ON THE MECHANISM OF HEARING

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CONTENTS

Summary

The aim of the investigation described in this thesis was to use data on the anatomy, physiology and dynamics of the ear and on hearing phenomena to design an electrical model of the ear which might be of some help in giving a clearer picture of the mechanism of hearing.

The first chapter describes the evolution of the ear, with special reference to the fact that the middle ear was developed before the cochlea.

The second chapter is devoted to the cochlea. After a brief description of the anatomy, the equation of motion of the cochlear partition is derived. It appears from this equation that the dynamic properties of the cochlea can be explained on the basis of the mechanical properties of the partition and of a thin layer of liquid on either side of it. In other words, the cochlea appears to contain a surplus of liquid, which explains Von Békésy's paradox. It is shown that the at first sight rather over-complicated structure of the cochlea is in fact necessary if it is to perform its function, and that other, simpler, structures would not work. The equation of motion derived here is compared with those given by Zwislocki, Peterson and Bogert, Fletcher and Ranke. The electrical model of the cochlea is then described. This is based mainly on data given by Von Békésy. It consists of one hundred discrete units linked to each other, each unit giving an output voltage proportional to the displacement at the corresponding place on the cochlear partition. One hundred units are used because this allows the frequency difference between tones giving maximum signals at neighbouring units to be made about a semi-tone, while the total range of the model is about eight octaves, i.e. about the same as that of the ear. The behaviour of the model for sinusoidal input signals and the input impedance are also calculated.

The third chapter deals with the middle ear. After an anatomical introduction, details are given of the reasoning underlying the design of the electrical model of the middle ear, which is more or less the same as Zwislocki's. There are however not enough data available on the mechanics of the middle ear to allow a completely satisfying model to be designed. Thus although this model represents certain aspects of the behaviour of the middle ear quite well, there are several reasons for doubting its universal validity. There is no point in trying to improve the model at present, until we have some data on the behaviour of the middle ear at frequencies above 2000 c/s. The model is compared with those built by other workers. An application of this model for the testing of artificial ears is also given. The most important information which we can derive from a study of the middle ear is the form of its overall response characteristic, i.e. the displacement of the oval window for a constant pressure on the eardrum as a function of the frequency. This characteristic is horizontal up to a certain point in the medium-frequency range, and then falls steeply.

The combination of the middle ear and inner ear is studied in the fourth chapter, and some explanation is given of the form of the threshold curve for pure tones. The maximum sensitivity of the ear at medium frequencies is determined by noise (i.e. not the noise produced by the mechanical motion of the system).

The decrease in sensitivity at low frequencies can be explained by the properties of the auditory nerve, while at high frequencies this is mainly due to the filter action of the middle ear.

The "spectroscope" used to represent the amplitude of the signals from the various taps of the cochlear model on a television screen is then described, and photographs are given of the cochlear spectrum and the wave form of the signals at various taps for input signals in the form of pure tones masked by other pure tones or by noise, of square-waves and filtered square-waves, amplitude-modulated signals (residue) and speech.

It is concluded that it is not yet possible to give a complete theory of hearing, but that there are reasons for doubting the correctness of several existing theories. Care must be taken when constructing a theory

of hearing not to bring in properties of the cochlea which do not harmonize with the physical limitations of the middle ear. It is however possible to give explanations of certain phenomena, such as the perception of pitch, timbre and loudness, and the reason for certain types of nerve deafness. Certain place and time correlation measurements between the nerve endings and at higher levels of the nervous system are essential for proper hearing, but a place-detection mechanism as postulated in the various place theories is not absolutely necessary.

Finally, the fifth chapter summarizes those results of this investigation which may be regarded as fairly reliable.

Résumé

Les recherches décrites dans cette thèse avaient pour but d'établir, par une combinaison des données nous fournies par l'anatomie, la physiologie, la dynamique de l'oreille et la phénoménologie de l'ouïe, un modèle électrique de l'organe auditif, afin d'acquérir une idée plus exacte du fonctionnement de l'oreille humaine.

Le premier chapitre traite de l'évolution de l'oreille et fait ressortir que l'oreille moyenne est née bien avant le cochléa.

Le second chapitre est consacré au cochléa. Une introduction anatomique est suivie de l'établissement de l'équation de mouvement qui s'avère particulièrement utile pour la description des phénomènes physiques qui se déroulent dans le cochléa. C'est ainsi que le comportement mécanique de la cloison cochléaire est déterminé par les propriétés mécaniques de cette cloison et par une mince couche de liquide qui se trouve de chaque côté de cette cloison. Le cochléa contient nettement un excès de liquide, ce qui permet d'expliquer le paradoxe de Von Békésy. La construction remarquable du cochléa semble la seule utilisable; d'autres constructions, plus évidentes, ne donneraient pas satisfaction. L'équation de mouvement établie est comparée avec celles données par Zwislocki, Peterson et Bogert, Fletcher et Ranke. Cette comparaison est suivie d'une description d'un modèle électrique du cochléa que nous avons réalisés à l'aide de données essentiellement puisées dans l'ouvrage de Von Békésy. Ce modèle est constitué par cent éléments discrets interconnectés, dont chacun fournit une tension équivalente à la déviation de la cloison cochléaire à l'endroit correspondant à un tel élément. La différence en fréquence de crête entre des éléments voisins est donc d'un demi ton. Les propriétés du modèle pour des signaux sinusoïdaux ainsi que l'impédance d'entrée sont mentionnées.

Le troisième chapitre traite de l'oreille moyenne. Après une introduction anatomique, on décrit comment on est arrivé à la construction d'un modèle électrique, en principe analogue à celui de Zwislocki. Toutefois, le nombre de données mécaniques connues ne suffit pas encore pour réaliser un ensemble satisfaisant. Les propriétés de ce modèle présentent certaines analogies avec celles de l'oreille moyenne, mais cela n'empêche que des doutes sérieux s'élèvent en ce qui concerne son exactitude. Il s'avéra cependant inutile de rechercher une amélioration étant donné que l'on ignore encore tout du comportement de l'oreille moyenne pour des fréquences supérieures à 2000 Hz. Le modèle établi est comparé avec d'autres. Une discussion relative à l'oreille moyenne est complétée par une description d'oreilles artificielles. Le résultat le plus important de l'étude de l'oreille moyenne est sa caractéristique de fréquence, c'est-à-dire la déviation de la fenêtre ovale, sous une pression constante sur la membrane du tympan, en fonction de la fréquence. Cette caractéristique est en palier jusqu'à une fréquence de la gamme moyenne pour tomber ensuite brusquement.

Le quatrième chapitre est consacré à l'étude de la combinaison oreille moyenne-oreille interne. La forme de la courbe de seuil de la tonalité peut s'expliquer dans une certaine mesure. La sensibilité maximale de l'oreille dans la partie horizontale de la courbe dans la gamme des fréquences moyennes est déterminée par un bruit (pas par le bruit que provoque l'ensemble du système mécanique). La pente de la courbe

dans la gamme des notes graves est due aux propriétés du nerf auditif, de celle dans la gamme des notes aiguës à l'effet de filtre de l'oreille moyenne.

Cette étude est suivie d'une description de l'appareillage utilisé pour photographier le spectre cochléaire. On donne des photographies de l'enveloppante de la déviation de la cloison cochléaire dans le cas de signaux composés, ainsi que ces déviations mêmes telles qu'elles se perçoivent en certaines endroits le long de la cloison. On a utilisé à cet effet des sons purs, masqués par d'autres sons purs ou du bruit, la somme de deux sons purs, des signaux en forme de blocs, filtrés et non filtrés, des signaux modulés en amplitude (résidu) et des signaux vocaux.

Il est encore impossible de formuler une théorie complète de l'ouïe mais l'exactitude de certaines théories déjà existantes est sujette à caution. Une explication possible est donnée de certaines phénomênes auditifs tels que la perception de la hauteur d'un son, du timbre, de l'intensité et de la cause de surdités des nerfs. Certaines mesures de corrélation en lieu et en temps doivent exister entre les récepteurs et les fibres nerveuses, mais un mécanisme de détection d'emplacement, tel que décrit dans les théories dites de localisation, n'est pas indispensable.

Le cinquième chapitre récapitule enfin, point par point, les résultats des recherches au sujet desquelles on dispose d'une certaine certitude.

Zusammenfassung

Die in dieser Dissertation beschriebene Untersuchung steckte sich das Ziel, durch Kombination bereits bekannter Daten aus der Anatomie, der Physiologie, der Dynamik des Ohres und der Gehörphenomenologie zum Bau eines elektrischen Modells des Gehörorganes zu gelangen, um damit ein besseres Verständnis der Arbeitsweise unseres Ohres zu erhalten.

Im ersten Kapitel wird die Evolution des Ohres beschrieben, wobei es besonders auffällt, daß das Mittelohr früher entstanden ist als die Cochlea.

Das zweite Kapitel behandelt die Cochlea. Nach einer anatomischen Einleitung wird die Bewegungsgleichung aufgestellt, die bei einer Beschreibung der physikalischen Vorgänge in der Cochlea dienlich ist. So zeigt sich, daß das mechanische Verhalten der Cochleamembran durch die mechanischen Eigenschaften dieser Membran sowie durch eine dünne Flüssigkeitsschicht zu beiden Seiten derselben bestimmt wird. Die Cochlea enthält offenbar einen Flüssigkeitsüberschuß, was eine Erklärung für das Paradox von Von Békésy ermöglicht. Die merkwürdige Konstruktion der Cochlea erweist sich als die einzig brauchbare, andere näherliegende Konstruktionen würden nicht entsprechen. Die abgeleitete Bewegungsgleichung wird mit denjenigen verglichen, die von Zwislocki, Peterson und Bogert, Fletcher und Ranke aufgestellt worden sind. Sodann wird die Beschreibung des elektrischen Modells der Cochlea gegeben, das wir mit Hilfe von Daten konstruierten, die wir in der Hauptsache der Arbeit von Von Békésy entlehnten. Dieses Modell besteht aus 100 diskreten aneinandergeschalteten Elementen, von denen jedes eine Spannung abgibt, die äquivalent der Auslenkung der Cochleamembran an einem solch einem Element entsprechenden Ort ist. Der Unterschied hinsichtlich der Scheitelfrequenz zwischen benachbarten Elementen beträgt einen halben Ton. Es werden die Eigenschaften des Modells für sinusförmige Signale sowie die Eingangsimpedanz gegeben.

Das dritte Kapitel handelt über das Mittelohr. Nachdem wieder eine anatomische Einleitung gegeben ist, wird beschrieben, wie es zur Konstruktion des elektrischen Modells gekommen ist, das im Prinzip dem von Zwislocki gleicht. Es sind jedoch noch zu wenig mechanische Daten bekannt, um zu einem befriedigenden Ganzen zu gelangen. Wohl zeigt dieses Modell gewisse Übereinstimmungen in seinen Eigenschaften mit denen des Mittelohrs, doch andererseits erheben sich starke Zweifel an seiner allgemeinen Richtigkeit. Es erwies sich jedoch als sinnlos nach einer Verbesserung zu suchen, da das Verhalten des Mittelohrs für

Frequenzen oberhalb 2000 Hz noch nicht bekannt ist. Es wird ein Vergleich mit Modellen anderer Untersucher gegeben. Mit der Diskussion über das Mittelohr ist zugleich die Besprechung von Kunstohren verknüpft. Das wichtigste Ergebnis der Untersuchung an dem Mittelohr ist seine Übertragungskennlinie, worunter die Auslenkung des ovalen Fensters bei konstantem Druck auf dem Trommelfell als Funktion der Frequenz verstanden wird. Diese Kennlinie verläuft horizontal bis zu einer Frequenz im Mittelbereich, um danach steil abzufallen.

Die Kombination Mittelohr - inneres Ohr wird im vierten Kapitel untersucht. Der Verlauf der Tonschwellenkurve kann bis zu gewissem Grade erklärt werden. Die größte Empfindlichkeit des Ohres im horizontalen Teil der Kurve im Mittelfrequenzbereich wird durch ein Rauschen bestimmt (aber nicht durch das Rauschen, das durch das ganze mechanische System hervorgerufen wird). Die Neigung der Kurve im Tieftongebiet wird durch Eigenschaften des Gehörnerves verursacht, diejenige im Hochtongebiet hauptsächlich durch die Filterwirkung des Mittelohres.

Sodann wird die Apparatur beschrieben, mit der das Cochleaspektrum photographiert wurde. Es werden Aufnahmen der Umhüllenden der Auslenkung der Cochleamembran bei zusammengesetzten Signalen gezeigt, sowie die Auslenkungen selbst, wie sie an bestimmten Stellen längs der Membran zu sehen sind. Es wurde mit reinen Tönen gearbeitet, die durch andere reine Töne oder Rauschen verdeckt werden, mit der Summierung zweier reiner Töne, mit gefilterten oder nicht gefilterten blockförmigen Signalen, mit amplitudenmodulierten Signalen (Residu) und Sprachsignalen.

Es kann noch keine geschlossene Gehörtheorie gegeben werden doch die Richtigkeit bestimmter bereits bestehender Theorien ist in Zweifel zu ziehen. Ein Gehörtheorie darf nicht auf vermeintliche Eigenschaften der Cochlea beruhen, von denen im Zusammenhang mit der Wirkungsweise des Mittelohrs kein Gebrauch gemacht werden kann. Wohl wird eine mögliche Erklärung bestimmter Gehörphenomene gegeben, wie der Wahrnehmung von Tonhöhe, Timbre, Lautheit und bezüglich der Ursache von einigen Formen von Nerventaubheit. Bestimmte Korrelationsmessungen hinsichtlich Ort und Zeit zwischen die Rezeptoren und zwischen den Nervenfasern müssen vorhanden sein, jedoch ein Mechanismus zur Anweisung des Ortes, wie er in den sog. Orttheorien beschrieben wird, stellt keine Notwendigkeit dar.

Im fünften Kapitel sind schließlich die Ergebnisse der Untersuchung, über die eine gewisse Sicherheit besteht, noch einmal punktweise zusammengestellt.

I. INTRODUCTION

I.1. The problem of hearing

The theory of hearing is a subject which has fascinated many investigators, especially during the last century. The importance of hearing for human existence and the excellent properties of the hearing organ stimulated many scientists from different fields to make a study of the ear, which is man's principal link with his surroundings.

If one inspects the enormous list of publications devoted to the problem of hearing by anatomists, physiologists, otologists, physicist-audiologists, acousticians, communication-engineers, mathematicians, philosophers and psychologists, one might imagine that this problem would have been solved now, and this impression is reinforced by the positiveness with which some of the propositions in these publications have been put. So it might seem rather ridiculous to add another contribution to the long line of papers dealing with this matter.

On the contrary, if one realises the number of divergent theories of hearing which still exists, as may be seen from e.g. the books of Wever [1]) and of Kostelijk [2]), and if one sees how much space is devoted to this field in modern books, periodicals and congresses, one may conclude that the subject is still open to investigation and that there are still problems to be solved. Anatomy and especially physiology are developing very quickly, also because new techniques enable us to penetrate deeper into the matter, literally as well as figurative. For example, physiologists can now study the behaviour of one single nerve fibre during its pulse firing, with the aid of new micro-electrodes.

Acoustics, communication engineering and audiology have made and are still making great progress without considering the mechanism of hearing at all. But there are some questions, which cannot be answered so easily in this way.

In acoustics, for example, we have the problem of the quality of reproduction. There are people who insist upon amplifiers with a frequency-range up to 40 kc/s or 50 kc/s, although one might think that 16 kc/s would be sufficient. We do hear a difference but we cannot tell in what it consists. In the phonograph industry, some people have the job of listening all day to samples taken at random, in order to hear if there are any defects in the records. Why are there no instruments which can indicate that? Everybody can hear a scratch on a record! Maybe this is a psychological problem, more typically physiological is the question why we can hear a difference between two recordings, one of which has been made with a microphone which has a frequency characteristic which is flat and smooth and exactly the same as that of the other microphone, except for a few octaves in the middle frequencies, where there is a difference of e.g. 1 dB. There are people who have a preference for one of the two, but nobody complains about the frequency-characteristics of loudspeakers, with peaks and dips of more than 1 dB lying close together. And what does phase mean for our ear? We can hear a change in phase, but in most cases it does not influence the quality of music or of the spoken word. And although our commercial telephone does not reproduce tones below 300 c/s, we hear fairly natural voices through it, because our ear nevertheless detects the missing fundamental. This phenomenon, known as "residue", can be understood and is generally accepted nowadays, (see below), but it is a further indication that we cannot expect that the ear makes a simple Fourier analysis of sounds. Most experiments on hearing have been done with pure tones, but in the next chapters we shall see that it is a pity that more data are not available concerning complex sounds, such as speech or noise. And what is masking? That is another question which still lacks an answer. This, together with the problem of loudness, especially for complex and interrupted sounds, is growing in importance, because of noise control.

Communication engineers all know that speech contains a lot of redundancy. They are searching for systems which avoid the transmission of this redundancy so that they can decrease their bandwidth in order to make more efficient use of their emitters and transatlantic cables, or to give better signal-to-noise ratios. Many systems have been brought already and give more or less satisfaction but they are all based upon phenomenological knowledge and developed by trial and error. There still remains the problem of how we understand speech. What is the essential part of the speech signal, what role is played by the formants, is their frequency-region the principal information, or is it the ratio of the frequencies, or perhaps neither of them? We are now beginning to understand how we distinguish vowels, but know very little about the consonants, the most important speech sounds in spite of the fact that they usually carry so little power. Scientists are searching for the answer to these questions in many laboratories all over the world.

But most of all, the audiologist is groping in the dark. He has already developed numerous measuring methods in order to obtain acoustical data about the ears of his deaf patients. Those data are often a good help for the otologist in making his diagnosis, but what can the audiologist do with e.g. a pure-tone-audiogram? If it is possible to help his patient with a hearing-aid, does he have objective methods to fit those aids to his patient? Of course, some systems which give fairly good results in some cases do exist, but generally we may say that these methods are only an indication of the direction into which the audiologist must start with his trial-and-error methods. And many times he will be surprised by his results. He understands conduction deafness and mechanical deviations of the middle ear, or rather he would understand these, if he knew the exact working of the middle-ear system, which is not true as we shall see below. But nerve deafness is practically a closed book. This review of some problems gives perhaps a rather pessimistic impression of the position of the above-mentioned sciences: of course, much can be done without exact knowledge of the hearing mechanism, but, in any case, it is quite understandable

that hearing problems are arousing interest all over the world nowadays. And not only monaural hearing, which we have discussed here; binaural and directional hearing, with which we will not deal, is in the news because of the rise of stereophonics.

