phase II), waarna tenslotte het zenuwgeleidingssysteem de impuls overbrengt naar de acoustische centra in de grote hersenen (phase III).

Na een korte beschrijving van de anatomische structuur

van het binnenoor en een historisch overzicht over de ontwikkeling van de gehoortheorieën tot het midden der 19de eeuw, wordt in dit proefschrift hoofdzakelijk de eerste phase van het proces, die der geluidsgeleiding, beschreven. Hierbij is onderscheid gemaakt tussen:
a. theorieën en experimenten betreffende de *geluidsgeleiding* en
b. theorieën en experimenten aangaande de *geluidsanalyse* in het oor.

Bij de bespreking van de eerste groep werd uitgegaan van de theorie van Weber-Helmholtz, waarbij de verschillende hypothesen, waarop deze theorie is gegrondvest, in het licht der experimentele gegevens nader worden bezien (Hoofdstuk IV). Het uitgangspunt voor de tweede groep vormde de klassieke resonantietheorie van Helmholtz, die tracht de geluidsanalyse, als een der fundamentele eigenschappen van het gehoororgaan, te verklaren door resonantie van verschillende segmenten van de basilairmembraan. De diverse argumenten voor en tegen deze opvatting worden in Hoofdstuk V nader besproken, waarbij mag worden geconcludeerd, dat een geluidsanalyse door resonantie in de oorspronkelijke zin van Helmholtz, als zeer onwaarschijnlijk mag worden beschouwd, doch dat de gelocaliseerde toonperceptie, zoals door Helmholtz aangegeven, door een groot aantal experimenten overtuigend is bewezen.

De hydrodynamische theorieën, die de geluidsanalyse in het algemeen trachten te verklaren zónder gebruikmaking van het principe der physische resonantie, gaan uit van de gedachte, dat als gevolg van een beweging van de stapes zich een lopende golf langs de basilairmembraan voortplant. Een plaatselijk optredend drukmaximum, bepaald door de verschillende physische factoren van de cochlea, zou dan als prikkel voor het orgaan van Corti fungeren. De modelexperimenten van von Békésy, waarbij inderdaad deze lopende golf kon worden aangetoond, alsmede de verschillende physisch-mathematische berekeningen over de voortplanting van een golf in een ten dele elastische buis worden in Hoofdstuk VI besproken.

Tenslotte is getracht, uitgaande van de gedachte dat het geluidsgeleidingssysteem een mechanisch systeem is, dat in staat is gedwongen trillingen uit te voeren, in Hoofdstuk VII

de verschillende physische eigenschappen van dit systeem na te gaan, waarbij de eigenschappen van geluidsontvangers in het algemeen als uitgangspunt werden genomen.

SUMMARY.

The entire process of hearing may be divided into three stages. The sound-conducting system transfers the sound-stimulus to the sensory organ proper, the organ of Corti (stage I). Here the physical energy is transformed into nervous energy (stage II), and the acoustic pathways finally conduct the impulse to the acoustic centres in the brain.

After a short description of the anatomical structure of the inner ear and a historical survey of the development of the theories of hearing up to the middle of the 19th century, this thesis deals essentially with the first stage of the hearing process. A distinction has been made between:
a. theories and experiments concerning *sound-conduction* and
b. theories and experiments concerning *sound-analysis* in the ear.

In the discussion of the first group an attempt was made to proceed from the theory of Weber-Helmholtz, in which the various hypotheses on which this theory is founded are studied in the light of experimental data (Chapter IV). The starting-point for the second group was the classic resonance-theory of Helmholtz, which tries to explain sound-analysis, as one of the basic principles of the hearing organ, by means of resonance of various segments of the basilar membrane. The arguments for and against this conception are discussed in Chapter V, and it may be concluded, that sound-analysis by resonance in the original sense of Helmholtz is highly improbable, but that a localized frequency-reception, as indicated by Helmholtz, has been confirmed by a great number of experiments.

The hydrodynamic theories, which attempt to explain sound-analysis without making use of the principle of physical resonance, proceed from the idea that consequent to a movement of the stapes a travelling wave travels up the vestibular scale, along the basilar membrane. A local pressure-maximum, determined by the various physical characteristics of the cochlea, would then constitute the stimulus for the organ of Corti. The experiments by von Békésy on models, in which such a travelling wave could actually be demonstrated, as well as the various physico-mathematical computations of the propagation of a wave in a partly elastic vessel, are discussed in Chapter VI.