Hearing is a typical fringe area where the physiologist, the otologist and the physicist can meet each other. They all have a lot of data about hearing in their own fields, but the co-operation between them has in most cases not been close enough to draw all the possible conclusions from the combination of their data. On the contrary, we shall see in the following that some points become clearer when different data, which were known for a long time already, are combined. It is therefore important to regroup these data and to make a new study of the existing theories of hearing.

As might be expected, the theoretical treatment of complex signals passing through the hearing organ, is very laborious and cannot be done without the help of an electronic computer. We decided to build one of the analogue type, in other words, we constructed an electronic model of the monaural hearing organ, as far as that was possible. The data for this model, which we will describe in the next chapters, were mainly obtained from anatomy and physiology. From these sciences we often can deduce the "how" of the elements, within certain limits of course, but we shall see that it is also desirable to know the "why", because the answer to the latter question often leads to the essential points of the construction and may save us from mistakes.

The best way to get a clear picture of the function of the various parts of our complex hearing mechanism, is to follow its history throughout evolution.

1.2. The evolution of the ear

At the beginning of the primary, about 500 million years ago, the seas were full of fishes, but no fauna existed on the land. To get an idea of how communication was established, one looks for hearing and sound making organs. A cursory inspection of the fishes leads however to the conclusion that most of them are mute, except for the drumming sorts 4). Moreover they are streamlined, so that their motion through the water will not make very much noise. We might imagine that, except at its surface, the sea is a relatively silent world where no hearing organ is needed. And indeed, a cursory inspection of the fishes shows us that they do not have ears. A balancing organ is much more necessary, as in deep water vision is poor and distinct points for orientation are sometimes lacking; and in fact fishes have one or more semi-circular canals which are sensitive to inertial forces, and an organ which is sensitive to their position with respect to the direction of gravitation, on each side in their head. The latter operates by detecting the position of a small calciferous mass, the otolith, in a little sac. Most fishes have two of these systems, the utricle and the saccule, just as in mammals. All are filled with liquid.

If fishes could not hear at all, we might ask ourselves how they could follow each other when swimming in shoals. Recent experiments have shown that fishes can indeed hear over a remarkably wide range of frequencies, though discrimination between frequencies is poor. It is supposed that they hear by detecting the vibrations of the otolith in the saccule, while the utricle looks after balancing. The sound is conducted through the body, no outer ears can be found.

During the Denovian, geological changes caused some of the inhabitants of the water to live on land. It is clear that these animals would not be able to hear at all well, since most of the airborne sound would be reflected from their bodies, and would not be able to penetrate to their ears. A primitive land animal having the simple ear of the fish would only be able to detect contact sound via the ground, although even that might be damped out on the way through the body. We cannot expect such an animal to be able to distinct between directions, however, for the signal received reaches both ears at the same time and depends on the place of contact with the surface of the earth. In this respect the amphibians are better off, because they have something like a middle ear.

Romer 3), when comparing the anatomy of the structures in the vestibular region of fishes, reptiles and mammals, ranked these species in a series of increasing technical (that is acoustical) perfection.

We may summarize his conclusions as follows: When the jaws were developed from the gill bars in fishes, both the upper jaw and the lower jaw were originally loose, the joint between them being fixed with respect to the skull by the hyomandibular bone (see fig. 1*A*). The upper jaw later became part of the skull and this little bone was without function except possibly as a sound conducting bridge between the skull and the saccule. Once on land, the gill openings were redundant and the first one, the spiracle (see fig. 1*A*), was reshaped to give the auditory meatus, the middle-ear cavity and the Eustachian tube (fig. 1*B*, *C*, *D*). The meatus was closed by the eardrum in reptiles and the hyomandibular bone was used to form a connection between the eardrum and the oval window, which also arose at about the same period (fig. 1*B*). This bone, which we still find in birds, where it is called the columella, is equivalent to the stapes of the mammals. The jaw junction was then again modified, making the quadrate and articular bones, which formed that junction (fig. 1*B*, *C*, *E*), redundant. The malleus and incus were now developed from these two bones (fig. 1*C*, *D*). The hearing organ, apart from the inner ear, was thus developed from the respiratory organ of fishes by various routes 3).

It will be clear from the above that Romer sees this series also as a temporal sequence, describing the way the evolution has taken throughout time. However alluring this view may be, we must not forget that there is no definite proof that a similar evolution has indeed taken place. It must be said, however, that

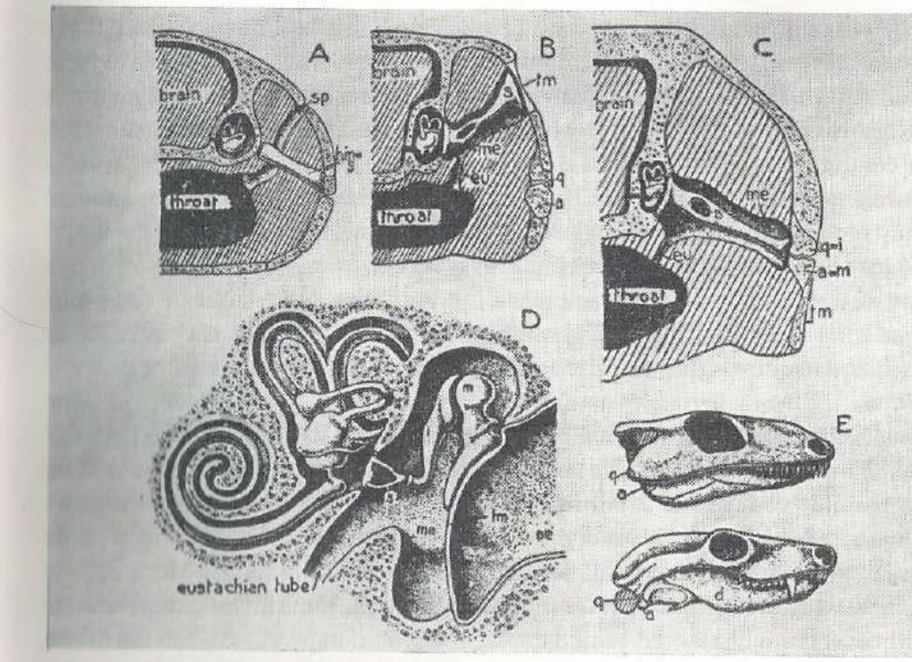

Fig. 1. *A-D*, a series of stages in the evolution of the ear apparatus. *A*, cross-section of half of the fishskull in the ear region. The ear consists of the internal ear, with its sacs and semicircular canals only. *B*, an amphibian. The hyomandibular bone (*hm*) of the fish is pressed into service as a sound transmitter, the stapes (*s*); the first gill slit, the spiracle (*sp*), becomes the Eustachian tube (*eu*) and the middle ear cavity (*me*), while the outer end of the spiracle is closed by the tympanic membrane (*tm*). *C*, a mammal-like reptile. The stapes passes close to two skull bones (*q*, *a*) which form the jaw joint. *D*, man (the ear region only, on a larger scale). The two jaw-joint bones have been pressed into service as accessory ossicles, the malleus (*m*) and the incus (*i*). *E*, a primitive land animal and a mammal-like reptile to show the relation of the eardrum to the jaw joint. At first in a notch high on the side of the skull (the otic notch) occupying the place of the fish spiracle, it shifts in mammal-like reptiles to the jaw region. In mammals the jaw becomes formed of one bone only (*d*, the dentary), and the bones of the jaw-joint region are freed to act as accessory hearing organs. (*oe*), tube of outer ear. From A. S. Romer, Man and the Vertebrates, A Pelican Book.

an applied scientist tends to find Romer's ideas most attractive because the human technical inventions have been perfected along the same line as Romer wants us to believe that evolution has taken place.

In any case, the ear of the mammal, with its lighter construction, perhaps together with a sort of transformer action of the middle ear, enables the animal to hear airborne sounds. The way to the hearing organ for airborne sounds is easier than and separated from the path for sounds conducted through the ground. Only the snake has to manage without eardrums, and is deaf for airborne sound.

The small microphone-like receiving organs of lower animals are probably not very good at discriminating between different frequencies and intensities. If a simple microphone action had been sufficient for the organ to detect the required information, it would have been "easier" to add it direct to the tympanic membrane, without liquid coupling, so that the middle ear could have been omitted. This seems to be impossible, as this line has not been taken by nature, probably because the receptors which had to be used were hair cells, connected to common nerve cells, which can discriminate between different frequencies and intensities up to a certain limit only. If this limit is to be raised, another construction is needed, and in the higher amphibians, the reptiles and the birds, we see the beginning of the cochlea. This is an extension of the receiving organ out of the saccule. In the amphibians the hair cells are set out in rows and connected to one membrane, whose motion stimulates them, and in reptiles, birds and mammals they are arranged between two membranes so that they are stimulated by the relative motion of one membrane to the other 4). Both constructions are still surrounded by liquid, which leads to believe that the liquid is essential for a suitable action. In the higher animals, e.g. the mammals, we see only changes of detail in this construction: the cochlea becomes still longer, and the hair cells are divided into two types in order, as far as we can see, to give a higher discrimination and a larger dynamic range. More details of these structures are given in the following chapters. Some investigators believe that the cochlea has lagged behind during the evolution process: when the fishes came to dry land it was "forgotten" to remove the liquid in the cochlea, so the middle-ear transformer was needed. On the contrary, if we take the teleological view of Romer, we believe that this liquid in the cochlea is essential for several reasons (see next chapter) and that a hearing organ with the properties it has in the higher organisms is impossible without that liquid. Moreover they are wrong in assuming that the cochlea already existed when the fishes came on land.

The structure consisting of a stretched membrane with hair cells arranged along it, transforms frequency differences into place differences, as we shall see later, and also enables us to discriminate simultaneously between two sounds coming from different directions 5), of course with the help of another such organ. This ability may be important for the preservation of life.

One of the latest developments added to the total organ is the pinna, the sound catcher in the air, with which mammals are provided. Some animals, e.g. the horse, can direct the pinna towards the sound source, while in other creatures, such as man, the pinna is so small, compared with the head, that it is practically useless.

The delicate eardrum is protected against damage by its position at some distance from the surface of the head. The auditory canal, through which it can be reached, gives a pressure increase by cavity resonance, often in the most important frequency range (about 3000 c/s in man).

In mammals, the simple columella has been replaced by the chain of three ossicles, the hammer, anvil and stirrup, which is far more sensitive to motions of the eardrum than to forces caused by movement of the head, yawning, walking, etc. We are tempted to say that this technical improvement is related to the heavy bodily vibrations of mammals that have to walk and jump. Little muscles connected to the hammer and the stirrup, which become active at higher intensities, protect the inner ear against very loud sounds 6).

It is interesting to see what has happened to the hearing organ of mammals which are believed to have gone back into the sea. In whales for example, one can speculate that the pinna disappeared, because it would give too much resistance during swimming. The highly developed cochlea and auditory nerve remained however, but the middle ear, as transformer from a low to a high impedance, had again to be changed. Whales have an auditory meatus which widens towards the inside, and is terminated by a rather rigid tympanic membrane. It is not yet clear whether this widening of the canal, which is filled with cerumen, has something to do with matching of water to the possibly smaller impedance of the inner ear. The ossicle chain is still present, but is considerably changed. The hammer is connected rigidly to a neighbouring bone, the stirrup is rigidly fixed in the oval window: the whole chain is a rigid, stiff conductor of sound. So the transformer action of the middle ear, if any, has been enormously changed, and the cochlea is especially sensitive to high frequencies. As the total hearing organ is surrounded by a heavy bony mass connected to the skull of the head by soft, heavily damped layers, the main path to the inner ear is still via the outer and middle ear and not via the whole body, so that good directional hearing is possible. Whales can hear much better than fishes 7).

We have seen, that starting from a part of the balancing organ in fishes, with which vibrations in the water could be perceived, the hearing organ is now a very sensitive tool in mammals, which can detect sounds over a remarkable range of frequencies and with a dynamic range which has never been equaled by technical transducers. Its resolving power is enormous, but combined with an onset and offset which are practically critically damped. It is provided with a feed-back mechanism which helps to protect it against damage. It is rather insensitive for the common low-frequency noises in nature but more sensitive for the more information-carrying signals in the higher frequency range. Its ability to distinguish between sounds coming from different directions is remarkable.

On the other hand, the human ear exhibits signs of degeneration. Our auricle is not much use, most of us cannot move it, and our frequency range is smaller than that of some other mammals. Most of us do not have an absolute pitch, while this has been detected in dogs and pigeons. Although it is sufficient for our way of life, our resolving power seems to be poorer than that of dogs, and our directional hearing is poor compared to that of bats. Still our hearing organ is our most important link with the world around us, and language is far more developed in man than in any animal whatever, though animals can use signals and show emotion. Maybe, however, the latter has nothing to do with our ear.

As mentioned already, the problem of hearing aroused great interest during the last century and is of increasing importance for human being. We will see that it is possible to cast new light on the problem by comparing existing data, and to construct an electrical model of the hearing organ which will be described in the following chapters.

Such a model will facilitate the study of the response of the ear to complex signals, but it must be remembered that this model cannot be a true picture of this very complex organ, because the model would be too complicated, and, moreover, there are still gaps in our knowledge of the construction and properties of different parts of the ear. We have a clear picture of the inner ear, but the behaviour of the middle ear is still a puzzle, especially at higher frequencies. The auditory pathways from the cochlea to the brain are so intricate that we have to stay in the periphery and can only make some suppositions about the more central regions.

We have not given references to all the other investigations and theories in this field. The interested reader is directed to the Bibliography on Hearing [8]) compiled by Stevens et al., which gives a survey of the total literature on this subject. The thickness of this work is an indication of the impossibility for one individual of being complete and up to date. The mention of a reference does not mean that it is more important than another one which has been omitted. We have referred only to those publications which have a direct bearing on the material discussed in this thesis.

Since the inner ear is the most important mechanical part of our hearing organ, and since it is also the part about which most is known, we will start with the cochlea in the next chapter. The middle ear, as the intermediary between the outer world and the cochlea will then follow.

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II. THE COCHLEA

II.1. Anatomy

The receptors of our hearing organ, the hair cells, are embedded in the organ of Corti and they are stimulated by the movement of this organ. It is therefore important to study this movement, and since the organ of Corti is a part of the cochlea we will have to study the whole cochlea in its mechanical behaviour. It is known from anatomical studies, that the part of the system containing the hearing organ is a tube filled with liquid, the perilymphe, and divided into two parts by the cochlear partition, except at the apical end, where the two parts are connected to each other by the helicotrema, a hole in the partition. The tube, which has a length of about 35 mm in human, is rolled up like a snail-shell to have a compact construction, but we do not believe that this affects the mechanics of the system very much. The upper part of the tube, the scala vestibuli, starts from a cavity, the vestibulum, above which are situated the three semicircular canals in which our balancing-organ is embedded. The system is set into oscillation by the middle ear ossicles via the oval window, which opens into the scala vestibuli; vibration is made possible by movement of the round window, a membrane in the wall at the basal end of the lower part of the tube, the scala tympani, as the liquid is practically incompressible. Figure 2 shows us the situation.

The cochlear partition is in fact a duct closed by two membranes and the bony wall. It is filled with another liquid, the more oil-like endolymphe. The upper membrane is called the Reiszner membrane and the lower one is the basilar membrane on which the organ of Corti is built. The hair cells are lying in the organ of Corti, and the ends of their cilia are embedded in the tectorial membrane, which is situated between the basilar and the Reiszner membrane. This can all be seen in fig. 3, a cross-section through the cochlea. The bony wall of the duct is covered with a layer of tissue containing many blood vessels to supply the organs with food via the endolymphe, as they have no blood vessels themselves.

II.2. Dynamics

II.2.1. *General theory*

Many investigators have given a theory of the dynamics of the cochlea. All these theories are based on the same principle, differing mainly in the approximations made in the calculations. The equation of motion given below is derived in more or less the same way, but is rather more general in form than the previously published equations which are discussed in section II.2.2.

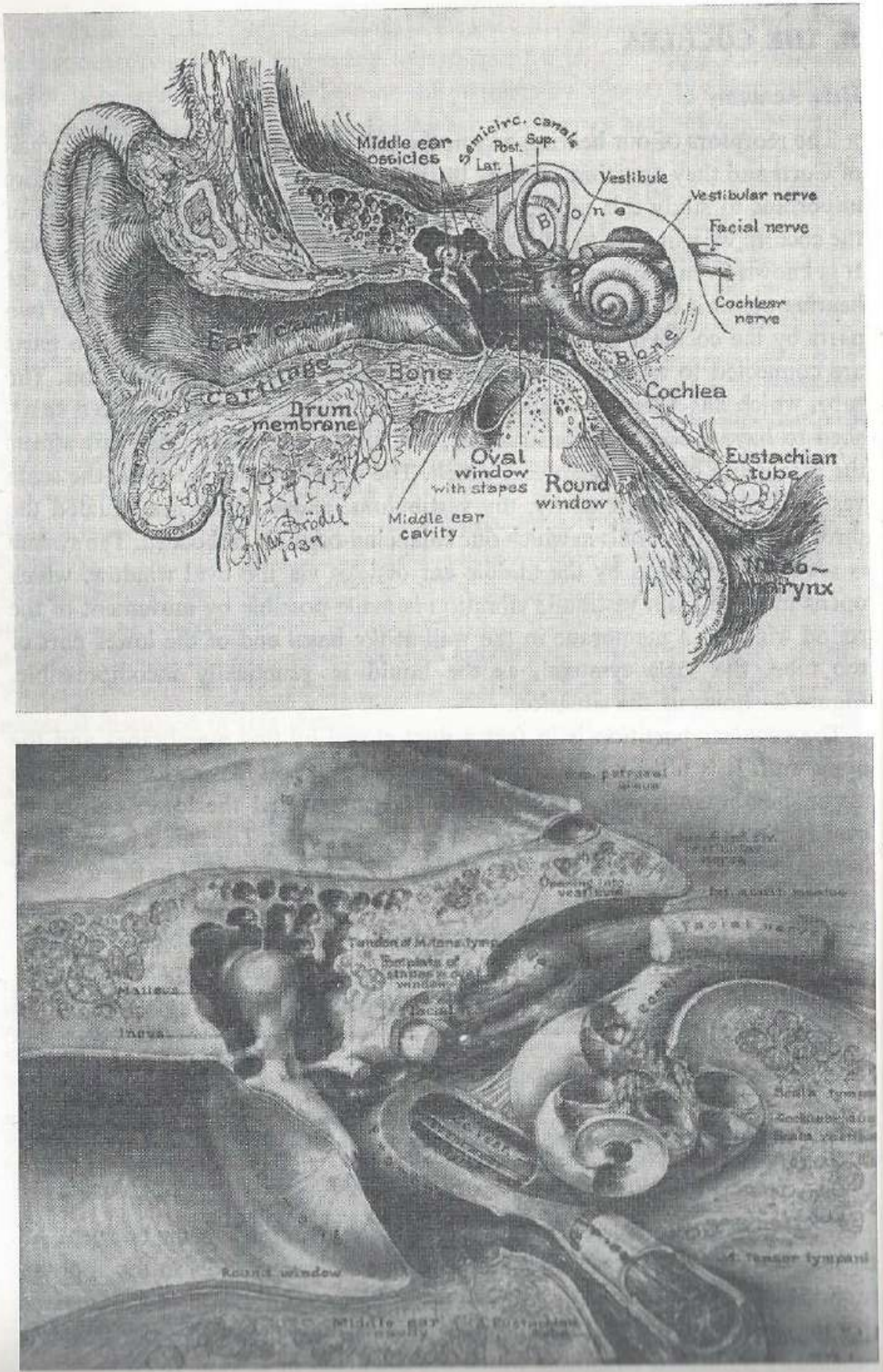


Fig. 2. Cross-sections through the human ear. Drawings by Max Brödel. From E. G. Wever

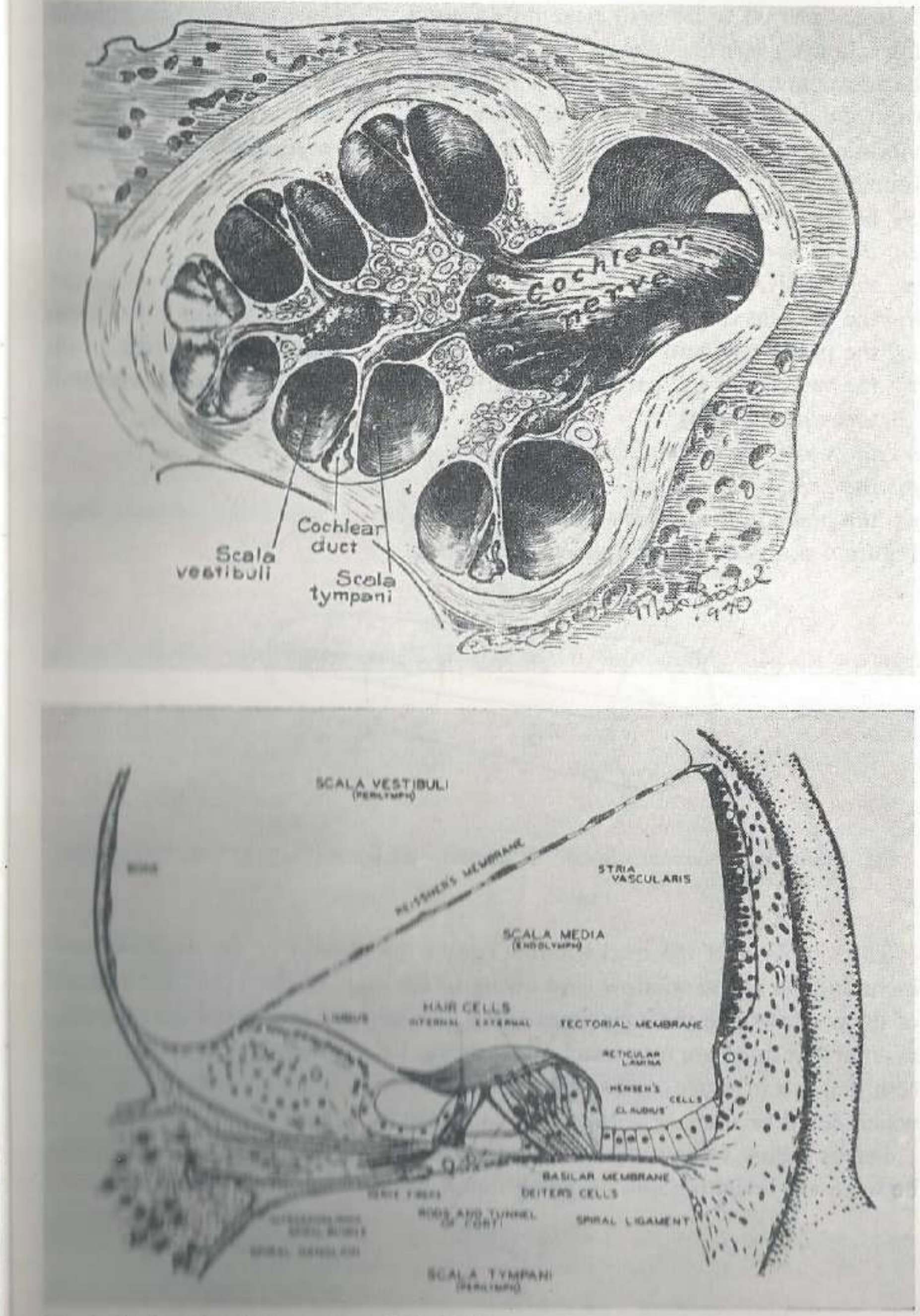


Fig. 3. (1) A midmodiolar section of the cochlea.
Drawing by Max Brödel, from the 1940 Year Book of the Eye, Ear, Nose and Throat.
(2) Cross-section of the cochlear partition in the second turn of a guinea pig cochlea.
From H. Davis, The Laryngoscope, 68, 367, 1958.

It has proved to be both elegant and permissible to simplify the system in the following way in order to treat its motion mathematically. Let the cochlea be a straight tube filled with liquid and divided by a membrane, which represents the total cochlear partition. This means that all the parts of the duct are vibrating in phase which is true for frequencies below 3000 c/s as Von Békésy found. Let

S_1 be the cross-section of the scala vestibuli,
S_2 the cross-section of the scala tympani,
ρ the density of the perilymphe,
u_1 the particle-velocity of the liquid in the scala vestibuli in the x direction,
u_2 the particle-velocity of the liquid in the scala tympani in the x direction,
v the velocity of the partition (positive in the direction from scala vestibuli to scala tympani),
b the width of the partition,
p_1 the pressure in the scala vestibuli,
p_2 the pressure in the scala tympani.

Figure 4 shows us this simplified situation.

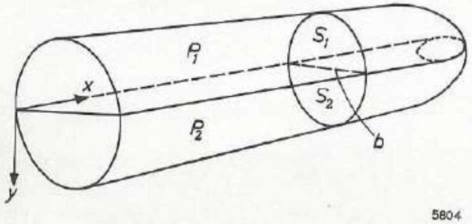


Fig. 4. Simplified representation of the cochlea with the partition and the helicotrema.

The vibration of the oval window causes the motion of the whole system, including the round window, and owing to the mass of the liquid, the stiffness of the windows and the impedance of the partition and the helicotrema, we may assume that there are losses and phase delays between oval and round window resulting in a pressure difference across the partition at the entrance of the canal which could be used as a boundary condition.

Let us follow what happens in an element of volume $S_1 dx$. The difference between the incoming and outgoing liquid per unit time will be

$$\frac{\partial (S_1 u_1)}{\partial x} dx ,$$

and the change in volume per unit time will be

$$v\, b dx,$$

so we obtain the continuity equation:

$$\frac{S_1 dx}{\rho} \frac{\partial \rho}{\partial t} + \frac{\partial (S_1 u_1)}{\partial x} dx + v\, b\, dx = 0,$$

and for the other scala

$$\frac{S_2\, dx}{\rho} \frac{\partial \rho}{\partial t} + \frac{\partial (S_2 u_2)}{\partial x} dx - v\, b\, dx = 0\,.$$

Newton's laws of motion give:

$$-\frac{\partial (S_1 p_1)}{\partial x} = \rho S_1 \frac{\partial u_1}{\partial t}\,,$$

$$-\frac{\partial (S_2 p_2)}{\partial x} = \rho S_2 \frac{\partial u_2}{\partial t}\,.$$

Moreover, we know that

$$\frac{\partial \rho}{\partial t} = \frac{1}{c^2} \frac{\partial p}{\partial t}\,,$$

where c is the velocity of sound in the liquid. Combining this all we find

$$\frac{S_1}{\rho c^2} \frac{\partial p_1}{\partial t} - \frac{1}{\rho} \int_0^t \frac{\partial^2 (S_1 p_1)}{\partial x^2} dt + v\, b = 0\,,$$

$$\frac{S_2}{\rho c^2} \frac{\partial p_2}{\partial t} - \frac{1}{\rho} \int_0^t \frac{\partial^2 (S_2 p_2)}{\partial x^2} dt - v\, b = 0\,.$$

Let us simplify by taking $S_1 = S_2 = S$, so

$$S_1 p_1 - S_2 p_2 = S\, p \text{ where } p = p_1 - p_2\,,$$

and consider the membrane executing a steady sinusoidal oscillation. If we put

$$Z(x) = \frac{p}{y}\,,$$

where

$$y \text{ is } \int_0^t v\, dt\,,$$

the equation thus becomes

$$\frac{\partial^2 (Sp)}{\partial x^2} - \left(\frac{1}{c^2} + \frac{2b\rho}{SZ}\right) \frac{\partial^2 (Sp)}{\partial t^2} = 0\,, \qquad (1)$$

which to a first approximation (because S and Z do not vary quickly) is a force wave with the velocity

$$\sqrt{\frac{1}{\dfrac{1}{c^2}+\dfrac{2b\rho}{SZ}}},$$

or, as the perilymphe is incompressible, with the velocity

$$\sqrt{\frac{SZ}{2b\rho}}.$$

We may write

$$Z(x) = S(x) + j\omega R(x) - \omega^2 M(x),$$

S, R and M being the stiffness, resistance and mass of the partition per unit area, and ω the angular frequency of the vibration. As long as the first term dominates the forcewave velocity is real. If the value of R is large, the velocity is complex, and it is imaginary if the mass term dominates, which means that all the points are in phase but their amplitudes fall exponentially with increasing x.

The displacement equation for the partition is thus

$$\frac{\partial^2(SZy)}{\partial x^2} - \left(\frac{1}{c^2}+\frac{2b\rho}{SZ}\right)\frac{\partial^2(SZy)}{\partial t^2} = 0 \tag{2}$$

or, if

$$c \gg \sqrt{\frac{SZ}{2b\rho}},$$

which is the case in the cochlea,

$$\frac{\partial^2(SZy)}{\partial x^2} - \frac{2b\rho}{SZ}\frac{\partial^2(SZy)}{\partial t^2} = 0\,.$$

Equation (2) cannot be solved explicitly, but only by numerical integration (see [8]). The solution corresponds to a wave travelling along the partition towards the apex. The amplitude of the wave reaches a maximum at a certain towards the apex. The amplitude of the wave reaches a maximum at a certain moment, behind which it decreases rapidly and vanishes. The point on the partition at which the maximum occurs and the vanishing point both lie closer to the stapes as the frequency increases. The form of the solution depends on the properties assumed for the perilymphe and the cochlear partition and on the approximations made, which may differ from one investigator to the other.

II.2.2. *Comparison with other theoretical treatments of the cochlea*

Zwislocki [5]) gives a differential equation for the pressure distribution over the cochlear partition which is similar to our eq. (1). The cross-section of the scalae is assumed constant, the velocity of sound in the liquids is assumed large, and the viscosity of the perilymphe is taken into account:

$$\frac{\partial^2 p}{\partial x^2} = \frac{2}{F_0}\,\frac{R_1 + j\omega\rho}{R_2 + j\left(\omega\sigma - \dfrac{1}{\omega C}\right)}\,p\,,$$

where F_0 is the cross-sectional area of the scalae,
ρ the density of the perilymphe,
R_1 the viscosity per unit length of the perilymphe,
R_2 the viscosity per unit length of the cochlear partition,
σ the mass per unit length of the cochlear partition,
C the compliance per unit length of the cochlear partition,

$$C = C_0 \exp \beta x\,.$$

He first tried neglecting R_1, R_2 and σ, which means that the variation of C determines the pressure distribution, but this gave poor agreement with Von Békésy's measurements [6]). When only R_1 and R_2 were neglected, the system had a maximum displacement at a position which is nearer to the helicotrema than was found by Von Békésy. Moreover, neglecting R_1 and R_2 gives standing waves on the cochlear partition (in such a way, however, that the system still has no characteristic frequencies, because the envelope of the vibration pattern remains principally the same if friction is neglected or not, see Zwislocki's thesis p. 39, Zürich 1948, Acta otolaryng. Suppl. LXXII). Zwislocki says that the best agreement is found if only σ is neglected but not R_1 and R_2, which are kept constant over the whole length of the partition. This gives the equation

$$\frac{\partial^2 p}{\partial x^2} = \frac{2}{F_0}\,\frac{R_1 + j\omega\rho}{R_2 - \dfrac{j}{\omega C_0 \exp \beta x}}\,p\,.$$

The only numerical value given is $\beta = 1{\cdot}5$ 1/cm. The author thought that the results would have been in better agreement with experiment if he had made F_0 vary along the length of the cochlea. Figure 5 gives these results for a pure tone of 1000 c/s, compared with those of other theoretical investigations, the measurements of Von Békésy [6]), and measurements on our electrical model (see below).

Peterson and Bogert [7]) also start with a similar differential equation, taking the cross-section of the scalae as $S_0(x) = 0{\cdot}029 - 0{\cdot}005\,x$ cm², the width of the partition as $b(x) = 0{\cdot}019 + 0{\cdot}0093\,x$ cm, the stiffness of the partition as $k(x) = 1{\cdot}72.10^9\,e^{-3x}$ dyn/cm³, and a constant mass per unit area of $m = 0{\cdot}143$ g/cm². The density of the perilymphe has been taken as 1 g/cc, the viscosity as 3 times that of water, and the velocity of sound in the liquid as $1{\cdot}43.10^5$ cm/s. Their result can also be seen in fig. 5.

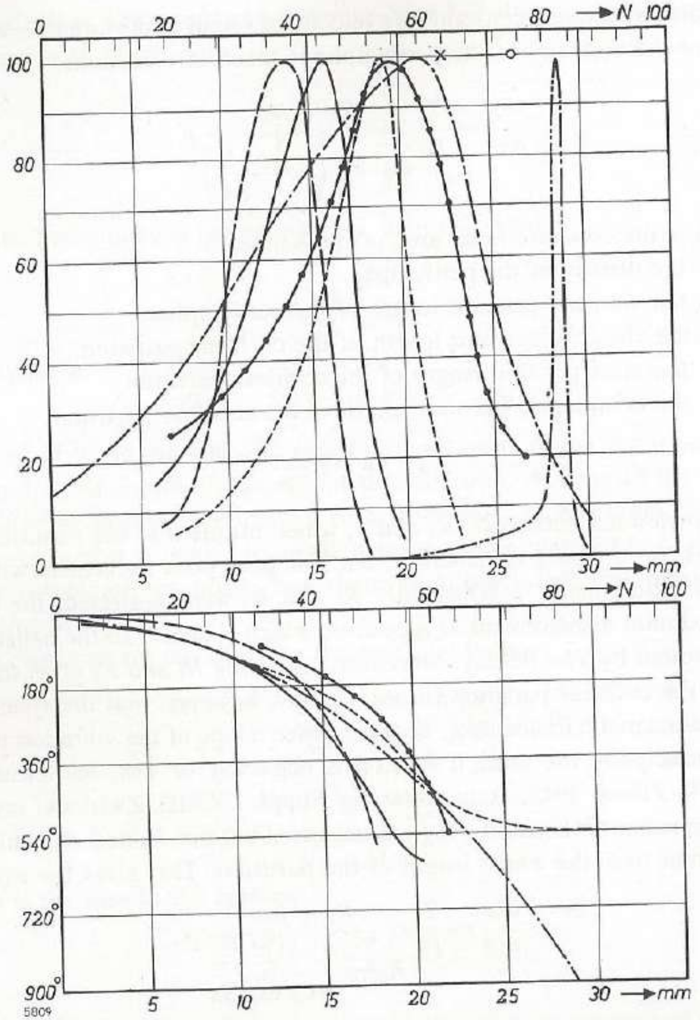


Fig. 5. The amplitude and phase of the cochlear partition at 1000 c/s. Comparison of the theoretical or experimental results of some investigators. Hor: distance from stapes and its corresponding tapnumber.

·—·—·— Von Békésy, J. acoust. Soc. Amer. **19**, 452, 1947.
— - — - Zwislocki, J. acoust. Soc. Amer. **22**, 778, 1950.
— — — Ranke, J. acoust. Soc. Amer. **22**, 772, 1950.
- - - - - - - Fletcher, Speech & Hearing in Commun. p. 250.
— - - — - - Peterson & Bogert, J. acoust. Soc. Amer. **22**, 369, 1950.
———— Our model.
X place of maximum observed another time by Von Békésy.
0 place of maximum concluded from hearing loss measurements, J. acoust. Soc. Amer. **21**, 253, 1949.

Fletcher [8]) gives the same derivation of the differential equations for the pressure distribution in the scalae, although slightly more precise than those mentioned above. Newton's laws of motion have been corrected for hydrodynamic effects, and the radiation mass of the partition in the liquid has been added to the mass of the partition itself.