Finally an attempt has been made, originating from the idea that the sound-conducting system is a mechanical one, capable of executing forced vibrations, to determine the various physical properties of this system, in which the properties of sound-receivers in general were taken as a starting-point.

RÉSUMÉ.

Schématiquement il est possible de diviser le processus de perception auditive en trois phases. Par l'appareil de transmission, l'excitation sonore est transmise à l'organe spécifique de l'audition: l'organe de Corti (Phase I). Celui-ci transforme l'énergie physique en énergie nerveuse (Phase II). Enfin l'influs est transmis par voie nerveuse au centre acoustique du système nerveux central (Phase III).

Après une courte description de la structure anatomique de l'oreille interne et quelques considérations historiques sur l'évolution des théories de l'audition jusqu'au milieu du dix-neuvième siècle, l'auteur dans sa thèse ne prend en considération que la première phase du processus auditif: celle de la transmission des sons à l'organe de Corti. Il faut distinguer:

a. les théories et expérimentations touchant la *transmission des sons.*

b. celles touchant l'*analyse des sons* dans l'oreille.

La première partie est traitée en prenant comme point de départ la théorie de Weber-Helmholtz. Les diverses hypothèses, sur lesquelles la théorie repose seront étudiées de plus près à la lumière de données expérimentales. (Chapitre IV). La seconde partie est basée sur la classique théorie de résonance de Helmholtz. Celle-ci tend à expliquer l'analyse des sons, propriété essentielle de l'organe de l'audition, comme résultant de la résonance de différents segments de la membrane basilaire. Les divers arguments pour et contre ce point de vue sont traités dans le Chapitre V. Par suite on peut conclure, qu'une analyse des sons par résonance dans le sens où Helmholtz l'entendait originalement, ne peut plus être considérée que comme peu vraisemblable, bien que l'on reste vaincu de la perception localisée des sons telle qu'il l'avait consignalée et telle qu'elle a été démontrée par nombre d'expériences.

Les théories hydrodynamiques ou ondulatoires, qui en général tendent à expliquer l'analyse des sons sans l'aide du principe physique de la résonance, partent de l'idée qu' à la suite d'un mouvement de l'étrier une onde se propage le long de la membrane basilaire. L'apparition d'une pression maximale à localisation déterminée par la fréquence des vibrations et les propriétés de la cochlée, fonctionnerait comme excitant de l'organe de Corti.

Les expériences de v. Békésy sur un modèle de l'oreille interne, par lesquelles fût en effet démontrée l'existence de cette onde de propagation, ainsi que les différents calculs physico-mathématiques de la propagation d'une onde sonore dans un canal partiellement élastique, seront traitées au Chapitre VI.

Partant du principe que l'appareil de transmission des sons est un système mécanique, apte d'exécuter des vibrations forcées, l'auteur poursuit enfin au Chapitre VII l'étude des diverses propriétés physiques de ce système comparées aux propriétés des récepteurs du son en général.

ZUSAMMENFASSUNG.

Der ganze Hörprozess lässt sich in drei Phasen einteilen: Durch das Schalleitungssystem wird der Schallreiz nach dem eigentlichen Sinnesorgan, dem Corti'schen Organ, geleitet (Phase I). Hier wird die physikalische Energie in nervöse umgewandelt (Phase II), worauf schliesslich das nervöse Leitungssystem den Impuls nach den akustischen Zentren im Grosshirn überführt (Phase III).

Nachdem der anatomische Bau des Innenohres kurz beschrieben und in einem geschichtlichen Ueberblick die Hörtheorien in ihrer Entwicklung bis in die Mitte des 19. Jahrhunderts dargestellt wurden, kommt in der vorliegenden Dissertation hauptsächlich die erste Phase des Prozesses, die der Schalleitung, zur Behandlung. Dabei sind zu unterscheiden Theorien und Experimenten

a. über die *Schalleitung*

b. über die *Schallanalyse* im Ohr.

In der Besprechung der ersten Gruppe wird ausgegangen von der Weber-Helmholtz'schen Theorie. Die verschiedenen Hypothesen, auf die sich diese Theorie stützt, werden im Hinblick auf die experimentellen Ergebnisse näher betrachtet (Kapitel IV). Den Ausgangspunkt für die zweite Gruppe bildete die klassische Resonanztheorie von Helmholtz. Dieselbe sucht die Schallanalyse — als eine der fundamentalen Eigenschaften des Gehörorgans — zu erklären als Resonanz verschiedener Segmente der Basilarmembran. Die für und wider diese Auffassung sprechenden Argumente werden in Kapitel V näher auseinandergesetzt. Dabei darf wohl die Schlussfolgerung gezogen werden, dass eine Schallanalyse durch Resonanz im ursprünglichen Sinne Helmholtz's als sehr unwahrscheinlich zu betrachten ist, dass jedoch die lokalisierte Tonperzeption, wie sie durch Helmholtz angegeben wurde, durch eine grosse Anzahl Untersuchungen überzeugend bewiesen ist.