The values of the quantities are derived from Von Békésy's measurements. The variation of the width and cross-sectional area of the scalae are given in a diagram, and the mass and stiffness of the squares into which the partition was divided are expressed by the equations:

$$m \approx 10^{-5\cdot31+0\cdot50x}\ \mathrm{g} = 0{\cdot}5.10^{-5} \exp(1{\cdot}16\, x)\ \mathrm{g}.$$

$$S \approx 10^{5\cdot07-0\cdot94x}\ \mathrm{dyn/cm} = 1{\cdot}18.10^{5} \exp(-2{\cdot}17\, x)\ \mathrm{dyn/cm}.$$

The resistance r of the partition has been calculated from decay-time measurements made on the partition by Von Békésy [1]). m and r are corrected in the neighbourhood of the helicotrema by the addition of terms Δm and Δr. The density of the liquid is 1, its viscosity has been neglected. Fletcher's results are also shown in fig. 5.

All the theories mentioned up to now have some points in common: only the liquid displacement in the x direction has been taken into account, the cochlear partition has been conceived as a vibrating membrane consisting of independant elements coupled only by the liquid. They differ in the different values assumed for the quantities of the system, the different approximations made to simplify the calculations and the different boundary conditions especially at the helicotrema end, where Peterson and Bogert assume the same pressure in both scalae but Fletcher a pressure difference.

TABLE I

Fletcher gives his data for elements of the cochlear partition with the same length and width. The numbers between brackets of Peterson and Bogert are calculated for the same elements in order to compare them with Fletcher's data.

	Fletcher	Zwislocki	Peterson and Bogert
Mass of the cochlear partition	$0{\cdot}5.10^{-5}\,e^{1\cdot16x}$ g	neglected	$0{\cdot}143$ g/cm^2 ($\approx 5.10^{-5}$ g)
Stiffness of the cochlear partition	$1{\cdot}18.10^{5}\,e^{-2\cdot17x}$ dyn/cm	$S_0\,e^{-1\cdot5x}$	$1{\cdot}72.10^{9}\,e^{-2x}$ dyn/cm^3 ($6{\cdot}2.10^{5}\,e^{-1\cdot2x}$ dyn/cm)
Damping of the cochlear partition	varying with x, giving $Q = 0{\cdot}5$ at each point	constant along the partition	neglected (corrections for friction are given at the end of the calculations)
Cross-section of the coupling liquid layer	total cross-section of the scalae, varying with x	total cross-section of the scalae, kept constant	total cross-section of the scalae: $0{\cdot}029$-$0{\cdot}005x$ cm^2
Density of the perilymphe	1 g/cm^3	1 g/cm^3	1 g/cm^3
Viscosity of the perilymphe	neglected	taken into account	three times that of water

Table I shows the different values of the mass and the stiffness of the membrane, assumed by the above-mentioned authors.

Despite the differences shown in table I, their results all agree more or less with the membrane motion observed by Von Békésy. The transverse flow of the liquid must also be taken into account in order to give a better approximation to the real situation. This was first done by Ranke [9][10]) about 30 years ago.

He also conceived the cochlear partition as one single membrane with features changing with the distance from the stapes. The derivation of the equations is similar to that of the simpler theories mentioned above, except that one more dimension is considered. The equations are not given in terms of the pressure p; Ranke works with a velocity potential F defined by the equation:

$$\frac{\rho \partial F}{\partial t} = p\,,$$

but this makes no fundamental difference. The liquid is assumed to be incompressible. Ranke keeps his theory as general as possible; he assumes however that the mass ratio

$$\frac{\sigma q}{\rho h}\,,$$

where σ is the density of the membrane,

q half of the thickness of the membrane,

ρ the density of the liquid,

h the height of one scala,

does not change too much over the whole length of the cochlea. This is in good agreement with the facts, for although the mass of the partition increases with distance as the partition becomes broader, if we assume that only a small layer of liquid at both sides of the partition is important (see below), this layer will also grow broader, leaving $\sigma q/\rho h$ more or less constant (Ranke's mathematical model had a membrane of constant width). He also assumes that

$$D = f/2\sqrt{\sigma q E} \quad \text{is constant}\,,$$

where f is the friction per unit area of the partition and E the stiffness per unit area of the partition.

This assumption is in agreement with Von Békésy's observations that the decay time of the partition is independent of frequency [1]), thus independent of the place on the membrane. From anatomical considerations Ranke supposes

$$\frac{\sigma q}{\rho h} = 0{\cdot}1$$

near the stapes and 0·3 near the apex and calculates in a rather complex way the curves with $D = 0{\cdot}1$, and $D = 0{\cdot}25$ and a constant

$$\frac{\sigma q}{\rho h} = 0{\cdot}1415 \text{ (i.e. } \pi - 3)\,.$$

One of the most interesting things in his papers is that he shows that with other values of $\sigma q/\rho h$ we obtain the models of other investigators, from Ewald for very large ρ, via Kucharski, to Helmholtz with $\rho = 0$, the independent vibrating elements, although in the latter case the direct coupling between the elements cannot be neglected. Our eqs.(1) and (2) also show the importance of $b\rho/Z$.

Ranke later corrected on his theories by taking hydrodynamic effects into account [11]). The curve drawn in fig. 5 is taken from the more recent paper.

As we have seen, the behaviour of the cochlear partition can be understood in terms of the simple theories and more complexity is not necessary, as this will give only second order corrections. The most important thing is to take values of the characteristic qualities which give best agreement with Von Békésy's observations, and enough anatomical data are now available to calculate all these quantities. The travelling wave caused by a pure tone increasing in amplitude up to a certain distance from the stapes, which depends on the frequency, and falling steeply after the peak, is characteristic of the cochlea, and as we can expect a large variation between different cochlea, the slopes, position of the peak, and phase-difference between stapes and peak (see fig. 5) will not be so critical.

Since our equations can be solved only very laboriously by numerical methods, we decided to use an electronic computer and built one of the analogue type.

It should be mentioned, however, that the circuit described below is not a true analogue computer, since eqs. (1) and (2) cannot be derived from a consideration of the circuit. General considerations make it likely that the circuit will behave in a similar manner to the cochlea, and measurements made on the circuit agree well with data obtained from the cochlea and from the differential equations. It is thus perhaps better to speak of a model of the cochlea rather than of an analogue computer.

II.1.3. *Discussion of the mathematical motion-equation*

If the cochlea were filled with a gas instead of a liquid (or rather, if the cochlea were filled with a compressible fluid instead of an incompressible one), it might be possible that

$$c \ll \sqrt{\frac{SZ}{2b\rho}}\,,$$

which leads to

$$\frac{\partial^2(SZy)}{\partial x^2} - \frac{1}{c^2}\,\frac{\partial^2(SZy)}{\partial t^2} = 0\,,$$

having a solution of the form

$$y = \frac{A}{SZ} \sin \omega \left(t \pm \frac{x}{c} \right).$$

It would then be possible for the wave to travel in both directions, so it would make difference if we excited the system at the basal or at the apical end.

In this case it is the fluid which mainly determines the propagation. The membrane is only a boundary condition, provided that we neglect the coupling of neighbouring elements through the membrane, which is allowed, as we shall see below. The membrane follows the wave through the fluid, which has a constant velocity. The displacement y is, of course, still determined by Z and the cross-section S.

If, however, $c \gg \sqrt{\frac{SZ}{2b\rho}}$,

which is the case with the cochlea, we have a totally different situation. The wave travels through the perilymphe very quickly compared with the phenomenon at the membrane.

Initially, just after the onset of the signal, this quick liquid wave will reach the helicotrema and later on the round window, all before most of the membrane has started to move. Phase and amplitude differences arise between the pressures in the two scalae because of the different impedances of fluid in the scalae, helicotrema and round window, and this brings the membrane into motion. The displacement of the membrane elements will modulate the pressure distribution in the scalae near the partition so that in the steady state this pressure distribution can be described by eq. (1). There is no membrane at the stapes end, but a bony partition, so there is no pressure modulation and we will find a pressure difference between the two windows which is the boundary condition at the beginning of the membrane. The boundary condition at the other end is determined by the helicotrema.

During the derivation of our equations we had assumed that S_1 and S_2 were the total cross-sections of the scalae. Von Békésy [1]), however, found that not all the liquid in the cochlea but only thin layers about 0·3 mm on both sides of the membrane need be considered. The rest of the liquid (about 1-5 mm) can be omitted. Considering the hydrodynamic theory of surface waves and the fact, that the width of the membranous part of the partition is smaller than its total width, we come to the same conclusion.

Tonndorf [2]) has shown in his model of the cochlea that only a thin layer near the membrane will be influenced by motion of the membrane. He observed the liquid particles and saw the particles near the outer wall making longitudinal motions only, while those near the membrane described ellipses, a combination of the longitudinal motion of the bulk of the liquid and the transversal motion of the membrane.

The velocity of sound in the liquid is about $1{\cdot}5.10^5$ cm/s, and as we shall see later the motion of the partition is a travelling wave with a wavelength of at the most 1/100 of its wavelength in the liquid, so the cochlear partition is a very bad radiator and we can understand why we do not notice any transverse motion of the liquid near the walls of the scalae.

The excess of liquid in the cochlea gives us the explanation of Von Békésy's paradox. If we should drive the system at another place than the stapes, the waves going in the two directions would meet different impedances on their way (e.g. passing the helicotrema) and at the end at the two windows, which would again give amplitude and phase differences between the two scalae, leading to the motion of the membrane. In the steady state, eq. (1), where S is now the cross-section of the thin layers, would be valid again. We can understand Von Békésy's paradox [3]), which states that, driving with an artificial window near the helicotrema, we see a travelling wave coming towards the sound source! It is fortunate for people with conduction deafness that Von Békésy's paradox exists, since it means that they can still hear by bone conduction, with a hearing aid.

Perhaps it would be better to speak here of a pseudo-travelling wave, since we have assumed that the membrane elements were coupled to each other only by the mass of liquid and not by stiffness. The resulting movement of the successive elements behind each other thus seems to be a travelling wave. Von Békésy's paradox would be scarcely credible if we were dealing with real travelling waves in membranes or strings. In a mechanical model, Von Békésy made with reeds loaded with masses [3])[4]), it was also possible to demonstrate the paradox. Thinking of the cochlea with its too much liquid, we can understand those travelling waves starting from the stapes end of the model when it was driven at the stapes end or at all the reeds together by magnetic forces, but when only one reed in the middle was driven we have the situation of the membrane with its thin just sufficient layers, and a wave can only travel from that tongue to the helicotrema. The same will be demonstrated in our electrical model. The easiest image for the whole situation is the exaggerated case of thinking both scalae divided into a series of layers. The outher layers have only longitudinal movements, merely the inner layers are influenced by the membrane and are "rolling underneath the outer layers". At the basal end, where is no membrane any more, both types of layers join each other.

We are now in a position to appreciate the complicated construction of the ear rather better. When some of the fishes left the water and came on land, they could not do much with their crude hearing organ, which was really a balancing organ which could detect sound in a certain way. Air-borne sound was reflected against their skull and could not reach the saccule. One might think that it would be easy to create some receptors lying near the skin, responding to the vibration of the latter under the influence of sound pressure. This part of the skin might be transformed into a membranelike tissue, giving a hearing organ of the microphone type. Instead of that, we find the construction of the middle ear, in order to abolish to a certain extent the mismatch of the air to the impedance of the rather primitive internal ear, for which an existing organ has been modified. This sort of thing seems to have happened quite often during evolution. We know from the fishes that they can hear sounds in a remarkable frequency-range. More receptors were probably needed to improve the sensitivity and the discrimination of the system and the cochlea arose. Because of its development from the saccule, the cochlea is filled with liquid. In fact it contains two liquids, one for feeding (the endolymphe) and one for loading and coupling (the perilymphe) thus making the middle ear necessary. A construction without perilymphe would probably have given a lower impedance, but it appears that the liquid coupling is essential if the cochlea is to function as it must.

We may assume that the ear will have to detect the frequencies which are most important for the organism without some of them dominating the others. The sensitivity does not need to be the same for all frequencies but abrupt changes of this sensitivity as a function of frequency would hinder the transfer of information, as in nature we do not find certain frequencies dominating others. This means that the transmitting and detecting mechanisms of the sound must have fairly smooth frequency characteristics without pronounced peaks and dips. A damped microphone system could perform this task without the help of liquid loading or coupling, but the liquid seems to be necessary if we have a stretched membrane, as indeed we do. We can say that one thing may not occur on such a membrane: reflection at the end. No frequencies may dominate the others, i.e., no characteristic frequencies may exist. Would it be possible to construct a stretched membrane with these properties without liquid coupling? In any case a uniform membrane with features not changing over its length, will not do.

For a cochlea which is uniform over its length, all the derivatives of S and Z with respect to x are zero, so that eq. (2) would be

$$\frac{\partial^2 y}{\partial x^2} - \left(\frac{1}{c^2} + \frac{2b\rho}{SZ}\right)\frac{\partial^2 y}{\partial t^2} = 0 .$$

This gives a solution of the form:

$$y = A \sin \omega \left(t \pm \frac{x}{c'}\right),$$

which represents a wave which can travel in both directions along the partition with a velocity

$$c' = \sqrt{\frac{SZc^2}{SZ + 2b\rho c^2}} = \text{constant}.$$

If the cochlea is driven by the stapes and if the impedance of the helicotrema is not equal to the characteristic impedance of the system, reflection will occur at the apical end, leading to standing waves and thus to characteristic frequencies. Such a system does not perform in the way we want, unless it is heavily damped, which diminishes its sensitivity.

We will now consider the motion of a membrane with characteristics which are a function of the distance along its length. The membrane is not surrounded by liquid.

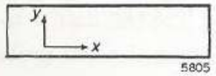


Fig. 6. The membrane clamped at its edges.

Figure 6 shows a thin membrane of constant width fixed at its edges. Let us assume that it is not homogeneous, $T(x)$ being the bending stiffness per unit length, and $M(x)$ the mass per unit area.

If we neglect friction we get the equation

$$T(x)\frac{\partial^2 A}{\partial y^2} + \frac{\partial}{\partial x}\left(T(x)\frac{\partial A}{\partial x}\right) = M(x)\frac{\partial^2 A}{\partial t^2},$$

where A is the amplitude at (x, y).

Writing

$$A = P(y)\,Q(x)\,e^{j\omega t},$$

we find

$$\frac{1}{P}\frac{\partial^2 P}{\partial y^2} + \frac{1}{Q}\frac{\partial^2 Q}{\partial x^2} + \frac{1}{T(x)}\frac{\partial T(x)}{\partial x}\frac{1}{Q}\frac{\partial Q}{\partial x} + \omega^2\frac{M(x)}{T(x)} = 0$$

or

$$T(x)\frac{\partial^2 Q}{\partial x^2} + \frac{\partial T(x)}{\partial x}\frac{\partial Q}{\partial x} + \left(\omega^2 M(x) - CT(x)\right) Q = 0,$$

where C is a constant.

As $T(x)$ will be differentiable and larger than 0, and as $\omega^2 M(x) - CT(x)$ will be continuous in the interval from $x = 0$ to $x = 1$, we can supply Sturm's first theorem, which states that if

$$T_1(x)\frac{\partial^2 Q}{\partial x^2} + \frac{\partial T_1(x)}{\partial x}\frac{\partial Q}{\partial x} + \left(\omega^2 M_1(x) - CT_1(x)\right) Q = 0$$

has a solution Q_1 and

$$T_2(x)\frac{\partial^2 Q}{\partial x^2} + \frac{\partial T_2(x)}{\partial x}\frac{\partial Q}{\partial x} + \left(\omega^2 M_2(x) - CT_2(x)\right) Q = 0$$

has a solution Q_2 and if

$$T_1(x) \geqslant T_2(x) > 0 \text{ and } \omega^2 M_1(x) - CT_1(x) < \omega^2 M_2(x) - CT_2(x),$$

then there exists at least one zero of Q_2 between two zeroes of Q_1.

Let M_0 be smaller than the smallest value of $M(x)$ of our membrane and T_0 larger than the largest value of $T(x)$.
Then

$$T_0 > T(x) > 0$$

and $\omega^2 M_0 - CT_0 < \omega^2 M(x) - CT(x)$.

The equation

$$T_0 \frac{\partial^2 Q}{\partial x^2} + (\omega^2 M_0 - CT_0)\, Q = 0$$

has the solution

$$Q = B \sin\left(\sqrt{\frac{\omega^2 M_0 - CT_0}{T_0}}\, x + \varepsilon\right).$$

We can imagine our membrane stretched from $-\sim$ to $+\sim$, so the interval in which Sturm's theorem may be applied is infinitely long. The zeroes of the sinusoidal function come closer together as the frequency increases, and according to Sturm the zeroes of the original function will do the same. On our finite membrane Q must be zero for $x = 0$ and $x = 1$, thus the solution of our equation exists for certain frequencies only, the characteristic frequencies. At intermediate frequencies no solution exists. Such a system cannot therefore perform in the way we want, unless it is heavily damped, which diminishes its sensitivity.

The cochlear partition, however, could not even have any characteristic frequencies if it were not damped, as is shown clearly by Zwislocki in his thesis. It differs in this respect from all the other possible systems based on a stretched membrane, as we have shown above, which is due to the fact that it is inhomogeneous and surrounded by a heavy incompressible fluid.

There is one other possibility, which we have not considered until now, i.e. independent resonators which could be driven by air filled scalae, or even by bone conduction. But it seems most improbable that such a delicate structure would be strong enough. We do not find it in nature in organs which have to work for a long time. Besides, how would these strings be fed? Again via liquid? Then we have come back to the picture Helmholtz made of the function of the cochlea; and these independent resonators surrounded by liquid are in fact just what we assumed in our calculations, which give results in agreement with the observations. In these results, however, resonance does not play an important role.

II.3. The electrical model of the cochlea

II.3.1. *The circuit*

Many electrical models of the cochlea have been built already [12][13][14]. They are based upon the same principal circuit and differ only in the choice of the circuit elements. The model represents the cochlear partition with the thin liquid layers at each side of it, which are so important for its motion. It is not necessary to depict the whole cochlea, unless we require to study Von Békésy's paradox or the activation by bone conduction. Let us imagine the partition split up into small elements of which the *N*th has a mass, a compliance and a frictional resistance corresponding to an inductance L_N, a capacitance C_N and a resistance $1/Y_N$ (fig. 7). These elements are coupled together by the incompressible fluid at both sides of the partition, which means that in our network the circuits are coupled together by an inductance and resistance in series at both sides, but because of the symmetry of the system these can be combined to give a single inductance λ_N and a resistance R_N at only one side of the elements (fig. 7). The voltage U_N across an element corresponds to the mechanical force upon it, the current Δi_N corresponds to the velocity, the charge across the capacitor to the displacement. The capacitance C_N of the *N*th element has been split up in a constant capacitance K and a variable one C_{lN}, giving together the value C_N, so that the voltage V_N across K corresponds to the displacement of the partition at the position of the *N*th element (fig. 7). The velocity of the liquid layer between the $(N-1)$th and *N*th element corresponds to i_N. The conversion from the mechanical system to the electrical model is made on the following basis:

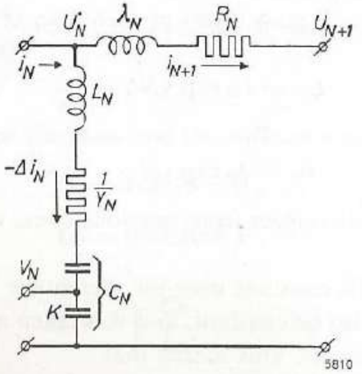


Fig. 7. The *N*th element of our electrical model.

$$1\ \text{g} = 1\ \text{H},$$

$$1\ \frac{\text{g}}{\text{sec}} = 1\ \Omega,$$

$$1\,\frac{\text{cm}}{\text{dyn}} = 1\ \text{F}\,.$$

Fletcher divided the partition into squares, and calculated the mass and compliance of these elements from the anatomical data of Von Békésy, who found that the width of the partition increases from the stapes to the apex. Applying Fletcher's formulae to our model, we obtain:

$$L_N = L_0 \exp \gamma N$$

and

$$C_N = C_0 \exp\,[(2\alpha - \gamma)N].$$

The total amount of liquid which supplies the coupling between neighbouring elements will vary with the width of the membrane. If we think of the partition, with its radiation-mass layers at each side, as a flat plate, then since we have taken

$$L_N = L_0 \exp \gamma N\,,$$

it seems natural to take

$$\lambda_N = \lambda_0 \exp \gamma N\,.$$

Our model differs in this respect from previous ones, where λ_N was assumed constant.

As the decay period is constant over the membrane [1]), the Q factor of the circuit elements must also be constant, and was taken as $\frac{1}{2}$ in accordance with Von Békésy's measurements. This means that

$$\frac{1}{Y_N}\sqrt{\frac{C_N}{L_N}} = \frac{1}{Y_N}\sqrt{\frac{C_0}{L_0}}\exp\,[(\alpha-\gamma)N] = \tfrac{1}{2}\,,$$

i.e.

$$Y_N = Y_0 \exp\,[(\alpha - \gamma)N]\,,$$

where

$$Y_0 = 2\sqrt{\frac{C_0}{L_0}}\,.$$

Similarly, we took

$$R_n = R_0 \exp\,[(\gamma - \alpha)N]\,.$$

Let us now calculate the value of these constants. Fletcher [8]) gives the following expressions for the stiffness S of the membrane:

$$S = 10^{5\cdot 07 - 0\cdot 94x} = \exp\,(11\cdot 7 - 2\cdot 17x)\ \text{dyn/cm}$$

and its total mass (membrane + radiation mass):

$$m = 1\cdot 4.10^{-5\cdot 31 + 0\cdot 50x} = \exp\,(-12\cdot 5 + 1\cdot 16x)\ \text{g}$$

where x is the distance from the stapes in cm.

The factor 1·4 is due to the fact that we divided the total length into 100 pieces, and Fletcher into 140. We decided to make the frequency difference between the taps of our partition panel about a semitone, which is not larger than the critical bandwidth, so there is no reason for making the distance between the taps smaller. Moreover the construction would become more difficult, since the tolerances in the network elements would have to be smaller. The semitone interval implies a total number of 100 circuit elements. If we take the average length of the cochlear partition as 3·4 cm, we get

$$\gamma = \frac{3\cdot 4 \times 1\cdot 16}{100} = 0\cdot 0394\,.$$

For simplicity, we took $\gamma = 0\cdot 04$. Then:

$$2\alpha = \frac{3\cdot 4}{100}\,(2\cdot 17 + 1\cdot 16) = 0\cdot 116, \text{ so } \alpha = 0\cdot 058$$

and we took $\alpha = 0\cdot 06$.

The above equations for the mass and the stiffness also lead to:

$$L_0 = 0\cdot 68.10^{-5}\ \text{H}\,,$$

$$C_0 = 0\cdot 85.10^{-5}\ \text{F}\,,$$

whence

$$Y_0 = 2\sqrt{\frac{C_0}{L_0}} = 2\cdot 24\ \Omega\,.$$

It may be shown that damping in the perilymphe is only important at frequencies below

$$\nu = \frac{1}{2\pi}\,\frac{R}{\lambda} = \frac{1}{2\pi}\,\frac{8\pi\eta}{\rho A}\,,$$

where η is the viscosity of the perilymphe, which is $\approx 0\cdot 02$ g/s.cm, ρ is its density, which we have taken as 1 g/cc, and A is the cross-sectional area of the active liquid layer, which is still assumed to be independent of frequency.

Now Von Békésy [1]) has shown that the active liquid layer is about 0·3 mm thick, and the width of the partition (near the helicotrema) is about 0·5 mm, so the cross-sectional area of the liquid layer coupling neighbouring elements will be of the order of

$$2 \times 0\cdot 03 \times 0\cdot 05 = 3.10^{-3}\ \text{cm}^2.$$

Substituting these values into the expression for ν, we find:

$$\nu = \frac{4 \times 0\cdot 02}{3.10^{-3}} \approx 23\ \text{c/s}\,,$$

i.e. above about 20 c/s, damping in the liquid can be neglected. We may therefore set $R_0 = 0$.

The value of λ_0 may now be calculated from other data in Fletcher's book [8]). For a given frequency, the circuit element at which the amplitude is maximum will be roughly equivalent to that shown in fig. 8 (bearing in mind that $R_N = 0$).

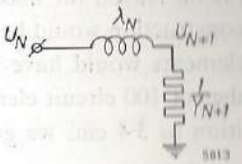


Fig. 8. Simplification of the $(N + 1)$th tap at its resonance frequency.

It follows that:

$$\frac{U_{N+1}}{U_N} = \frac{1/Y_{N+1}}{(1/Y_{N+1}) + j\omega\lambda_N} = \frac{1}{1 + j\omega\lambda_0 Y_0 \exp\{\alpha(N+1) - \gamma\}}\,.$$

We found that the maximum amplitude for $\nu = 600$ c/s ($\omega = 3770$ s^{-1}) occurred 22 mm from the stapes, according to fig. 157 of Fletcher's book, i.e. at the element designated by:

$$N + 1 = \frac{22 \times 100}{35} = 63\,.$$

We measured $U_{N+1}/U_N = 8/9$ from this figure, so

$$8/9 = \sqrt{\frac{1}{1 + (3{\cdot}770.10^3\,\lambda_0 \times 2{\cdot}24 \exp(0{\cdot}06 \times 63 - 0{\cdot}04))^2}}\,,$$

i.e. $\lambda_0 = 1{\cdot}36 \times 10^{-6}$ H.

In fact, the value should be rather less, since we have neglected the rest of the filter after tap $N + 1$.

The phase delay at the same position may also be used to calculate λ_0:

calculated phase delay $U_N \rightarrow U_{N+1} = \omega\lambda_0 Y_0 \exp\{\alpha(N+1) - \gamma\} = 3{\cdot}37.10^5\,\lambda_0$,

measured phase delay $= \tan -2\pi/14$, so $\lambda_0 = 1{\cdot}36.10^{-6}$ H.

In this case, if we took the rest of the filter behind tap $N + 1$ into consideration we would obtain a larger result. We therefore decided to take $\lambda_0 = 0{\cdot}2\, L_0 = 1{\cdot}36.10^{-6}$ H. A further check on this result is provided as follows: the largest value of λ in our model is

$$\lambda_{100} = \lambda_0 \exp 100\gamma = 1{\cdot}36.10^{-6} \exp 4 = 75.10^{-6}\text{ H}\,,$$

which corresponds to a weight of liquid of 75.10^{-6} g. The length of this liquid element may be taken as 35/1000 cm, for the sake of simplicity, and since we have supposed the density of the liquid to be 1 g/cc, the cross-sectional area of this liquid element is

$$S = \frac{75.10^{-6}}{1 \times 35.10^{-3}} = 2.10^{-3}\text{ cm}^2\,,$$

which agrees well with the value of 3.10^{-3} cm² calculated above from Von Békésy's experimental data. Other estimations of λ_0 derived from the membrane-motion pictures gave similar results.

II.3.2. *Calculated results*

In order to check the design of our model before actually building it (in particular to check whether our value of λ_0 is acceptable), and in order to compare our theoretical results with those to be measured, we calculated the amplitude and phase of the voltage at the different taps for a frequency of 600 c/s.

We may write now, operating the system by a signal of frequency ω:

$$\left\{\begin{aligned} U_N &= i_{N+1}(j\omega\lambda_N + R_N) + U_{N+1}\,,\\ U_N &= -\Delta i_N\left(j\omega L_N + \frac{1}{Y_N} + \frac{1}{j\omega C_N}\right),\\ V_N &= \frac{-\Delta i_N}{j\omega K}\,,\\ i_{N+1} - i_N &= \Delta i_N\,. \end{aligned}\right.$$

After some calculation we find

$$V_{N+1}\,\frac{j\omega L_{N+1} + \dfrac{1}{Y_{N+1}} + \dfrac{1}{j\omega C_{N+1}}}{j\omega\lambda_N + R_N} =$$

$$V_N\left(1 + \frac{j\omega L_N + \dfrac{1}{Y_N} + \dfrac{1}{j\omega C_N}}{j\omega\lambda_N + R_N} + \frac{j\omega L_N + \dfrac{1}{Y_N} + \dfrac{1}{j\omega C_N}}{j\omega\lambda_{N-1} + R_{N-1}}\right) +$$

$$- V_{N-1}\,\frac{j\omega L_{N-1} + \dfrac{1}{Y_{N-1}} + \dfrac{1}{j\omega C_{N-1}}}{j\omega\lambda_{N-1} + R_{N-1}}\,. \tag{3}$$

Let us write eq. (3) as

$$V_{N+1}B_{N+1} = V_N(1 + A_N + B_N) - V_{N-1}A_{N-1}\,,$$

with

$$A_N = \frac{j\omega L_N + \dfrac{1}{Y_N} + \dfrac{1}{j\omega C_N}}{j\omega\lambda_N + R_N}$$

and

$$B_N = \frac{j\omega L_N + \dfrac{1}{Y_N} + \dfrac{1}{j\omega C_N}}{j\omega\lambda_{N-1} + R_{N-1}}.$$

Substitution gives

$$A_N = \frac{j\omega L_0 \exp\gamma N + \dfrac{1}{Y_0}\exp(\gamma-\alpha)N + \dfrac{1}{j\omega C_0}\exp(\gamma-2\alpha)N}{j\omega\lambda_0 \exp\gamma N + R_0\exp(\gamma-\alpha)N}.$$

Let us write

$$L_0C_0 = \frac{1}{\omega_0{}^2}, \qquad Y_0{}^2\,\frac{L_0}{C_0} = \beta^2, \qquad R_0 = \frac{\delta}{Y_0}, \qquad \lambda_0 = \varepsilon L_0 .$$

Then we find

$$A_N = \frac{j\omega L_0 \exp\,\alpha N + \dfrac{1}{j\omega C_0}\exp(-\alpha N) + \dfrac{1}{\beta}\sqrt{\dfrac{L_0}{C_0}}}{j\omega\varepsilon L_0 \exp\alpha N + \dfrac{\delta}{\beta}\sqrt{\dfrac{L_0}{C_0}}} =$$

$$= \frac{j\dfrac{\omega}{\omega_0}\exp\alpha N - j\dfrac{\omega_0}{\omega}\exp(-\alpha N) + \dfrac{1}{\beta}}{j\dfrac{\omega}{\omega_0}\varepsilon\exp\alpha N + \dfrac{\delta}{\beta}} = \frac{\dfrac{1}{\beta} + 2j\sinh\left(\alpha N + \ln\dfrac{\omega}{\omega_0}\right)}{j\dfrac{\omega}{\omega_0}\varepsilon\exp\alpha N + \dfrac{\delta}{\beta}}.$$

In the same way we can calculate that

$$B_N = \frac{\exp\gamma}{\exp\alpha}\cdot\frac{\dfrac{1}{\beta} + 2j\sinh\left(\alpha N + \ln\dfrac{\omega}{\omega_0}\right)}{j\dfrac{\omega}{\omega_0}\varepsilon\exp\alpha(N-1) + \dfrac{\delta}{\beta}}.$$

In total we find for eq. (3)

$$V_{N+1}\frac{\exp\,\gamma}{\exp\,\alpha}\cdot\frac{\dfrac{1}{\beta} + 2j\sinh\left\{\alpha(N+1) + \ln\dfrac{\omega}{\omega_0}\right\}}{j\,\varepsilon\exp\left(\alpha\,N + \ln\dfrac{\omega}{\omega_0}\right) + \dfrac{\delta}{\beta}} = V_N\left(1 + \frac{\dfrac{1}{\beta} + 2j\sinh\left\{\alpha N + \ln\dfrac{\omega}{\omega_0}\right\}}{j\,\varepsilon\exp\left(\alpha N + \ln\dfrac{\omega}{\omega_0}\right) + \dfrac{\delta}{\beta}} + \right.$$

$$\left. + \frac{\exp\dot{\gamma}}{\exp\alpha}\cdot\frac{\dfrac{1}{\beta} + 2j\sinh\left\{\alpha N + \ln\dfrac{\omega}{\omega_0}\right\}}{j\varepsilon\exp\left\{\alpha(N-1) + \ln\dfrac{\omega}{\omega_0}\right\} + \dfrac{\delta}{\beta}}\right) - V_{N-1}\frac{\dfrac{1}{\beta} + 2j\sinh\left\{\alpha(N-1) + \ln\dfrac{\omega}{\omega_0}\right\}}{j\varepsilon\exp\left\{\alpha(N-1) + \ln\dfrac{\omega}{\omega_0}\right\} + \dfrac{\delta}{\beta}}. \qquad (4)$$

We have seen already that it is allowed to take $\delta = 0$. Let us call

$$V_N = p_N + j\,q_N\,.$$

Then the amplitude at position N is

$$A_N = \sqrt{p_N{}^2 + q_N{}^2}$$

and the phase shift at position N is

$$\varphi_N = \tan^{-1}\frac{q_N}{p_N}.$$

After some manipulations, eq. (4) becomes

$$\left\{\begin{aligned} & p_{N+1}\exp(\gamma)\,D_{N+1} - p_N\,\{1 + (1+\exp\gamma)D_N\} + p_{N-1}D_{N-1} + \\ & \qquad + \{q_{N+1}\exp(\gamma-\alpha) - q_N(1+\exp\gamma) + q_{N-1}\exp\alpha\}\,E_N = 0, \\ & q_{N+1}\exp(\gamma)\,D_{N+1} - q_N\{1 + (1+\exp\gamma)D_N\} + q_{N-1}D_{N-1} + \\ & \qquad - \{p_{N+1}\exp(\gamma-\alpha) - p_N(1+\exp\gamma) + p_{N-1}\exp\alpha\}\,E_N = 0, \end{aligned}\right.$$

with

$$D_N = \frac{2\sinh\left(\alpha N + \ln\dfrac{\omega}{\omega_0}\right)}{\dfrac{\omega}{\omega_0}\,\varepsilon\exp\alpha N} \quad\text{and}\quad E_N = \frac{\dfrac{1}{\beta}}{\dfrac{\omega}{\omega_0}\,\varepsilon\exp\alpha N}.$$

The manner in which our filter is terminated at the apical end will not influence its behaviour at 600 c/s much, since at this frequency, the amplitude of the partition near the helicotrema is very small.

To calculate the numerical values we started at the apical end; p_{100} and q_{100} may be chosen arbitrary. As we know that, for a frequency of 600 c/s, the signal is only seeing inductances near the termination of our filter we can expect that the absolute value of the voltage at the 99th tap will be larger than at the 100th one, and that the phase difference between the last circuits will be neglectible. So we took $p_{100} = q_{100} = 0$ and $p_{99} = 1$ with $q_{99} = 0$. Then we could calculate p_{98} and q_{98} from eq. (5), and so on. Our solution converged and was in good agreement with our expectations. Numerical values are given in Table II for each tenth circuit. χ is the phase angle relative to the base of the partition, i.e. $\chi = \varphi_0 - \varphi$ (see p. 37).