Die hydrodynamischen Theorien suchen die Schallanalyse im allgemeinen zu erklären, ohne auf das Prinzip der physikalischen Resonanz zurückzugreifen. Sie gehen aus von dem Gedanken, dass infolge einer Bewegung des Steigbügels sich eine laufende Welle entlang der Basilarmembran fortpflanze. Ein lokalisiert auftretendes Druckmaximum, bestimmt durch die verschiedenen physikalischen Eigenschaften der Cochlea, soll dann als Reiz für das Corti'sche Organ dienen. Die Modelversuche von Békésy's, mittels derer tatsächlich diese sich fortpflanzende Welle nachgewiesen werden konnte, samt den verschiedenen physikalisch-mathematischen Berechnungen über die Fortpflanzung einer Welle in einem teilweise elastischen Rohr, werden in Kapitel VI besprochen.

Von dem Gedanken ausgehend, dass das Schalleitungssystem ein mechanisches System ist mit der Fähigkeit, erzwungene Schwingungen auszuführen, wird in Kapitel VII schliesslich versucht, den verschiedenen physikalischen Eigenschaften dieses Systems nachzugehen. Als Ausgangspunkt dieten dabei die Eigenschaften der Schallempfänger im allgemeinen.

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SUBJECT INDEX

STELLINGEN

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I

Onder normale omstandigheden worden de geluidstrillingen via de gehoorbeentjesketen en het ovale venster op de vloeistof van het binnenoor overgebracht.

II

Het is echter zeer waarschijnlijk, dat na de fenestratie-operatie de geluidstrillingen het binnenoor via het ronde venster bereiken en dat de bij deze operatie in de horizontale booggang gemaakte opening als uitwijkplaats voor de vloeistof van het binnenoor fungeert.

III

Voor de functie van het binnenoor is de membrana tectoria waarschijnlijk van groter betekenis dan de membrana basilaris.

IV

De hydrodynamische gehoortheorieën, welke het binnenoor beschouwen als een hydrodynamisch systeem met ten dele elastische wand, zijn in staat een betere verklaring te geven voor de klankanalyse en de gelocaliseerde toon-perceptie in het binnenoor dan de klassieke resonantie-theorie van Helmholtz.

V

Bij lijders aan zogenaamde otosclerose is het, bij het overwegen van operatieve hulp, een zeer dringende eis de totale persoonlijkheid, dus ook de geestelijke zijde hiervan, mede in ogenschouw te nemen.

VI

In gevallen van lymphadenitis colli tuberculosa dient tonsillectomie ernstig in overweging te worden genomen.

VII

Het veelvuldig voorkomen van tuberculeuze afwijkingen in tonsillen en adenoid bij lijders aan niet-open tuberculose maakt een haematogeen ontstaan van deze tuberculeuze haarden waarschijnlijk.

VIII

Het verdient aanbeveling te trachten de eventuele secundaire shockverschijnselen tengevolge van ernstige verwondingen door vroegtijdig toedienen van antihistaminica te bestrijden.

IX

Men denke bij de aetiologie van de abortus in het begin van de zwangerschap aan banale infecties in de neus en nasopharynx.

X

Het geluidsgeleidingssysteem in het gehoororgaan, dat bestaat uit trommelvlies, gehoorbeentjesketen en de vloeistof van het binnenoor, kan als een trillend mechanisch systeem worden beschouwd.

XI

De physische eigenschappen van dit systeem dienen door een nauwe samenwerking tussen physici en biologen nader te worden bestudeerd.

XII

Er dienen in ons land enkele Centrale Instituten voor het onderzoek en de behandeling van slechthorenden te worden gesticht.

XIII

Het voorschrijven van een gehoorapparaat moet als een medische handeling worden beschouwd.

XIV

In verband met de grote hoekversnellingen bij de moderne jachtvliegtuigen is een onderzoek der vliegers op hun weerstandsvermogen tegen de hierbij optredende centrifugale krachten vereist.