Figure 9 gives our calculated and measured curves together with those of Fletcher and Von Békésy, which has been drawn on the assumption that our 100 taps are divided equally over the length of the partition of 35 mm. We see that our maximum lies about 10 circuits, which corresponds with about 3·5 mm, nearer the stapes side than Fletcher's and that our slope is greater after the maximum,

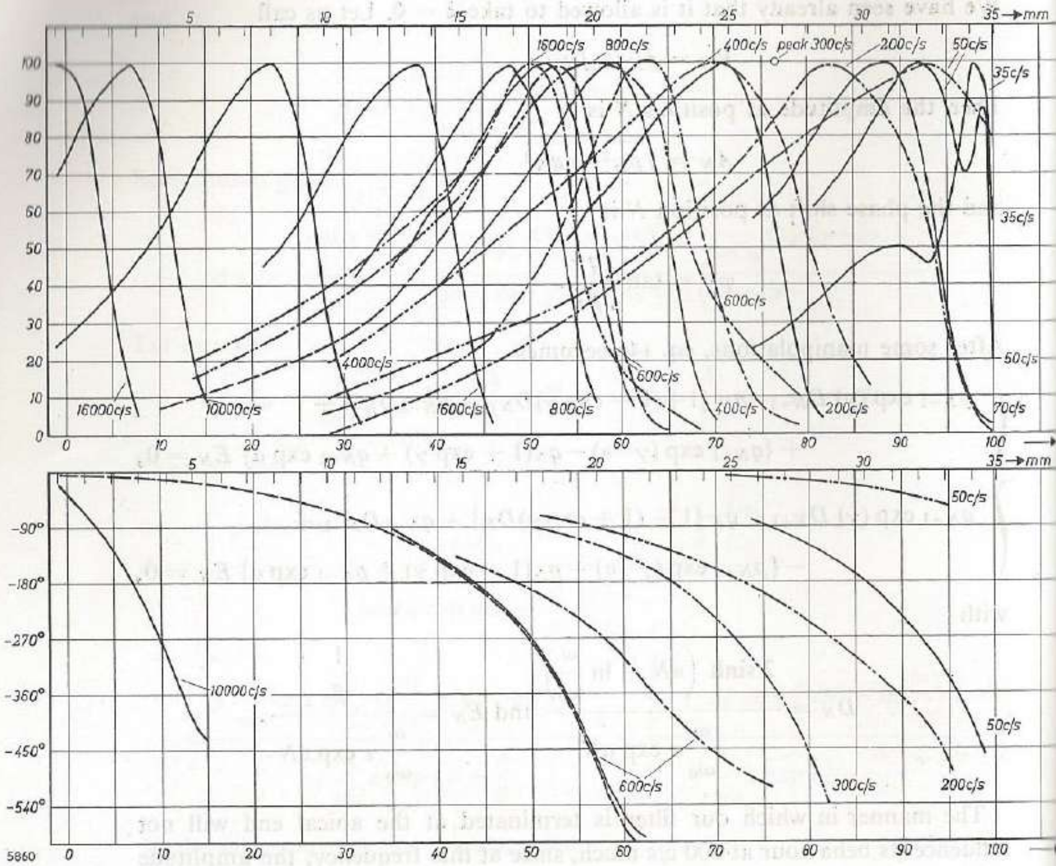


Fig. 9. The normalized amplitude and phase of the cochlear partition.
— - — - calculated by Fletcher
— — — calculated by us
——— measured on our electrical model
— - - — - - measured by Von Békésy, Akust. Z. **8**, 66, 1943, J. acoust. Soc. Amer. **19**, 452, 1947.

but less before the maximum, than Fletcher's. Moreover, our phase lag near the maximum is somewhat more than that of Fletcher. From figs. 6 and 9, we see that our curve is in good agreement with Von Békésy's measurements, especially as regards the phase change near the maximum, but that it has somewhat less damping and is closer to the stapes.

Searching for the differences between us and Fletcher, whose data were used, we have to realize in the first place that the Nth tap is not lying exactly at $(N/100) \times 3{\cdot}5$ cm from the base, because our mass function was calculated from Fletcher's who worked with mass elements of the same length as width. So his mass function was proportional to b^3, where $b(x)$ is the width of the partition. Probably we could

TABLE II

N	$\sqrt{p^2 + q^2}$	φ(deg)	χ(deg)
100	0	0	−775
90	$11{\cdot}1.10^1$	8·11	−767
80	$11{\cdot}3.10^3$	28·7	−746
70	$18{\cdot}5.10^5$	72·0	−703
60	$57{\cdot}1.10^7$	254	−521
54	$13{\cdot}5.10^8$	448	−327
50	$11{\cdot}9.10^8$	530	−245
40	$64{\cdot}7.10^7$	651	−124
30	$33{\cdot}4.10^7$	713	− 62
20	$19{\cdot}7.10^7$	742	− 33
10	$96{\cdot}0.10^6$	756	− 19
0	$32{\cdot}0.10^6$	775	0

better have taken a function proportional to b^2 which would have given a lower value of γ. This lower γ would have brought our maximum more towards the apex and would have resulted in a better agreement with Von Békésy's curves. However, let us not forget that there will be some inaccuracy in Von Békésy's curves which has already been indicated in fig. 5, and that there will be a large variation among the specimens. Moreover, we may assume that the steepness of the curves will not be so important within certain limits, and we designed our model so that successive taps give maxima at frequencies situated a semitone apart so it does not matter so much if all the curves are shifted by the same amount. Bogert has an L varying linearly with x, Bauch and Zwislocki neglect L and let the damping dominate. Peterson and Bogert, and Zwislocki and Bauch have a constant λ, Fletcher takes λ proportional to the cross-section of the scalae. All investigators have results which are in fairly good agreement with Von Békésy's measurements, because their theories are based upon the same principle: liquid coupling between the various parts of the partition. The current flowing through the λ-inductances corresponds to the velocity of the liquid layers in the cochlea and if we had followed another line of reasoning in our theory and expressed all the impedances in pressure per unit volume-velocity it would not matter if one took the total cross-section of the scalae or only the cross-section of the thin layers near the partition. Only the total amount of fluid flowing from x to $x + \mathrm{d}x$ is important, as can be seen from the derivation of eq. (1). Newton's law and the continuity equation are applied for the total of flowing liquid going from x to $x + \mathrm{d}x$. So we have a number of elements Z_N coupled by the mass of the liquid, and we neglect the coupling of

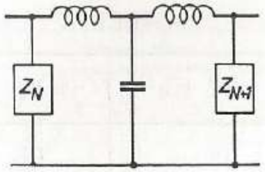


Fig. 10. Representation of two elements of the cochlear partition, coupled by a compressible liquid.

neighbouring elements by stiffness. That this can be done can be shown easily in the electrical model. As the liquid is not really incompressible our equivalent circuit should be as shown in fig. 10 or rather as in fig. 11. Stiffness coupling through the membrane can be represented by the coupling compliance C in

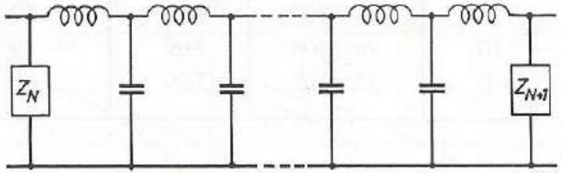


Fig. 11. Improved representation of fig. 9.

series with the compliances of the liquid as in fig. 12, but C will be so large in comparison with the rather incompressible fluid that it can be neglected. And as we have seen in the theory we may conceive the liquid as totally incompressible so we have come back to our starting-point.

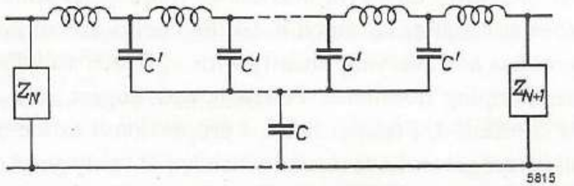


Fig. 12. Coupling of two neighbouring elements of the cochlear partition by the compressible liquid (L and C') and the stiffness of the membrane (C).

It might have been helpful to make our model a representation of the whole cochlea, instead of considering only the thin layers along the partition. Let us imagine that the liquid in the scalae has been built up by thin layers lying over each other. The liquid will flow transversally as well as longitudinally, especially near the partition. Figure 13 gives a picture of the situation. The (incompressible) liquid layers are represented by coupled inductances. These layers have been coupled by inductances to take the transversal motion into account. Friction has been neglected. At the entrance of the canal the pressure P acts on the layers

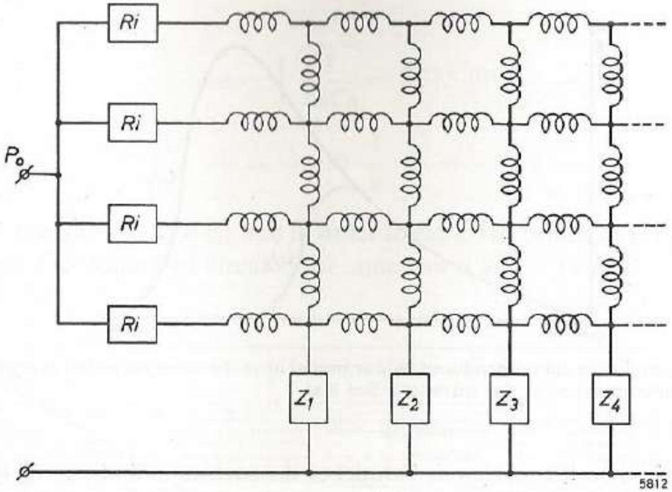


Fig. 13. Simplified representation of the whole cochlea near its base (see text).

via the internal impedance of the oval window (drawn as blocks). From this circuit we see that we will have a current which is mainly longitudinal in the upper layer, but the lower layers will send current into transversal directions too. The pressure modulation caused by the current through the Z's will have been obliterated near the upper layers where the pressure division is determined by longitudinal current. These things together gave us reason to approximate the picture by our simplified model which represents only the lowest layer, and we think that this is justified in the first place by the experiments of Von Békésy [1]), showing that the scalae could have been somewhat thicker or thinner without influencing the motion of the partition and that the position of excitation does not matter (Von Békésy's paradox). In the second place Tonndorf [2]) observed only longitudinal motions near the outer wall of his cochlear model (with the exception of the eddy motion, caused by non-linearities existing for high intensities only) and saw transversal motions of liquid particles near the partition. In the third place, our choice of $\lambda_N/L_N = 0{\cdot}2$, which covered only a part of the liquid in the scalae, gave good agreement with Von Békésy's measurements, and we decided to retain this value for λ_N/L_N in the model.

The curves have the same shape for all frequencies because the connection between V_{N+1}, V_N and V_{N-1} remains the same if

$$\alpha N + \ln \frac{\omega}{\omega_0} = \text{constant},$$

as we have seen already in eq. (4).

The envelopes of the displacement curves for two frequencies ω_1 and ω_2 will be similar if their amplitudes are in the ratio shown in fig. 14.

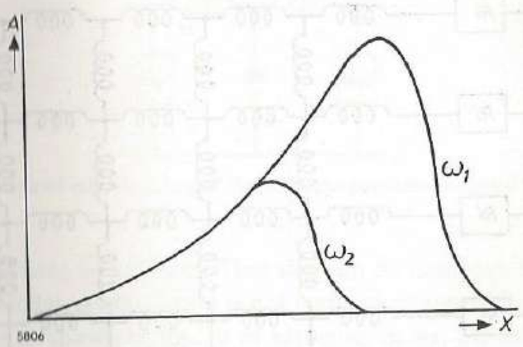


Fig. 14. The amplitude curves produced by our model have the same shape for every frequency ($\omega_1 > \omega_2$; same pressure at the entrance). See text.

Tonndorf [15]) built a mechanical model of the cochlea and measured the place of the maximum displacement as function of the frequency. He compared his results with the dimensionless equation

$$\frac{\rho f l^2}{\eta} = \text{constant},$$

where ρ is the density of the perilymphe,

f the frequency,

l the distance from the stapes,

η the viscosity of the perilymphe,

which equation was originally derived by Von Békésy in 1928, and gives

$$f \sim \frac{1}{l^2}.$$

From

$$aN + \ln \frac{\omega}{\omega_0} = \text{constant}$$

we find

$$f \sim \exp(-l).$$

It seems to us that the experimental data agree better with the latter theoretical relation.

From our example of 600 c/s we can calculate, that at the maximum the constant from our equation is $-0{\cdot}37$, and this allows us to calculate the frequency of the maxima at the other taps.

For $N = 100$ we find

$$\ln \frac{\omega}{\omega_0} = -0{\cdot}37 + 6,$$

where

$$\omega_0 = \sqrt{\frac{1}{L_0 C_0}} = 1{\cdot}315.10^5 \frac{1}{\mathrm{s}} \rightarrow$$

$$\rightarrow \omega_t = 210 \frac{1}{\mathrm{s}} \rightarrow \nu_t = 33 \text{ c/s}.$$

$N = 1$ gives $\nu_t = 13700$ c/s and in order to get a bandwidth of at least 15000 c/s we added another two circuits, the numbers 0 and -1; $N = -1$ gives $\nu_t = 15400$ c/s.

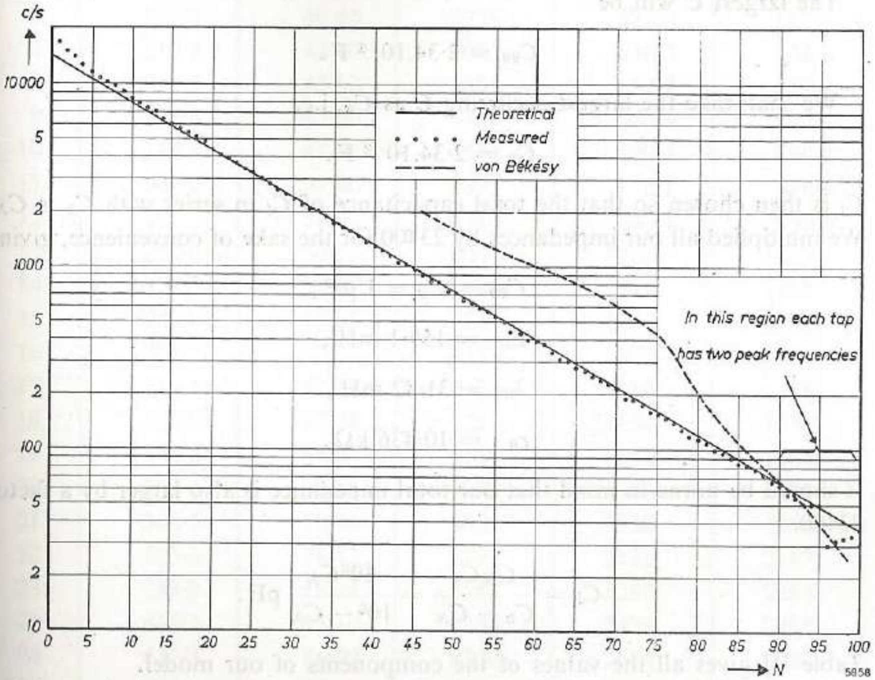


Fig. 15. Relation between the frequency and the number of the circuit where it has its maximum.

Figure 15 shows the relation between frequencies and the number of the tap where they have their maxima, together with the relation between the frequencies and the place upon the basilar membrane where they have their maxima according to Von Békésy [1]).

II.3.3. *The network elements*

We have seen above that the components of our model should have the following values:

$$L_N = L_0 \exp(0{\cdot}04N) \quad \text{with} \quad L_0 = 6{\cdot}8.10^{-6}\ \mathrm{H},$$

$$C_N = C_0 \exp(0{\cdot}08N) \quad \text{with} \quad C_0 = 0{\cdot}85.10^{-5}\ \mathrm{F},$$

$$Y_N = Y_0 \exp(0{\cdot}02N) \rightarrow r_N = \frac{1}{Y_N} = r_0 \exp(-0{\cdot}02N),$$

with $r_0 = 0{\cdot}446\ \Omega.$

$$\lambda_N = \lambda_0 \exp(0{\cdot}04N) \quad \text{with} \quad \lambda_0 = 0{\cdot}2 \times 6{\cdot}8.10^{-6} = 1{\cdot}36.10^{-6}\ \text{H},$$

$$R_N = 0\,.$$

We omitted circuit 100, thus N is going from −1 to 99, which gives a variation of 55·7 in the inductances, 2979 in the capacitances and 7·39 in the resistances.

The largest C will be

$$C_{99} = 2{\cdot}34.10^{-2}\ \text{F}\,.$$

We shall take the largest occurring C as C_k, i.e.

$$C_k = 2{\cdot}34.10^{-2}\ \text{F}\,.$$

C_l is then chosen so that the total capacitance of C_l in series with C_k is C_N. We multiplied all our impedances by 23400 for the sake of convenience, giving

$$C_{99} = C_k = 1\ \mu\text{F}\,,$$

$$L_0 = 159{\cdot}1\ \text{mH}\,,$$

$$\lambda_0 = 31{\cdot}82\ \text{mH}\,,$$

$$r_0 = 10{\cdot}436\ \text{k}\Omega\,.$$

It should be borne in mind that our total impedance is also larger by a factor 23400.

$$C_l = \frac{C_N C_k}{C_k - C_N} = \frac{10^6 C_N}{10^6 - C_N}\ \text{pF}\,.$$

Table III gives all the values of the components of our model.

N	L_N in mH	λ_N in mH	r_N in Ω	C_N in pF	C_l in pF
−1	152·9	30·57	10650	335·5	335·6
0	159·1	31·82	10440	363·4	363·6
1	165·6	33·12	10230	393·7	393·9
2	172·4	34·48	10030	426·4	426·6
3	179·4	35·88	9829	462·0	462.2
4	186·7	37·34	9634	500·4	500·7
5	194·3	38·86	9443	542·1	542·4
6	202·2	40·44	9256	587·3	587·7
7	210·5	42·10	9072	636·2	636·6
8	219·1	43·82	8893	689·2	689·7
9	228·0	45·60	8717	746·6	747·2
10	237·3	47·46	8544	808·7	809·4
11	247·0	49·40	8375	876·1	876·9
12	257·1	51.42	8210	949·1	950·0
13	267·6	53·52	8047	1028	1029
14	278·5	55·70	7888	1114	1115
15	289·9	57·98	7731	1207	1208
16	301·7	60·34	7578	1307	1309
17	314·1	62·82	7428	1416	1418
18	326·9	65·38	7281	1534	1536
19	340·2	68·04	7137	1662	1664
20	354·1	70·82	6996	1800	1803
21	368·5	73·70	6857	1950	1954
22	383·6	76·72	6721	2112	2117
23	399·2	79·84	6588	2288	2293
24	415·5	83·10	6458	2479	2485
25	432·5	86·50	6330	2685	2692
26	450·1	90·02	6205	2909	2917
27	468·5	93·70	6082	3151	3161
28	487·6	97·52	5961	3414	3426
29	507·5	101·5	5843	3698	3712
30	528·2	105·6	5727	4006	4022
31	549·8	110·0	5614	4339	4358
32	572·2	114·4	5503	4701	4723
33	595·6	119·1	5394	5092	5118
34	619·9	124·0	5287	5516	5547
35	645·2	129·0	5182	5976	6012

N	L_N in mH	λ_N in mH	r_N in Ω	C_N in pF	C_l in pF
36	671·5	134·3	5079	6474	6516
37	698·9	139·8	4979	7013	7063
38	727·4	145·5	4881	7597	7655
39	757·1	151·4	4784	8230	8298
40	788·0	157·6	4689	8915	8995
41	820·2	164·0	4596	9658	9752
42	853·7	170·7	4505	1046.10^1	1057.10^1
43	888·5	177·7	4416	1133.10^1	1146.10^1
44	924·8	185·0	4329	1228.10^1	1243.10^1
45	962·5	192·5	4243	1330.10^1	1348.10^1
46	1002	200·4	4159	1441.10^1	1462.10^1
47	1043	208·5	4077	1561.10^1	1585.10^1
48	1085	217·0	3996	1691.10^1	1720.10^1
49	1130	225·9	3917	1832.10^1	1866.10^1
50	1176	235·1	3839	1984.10^1	2024.10^1
51	1224	244·7	3763	2149.10^1	2197.10^1
52	1274	254·7	3689	2328.10^1	2384.10^1
53	1326	265·1	3616	2522.10^1	2588.10^1
54	1380	275·9	3544	2732.10^1	2809.10^1
55	1436	287·2	3474	2960.10^1	3050.10^1
56	1495	298·9	3405	3207.10^1	3313.10^1
57	1556	311·1	3338	3474.10^1	3599.10^1
58	1619	323·8	3272	3763.10^1	3910.10^1
59	1685	337·0	3207	4076.10^1	4249.10^1
60	1754	350·8	3143	4416.10^1	4620.10^1
61	1825	365·1	3081	4738.10^1	5023.10^1
62	1900	380·0	3020	5182.10^1	5465.10^1
63	1978	395·5	2960	5613.10^1	5947.10^1
64	2058	411·6	2902	6081.10^1	6475.10^1
65	2142	428·4	2844	6587.10^1	7051.10^1
66	2230	445·9	2788	7136.10^1	7684.10^1
67	2321	464·1	2733	7731.10^1	8379.10^1
68	2415	483·0	2679	8374.10^1	9139.10^1
69	2514	502·8	2625	9072.10^1	9977.10^1
70	2616	523·3	2573	9827.10^1	1090.10^2
71	2723	544·6	2523	1065.10^2	1191.10^2
72	2834	566·8	2473	1153.10^2	1304.10^2

N	L_N in mH	λ_N in mH	r_N in Ω	C_N in pF	C_l in pF
73	2950	590·0	2423	1249.10^2	1428.10^2
74	3070	614·1	2376	1353.10^2	1565.10^2
75	3196	639·1	2329	1466.10^2	1718.10^2
76	3326	665·2	2282	1588.10^2	1888.10^2
77	3462	692·3	2237	1720.10^2	2078.10^2
78	3603	720·6	2193	1864.10^2	2291.10^2
79	3750	750·0	2150	2019.10^2	2530.10^2
80	3903	780·6	2107	2187.10^2	2799.10^2
81	4063	812·5	2065	2369.10^2	3105.10^2
82	4228	845·6	2024	2567.10^2	3453.10^2
83	4401	880·1	1984	2780.10^2	3851.10^2
84	4580	916·1	1945	3012.10^2	4310.10^2
85	4767	953·5	1907	3263.10^2	4843.10^2
86	4962	992·4	1869	3535.10^2	5467.10^2
87	5164	1033	1832	3829.10^2	6205.10^2
88	5375	1075	1795	4148.10^2	7088.10^2
89	5594	1119	1760	4493.10^2	8160.10^2
90	5823	1165	1725	4867.10^2	9483.10^2
91	6060	1212	1691	5273.10^2	1116.10^3
92	6308	1262	1657	5712.10^2	1332.10^3
93	6565	1313	1625	6188.10^2	1623.10^3
94	6833	1367	1592	6703.10^2	2033.10^3
95	7112	1422	1561	7261.10^2	2651.10^3
96	7402	1480	1530	7866.10^2	3686.10^3
97	7704	1541	1500	8521.10^2	5761.10^3
98	8019	1604	1470	9231.10^2	1200.10^4
99	8346	1669	1441	10000.10^2	~

The real components from which our model has been built had of course some deviation from the theoretical values. The coils in particular gave a lot of difficulties because their inductances were dependent on the current, the temperature and the frequency, because the wire was wound on a ferroxcube core and cased in a ferroxcube pot with a small air gap which could be adjusted for correction. The μ of ferroxcube is dependent on frequency and intensity, and that of the small air gap on temperature. Especially the frequency dependence could not be neglected, variations of 10% or more from 100 c/s to 8 kc/s existed, while the other variations were much smaller, e.g.

$$\frac{\Delta L}{L} \approx \frac{1}{100} \quad \text{for} \quad \frac{\Delta I}{I} = 100\,.$$

It is impossible to correct for errors in L by altering the corresponding capacitances because this gives wrong impedances before the resonating circuit and those errors are additive. The only thing to do was therefore to adjust each L so that it has its proper value near the resonance frequency of its circuit. Before the resonating circuit, the impedances are determined by the capacitances which can be made within 1 % of their theoretical values without much trouble, and after the resonating circuit the inductance L is not so important because a somewhat steeper or slower fall of the curve will not matter so much.

Before the resonating circuit one filter element can be depicted by fig. 16.

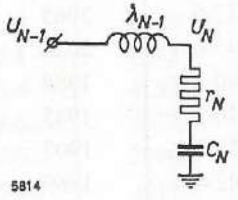


Fig. 16. Simplification of an element before the resonating circuit.

$$\frac{U_N}{U_{N-1}} \approx \frac{\dfrac{1}{j\omega C_N} + r_N}{\dfrac{1}{j\omega C_N} + r_N + j\omega\lambda_N} = \frac{1 + \dfrac{j}{\beta}\dfrac{\omega}{\omega_0}\exp aN}{1 + \dfrac{j}{\beta}\dfrac{\omega}{\omega_0}\exp aN - \varepsilon\left(\dfrac{\omega}{\omega_0}\ \exp\ aN\right)^2}.$$

For most circuits,

$$\frac{1}{\beta}\frac{\omega}{\omega_0}\ \exp\ aN > \varepsilon\left(\frac{\omega}{\omega_0}\ \exp\ aN\right)^2,$$

so that λ is not so important there.

At the resonance frequency

$$\frac{U_N}{U_{N-1}} \approx \frac{r_N}{r_N + j\omega\lambda_N} = \frac{\dfrac{1}{\beta}}{\dfrac{1}{\beta} + j\dfrac{\omega}{\omega_0}\ \varepsilon \exp aN}.$$

So λ is more important here.

So we gave the capacitances their theoretical values as near as possible, and it is quite easy do to this within 1 %, and did the same with the L's and λ's near the resonance frequency of their circuit. We have taken the theoretical values for the resistances, taking the resistance of the L coils into account. The λ coils will have some resistance too, which means that δ is not exactly zero. We measured that $\omega\lambda = R$ for a frequency which is at least 8 times smaller than the resonance frequency of the circuit to which λ is connected. So this coil resistance will not give much trouble.

Before giving the further results of the measurements we have to consider both ends of our filter separately. We started with an inductance direct behind the entrance, giving the right voltage across circuit −1 (fig. 17).

$$\lambda_{-2} = \lambda_{-1}\,\frac{1}{e}\exp(-\gamma) = 29{\cdot}37\ \text{mH}.$$

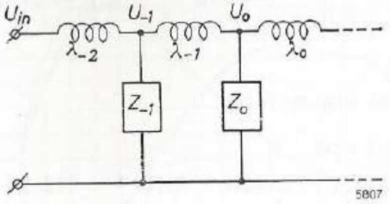


Fig. 17. The input of our circuit.

At the other end the filter will be terminated by the helicotrema. Some investigators have a short-circuit there, but one can even take an infinite resistance: it does not matter so much, except for the very low frequencies. Since we have tried to base our model of the cochlea on anatomical data, we decided to terminate our filter with an element constructed in accordance with anatomical considerations too.

Taking the helicotrema as a cylinder with a length of 0·1 cm and a cross-section of 25.10^{-4} cm², i.e. a radius of $2{\cdot}8.10^{-2}$ cm, we can calculate its impedance which will correspond to an inductance in series with a resistance. But here also we may wonder whether all the liquid has an effect.

The liquid mass which is responsible for the coupling at the end of the scalae can be represented by

$$\lambda_{100} = 1{\cdot}36.10^{-6}\exp 4 = 74{\cdot}3.10^{-6}\ \text{H}.$$

This corresponds to a volume of about $74{\cdot}3.10^{-6}$ cc perilymphe. The width of the basilar membrane at the end is $5{\cdot}2.10^{-2}$ cm, the length of our λ_{100} column 34.10^{-2} cm, so the height will be

$$\frac{74{\cdot}3.10^{-6}}{5{\cdot}2.10^{-2} \times 34.10^{-2}} = 4{\cdot}2.10^{-2}\ \text{cm}.$$

The real height of the scalae is 15.10^{-2} cm here, so we see that the loading layer is indeed smaller than the total amount of liquid.

Let us assume then that the active cross-section of the helicotrema is

$$4{\cdot}2.10^{-2} \times 5{\cdot}2.10^{-2} = 22.10^{-4}\ \text{cm}^2,$$

which is about the total cross-section.

The loading mass at the end is then

$$S.l_{eff}.\rho = 22.10^{-4}\ (0{\cdot}1 + 0{\cdot}8\sqrt{22.10^{-4}})\ 1 = 3.10^{-4}\ \mathrm{g}.$$

The resistance of the helicotrema will be

$$R = 8\pi l\eta = 8\pi \times 0{\cdot}1 \times 0{\cdot}02 = 50{\cdot}2.10^{-3}\ \mathrm{g/s}\,.$$

$R = \omega m$ for

$$\omega = \frac{50{\cdot}2.10^{-3}}{3.10^{-4}} = 170\ \frac{1}{\mathrm{s}} \rightarrow \nu = 27\ \mathrm{c/s}\,.$$

(Fletcher gives 50 c/s).

We see that m is most important.

In our network we get

$$L_H = 23400 \times 3.10^{-4} = 7\mathrm{H}$$

with the resistance

$$R = 23400 \times 50{\cdot}2.10^{-3} = 1250\ \Omega\,.$$

In total we have the filter of fig. 18.

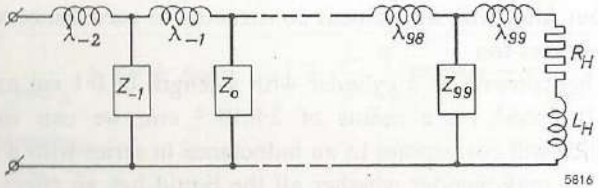


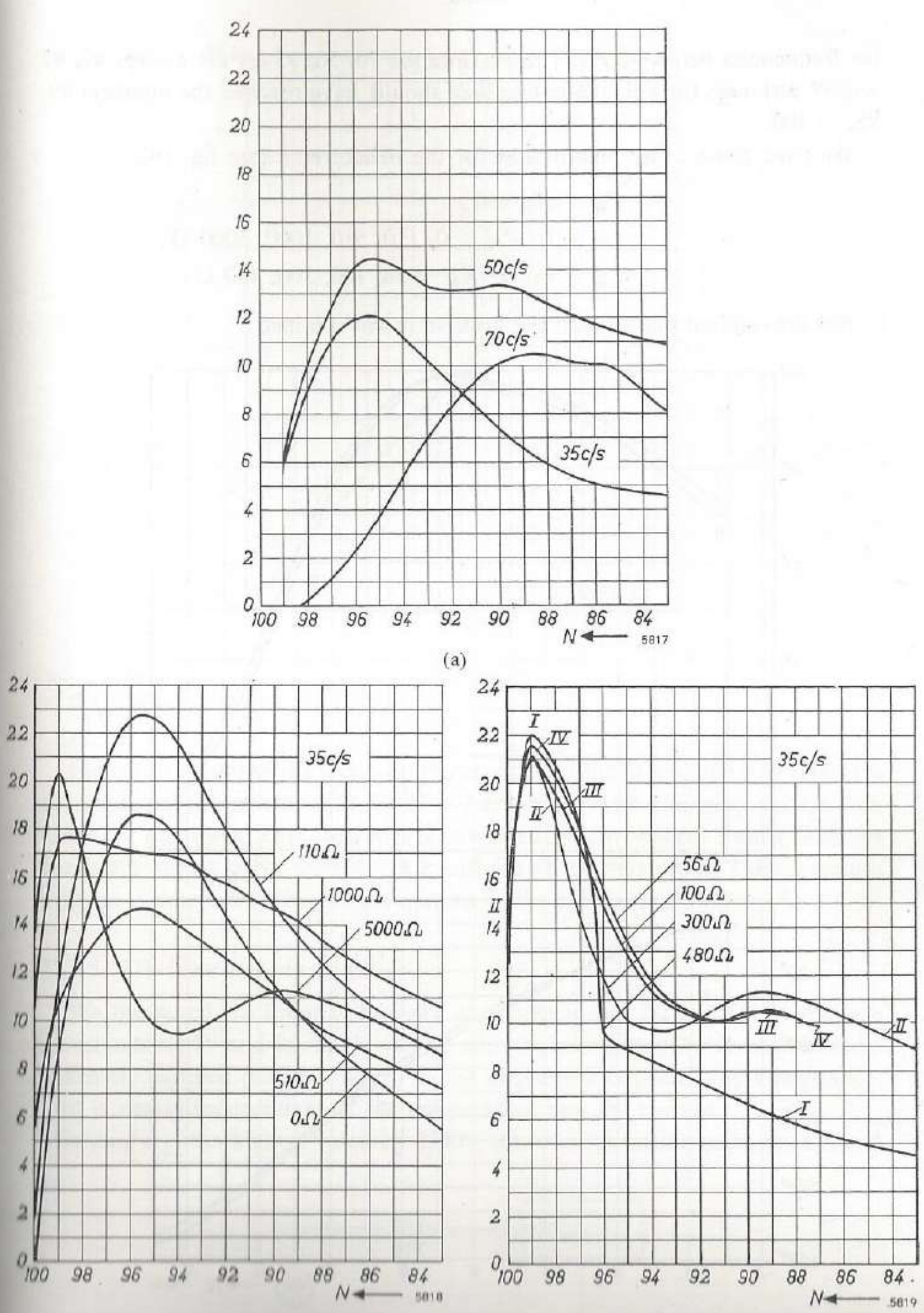
Fig. 18. The beginning and end of our circuit.

L_H is of the same order of magnitude as L_{100}, which means that near the apical end of our model the maxima for different frequencies will be crowded together, as was found by Von Békésy [1]). This means that at low frequencies, the distance between neighbouring taps will be more than a semitone.

II.3.4. *Results of the measurements*

We saw already in fig. 9 that there is only a slight difference between the calculated and measured curve at 600 c/s which is mainly due to the frequency dependence of the coils.

Figure 9 gives the amplitudes with normalized maxima, and the phases as functions of the circuit number for 35, 50, 70, 200, 400, 600, 800, 1600, 4000, 10000, 16000 c/s, compared with Fletcher and Von Békésy. They were measured with our theoretical helicotrema at the end of the filter. It may be seen that there are some reflections at that end and there is a beginning of standing waves



(a)

(b)

(c)

Fig. 19. Different possibilities for the helicotrema.
(a) $L_H = R_H = 0$.
(b) $L_H = 0$; $R_H = 0, 110, 500, 1000, 5000\ \Omega$.
(c) $L_H = 8{\cdot}7\ \mathrm{H}$; $R_H = 56, 100, 300, 480\ \Omega$.

for frequencies below 70 c/s. The maxima for 70, 50, 35 c/s are at taps 89, 92 and 99, although for an infinite line they should have reached the numbers 89, 95, > 100.

We tried some other possibilities for the helicotrema (see fig. 19).

$$L_H = R_H = 0\,,$$
$$L_H = 0;\; R_H = 0,\ 110,\ 510,\ 1000,\ 5000\ \Omega\,,$$
$$L_H = 8{\cdot}7\,\mathrm{H};\; R_H = 56,\ 100,\ 300,\ 480\ \Omega\,.$$

But the original one seemed the best, so it was retained.

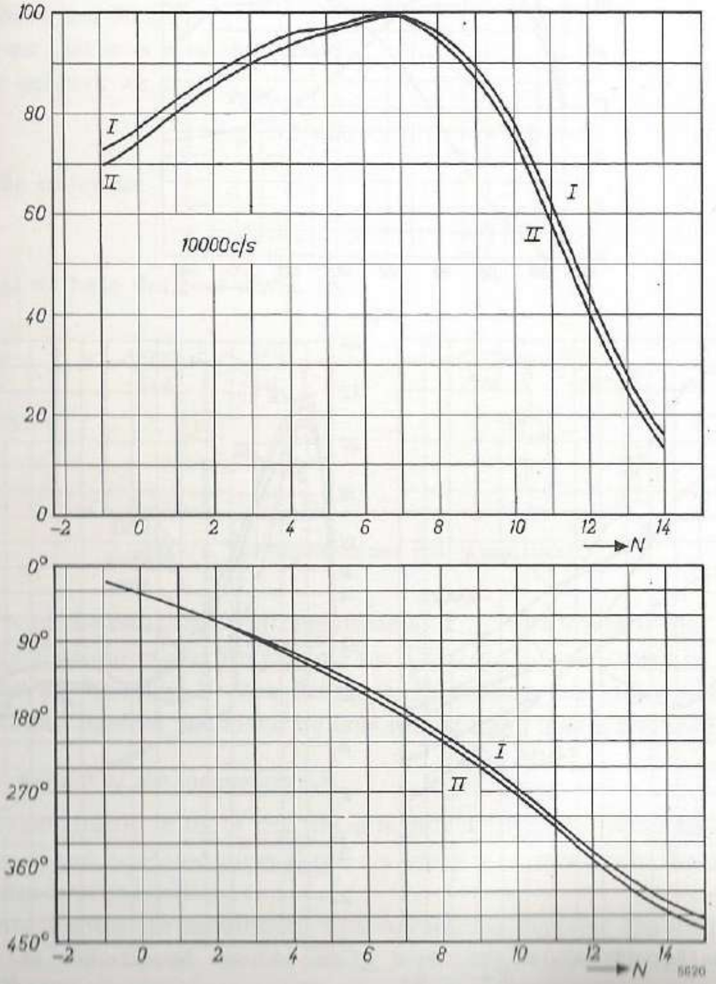


Fig. 20. The influence of temperature and voltage on the amplitude and phase at 10000 c/s in our model.
I. 19 °C with the tensions V and 10 V.
II. 21 °C with the tensions V and 10 V.

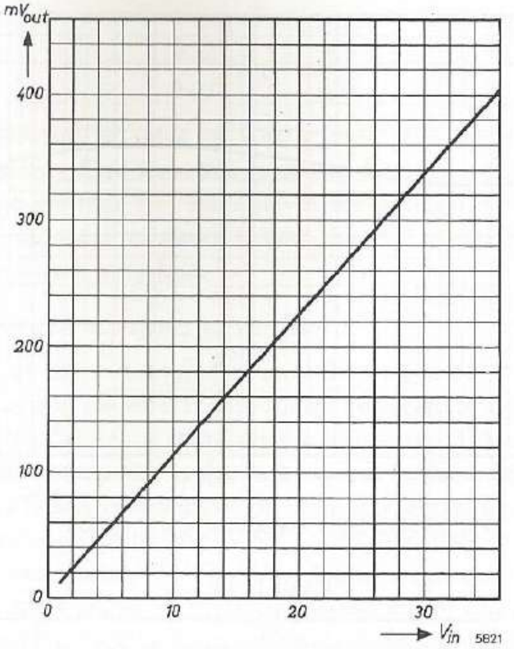


Fig. 21. The input-output curve measured at 600 c/s. V_{in} at the input of the circuit, V_{out} at the 52nd tap.

Figure 20 shows us the relative difference in amplitude and phase at 10000 c/s for changing temperature (19 °C-21 °C) combined with changing voltage (ten times) at the input. This difference is only small as can be seen. Figure 21 shows the input-output curve for 600 c/s, measured at the maximum. The maximum voltage is determined by the dissipation in the resistances.

II.3.5. *The input impedance*

We measured the input impedance as shown in fig. 22, and the results are given in table IV and fig. 23. It may be seen that the system behaves rather like a heavily damped parallel circuit, so the impedance is practically a resistance, and is nearly independent of the temperature and the current.

Dividing e.g. the highest value by 23400, the transformation ratio, mentioned

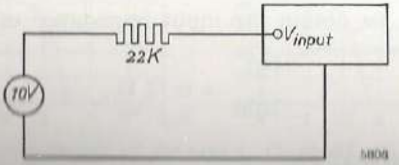


Fig. 22. Circuit for measuring the input impedance of our model.

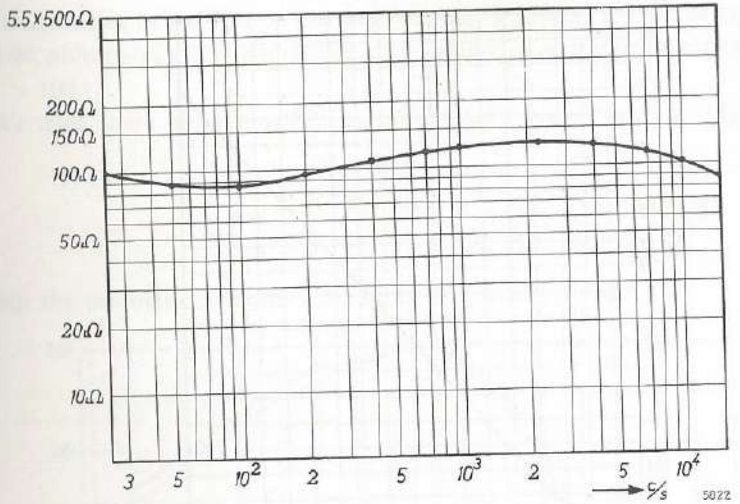


Fig. 23. The input impedance of our model.

TABLE IV

frequentie in c/s	amplitude in V	phase in degree	impedance in kΩ
25	2	+ 1	5.5
50	1·75	+ 2·5	4·66
100	1·75	+ 10·5	4·66
200	1·97	+ 14	5·38
400	2·15	+ 13·8	6·03
700	2·34	+ 11·5	6·71
1000	2·42	+ 9	7·04
2300	2·55	0	7·55
4000	2·50	— 10	7·33
7000	2·28	— 22	6·48
10000	2·05	— 30	5·66
15000	1·72	— 38	4·57
20000	1·53	— 40	3·97

already on page 42, we obtain the input impedance of our original model:

$$\frac{7550}{23400} = 0{\cdot}32\ \Omega\,,$$

which is equivalent to 0·32 g/s.

Since the area of the oval window is about 3 mm^2, our impedance may be

expressed as

$$\frac{0{\cdot}32}{0{\cdot}03} = 11\ \frac{\mathrm{g}}{\mathrm{cm^2 s}}\,.$$

Zwislocki calculates a value of 9000 g/cm^{2}s. The latter resistance is also measured for steady fluid flow and is caused by eddies or losses against the wall [1]). Thus we see that the resistance of the principal system is very small compared with the total resistance behind the oval window. The efficiency of our cochlear system is very bad.

II.3.6. *Frequency characteristics of the taps*

Up till now we have measured mainly the output of all the taps for one frequency. Let us now see what is happening at one tap for different frequencies. If we measure the frequency characteristic of one tap with a constant voltage across the input, we measure at constant current because the input impedance of our model is nearly independent of frequency. From fig. 14 we can expect that the frequency characteristic at one tap will be flat up to the frequency which gives its maximum at this tap. For higher frequencies the characteristic decreases. Figure 24 shows us these characteristics for circuits with an interspacing of one octave, together with the input voltage (40 dB lower than it was in

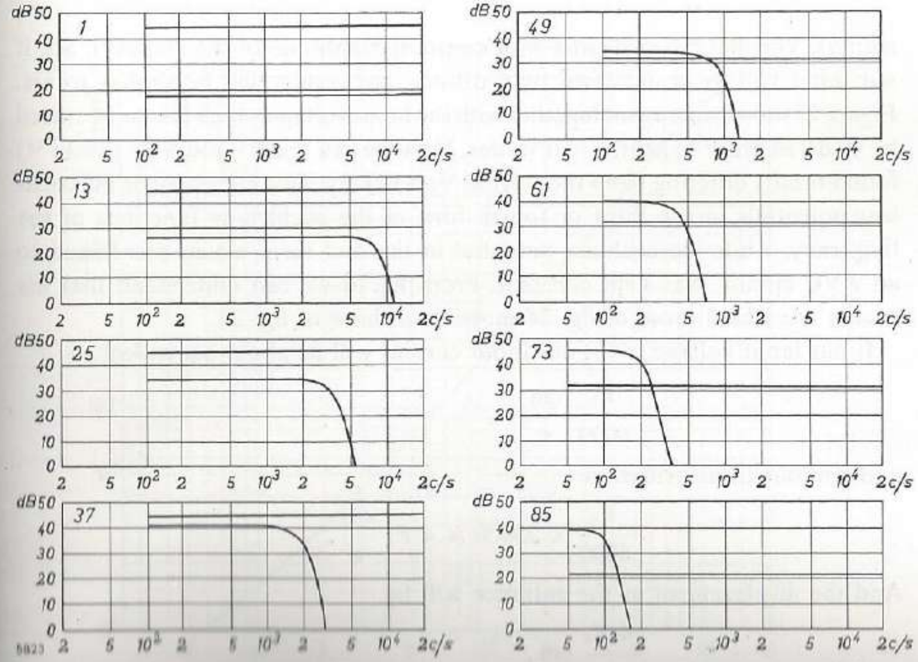


Fig. 24. The frequency characteristic of the taps 1, 13, 25, 37, 49, 61, 73, 85 (curved lines) for constant input voltage. The input voltage has been drawn in, 40 dB lower than its real value (straight lines).

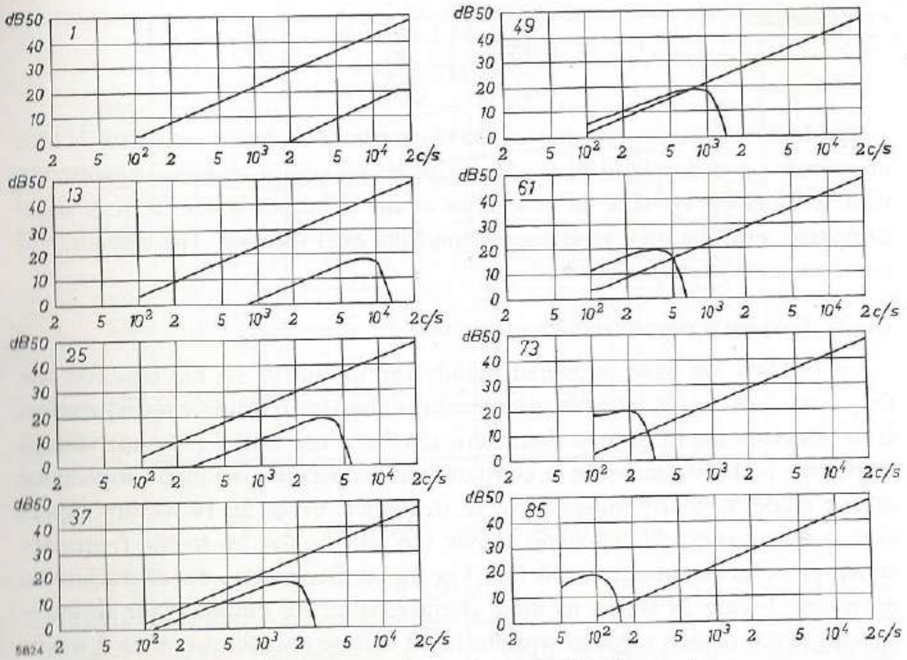


Fig. 25. The same as fig. 24, but raised 6 dB per octave.

reality). Von Békésy measured with constant amplitude of the stapes [6]). So, if our input voltage is increased by 6 dB/oct, our results will be similar to his. Figure 25 shows this, again together with the input voltage which has to be raised by 40 dB in order to get the real values. Now we can understand why Tasaki [16]) found results differing from those from Von Békésy. Tasaki measured the cochlear potentials in the third or fourth turn of the cochlea as functions of the frequency, while the cochlear potential in the first turn, which was linked to an AVC circuit, was kept constant. From fig. 14 we can understand that his results resembled those of fig. 24 more than those of fig. 25.

If our input voltage is V_1, our input current will be about equivalent to

$$\frac{V_1}{6000}\ \frac{\text{cm}}{\text{s}}$$

and without transformation

$$\frac{V_1}{6000} \times 23400 \approx 4\,V_1\,\frac{\text{cm}}{\text{s}}.$$

And the displacement at the entrance will be

$$\frac{4\,V_1}{\omega}\ \text{cm},$$

where ω is the frequency.

Assuming that the oval window has the same displacement, we find a volume displacement of

$$3.10^{-2} \times 4\,\frac{V_1}{\omega} = 12.10^{-2}\,\frac{V_1}{\omega}\ \text{cm}^3.$$

If V_2 is the maximum voltage for the frequency ω, the maximum amplitude will be

$$23400.10^{-6}\ V_2\ \text{cm}.$$

Thus the ratio of the volume displacement of the stapes to the maximum amplitude of the partition will be

$$12.10^{-2}\,\frac{V_1}{\omega} \times \frac{1}{2{\cdot}34.10^{-2}V_2} \approx \frac{5}{\omega} \times \frac{V_1}{V_2}\ \text{cm}^2.$$

From fig. 24 we can calculate that this will be

for 50 c/s: 0·16 cm^2
for 100 c/s: 0·125 cm^2
for 200 c/s: 0·125 cm^2
for 400 c/s: 0·11 cm^2
for 800 c/s: 0·12 cm^2.
for 1600 c/s: 0·12 cm^2
for 4000 c/s: 0·12 cm^2
for 8000 c/s: 0·12 cm^2
for 20000 c/s: 0·12 cm^2

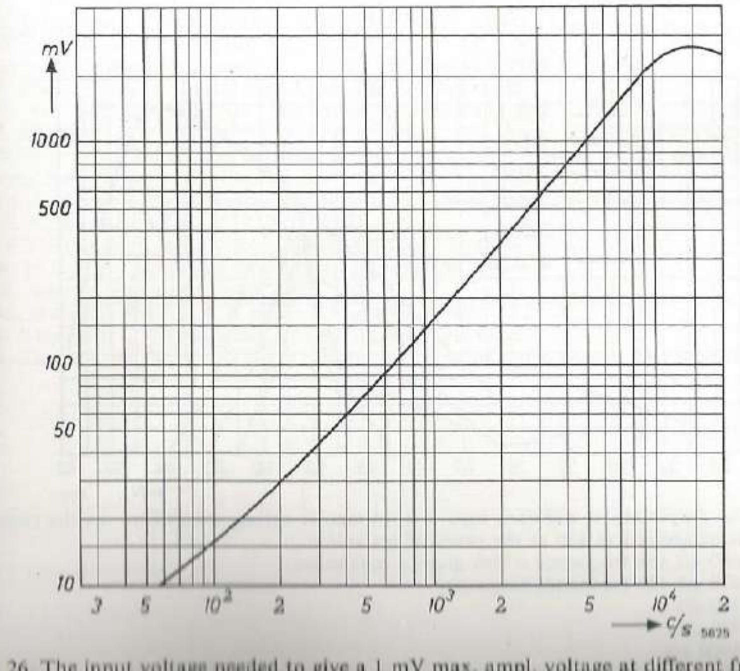


Fig. 26. The input voltage needed to give a 1 mV max. ampl. voltage at different frequencies,

Von Békésy 6) measured values varying from 4.10^{-2} cm^2 to 7.10^{-3} cm^2, which differs from our results by a factor 17, which is rather bad. But the assumption that the displacement of the oval window will be the same as that found at the entrance of the cochlear partition is a bit doubtful.

Figure 15 shows us the maximum frequency of the taps compared with a theoretical line for a filter with 12 circuits per octave. Some measurements by Von Békésy are also shown, assuming that our circuits are divided equally over 35 mm of length.

We see deviations from the theoretical line at both ends of our filter. Near the entrance we seem to be measuring the resonance frequency, near the apical end we get irregularities due to the manner in which we terminated our circuit. We measure two maximum frequencies for each circuit there, because of the reflections. The one with the larger amplitude has been drawn in fig. 15.

Figure 26 shows us the input voltage needed to give a constant maximum amplitude voltage of 1 mV at each tap. The measured input voltages are plotted against the measured maximum frequencies. We see that, except for both ends, this relation is a line with a slope of 6 dB/oct.

II.3.7. *Von Békésy's paradox*

As our model does not depict the whole scalae with the whole perilymphe, but only the partition with a thin liquid layer at both sides, it must not show Von Békésy's paradox.

We operated the filter at the tap where the maximum of 600 c/s occurs. That means that we brought a force upon the partition at a certain position with a frequency of 600 c/s, the maximum frequency; 870 c/s, the resonance frequency; 300 c/s, a frequency lower than the maximum frequency; 720 c/s, a frequency between maximum and resonance frequency; and 1800 c/s, a frequency much higher than the resonance frequency.

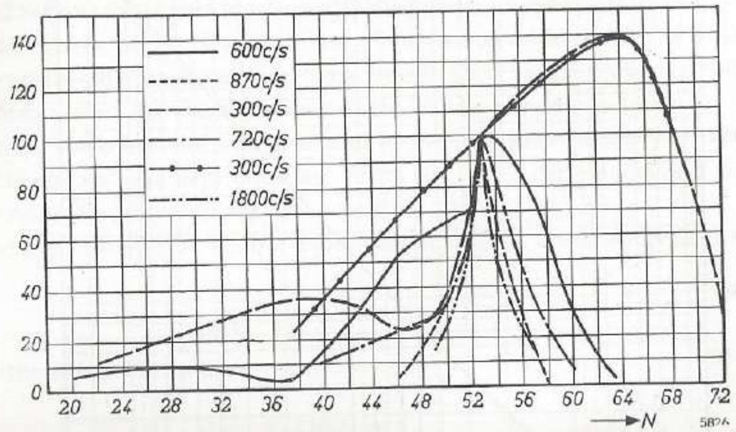


Fig. 27. The amplitude at different taps if a voltage is acting somewhere on the cochlear partition, standardized at 100 at the point of activation.
——— 600 c/s the frequency which gives a maximum
------- 870 c/s the resonance frequency
— — — 300 c/s
—·—·— 720 c/s
—··—·· 1800 c/s
—•—•— 300 c/s driven by the stapes.

Figure 27 shows the voltages measured at different taps, being normalized at 100 at the position where the force impacts.

We see that for frequencies higher than the maximum frequency the partition moves only up and down, which could be expected, because those frequencies are seeing only mass around them. Thus there is no travelling wave, all points are in phase. For frequencies lower than or the same as the maximum frequency we see that to the apical side we have the common travelling wave, as if the system were driven by the stapes. This can be controlled by the curve for 300 c/s, driven by the stapes, which has been drawn in too. This could be expected, because for an infinite line the stapes is an arbitrary driving point. To the basal side we see the beginning of standing waves, but for no frequency we see the same picture as with the driving stapes over the whole length.

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III. THE MIDDLE EAR

III.1. Anatomy

We already know that the columella, the simple bone between the eardrum and the oval window of e.g. birds, has evolved into a number of more or less independent ossicles: the malleus or hammer, which is connected to the tympanic membrane; the incus or anvil, the middle ossicle, and the stapes or stirrup, which is connected to the oval window. Those three ossicles are generally known, but there exists another one, a small round bone between the anvil and the stirrup, so in fact we have four middle-ear ossicles. We have however neglected the effect of the fourth ossicle in our consideration of the middle ear. The shape of these ossicles is described by their names. Two muscles, the tensor tympani and the stapedius, joined to the malleus and the stapes respectively, together with some ligaments, keep the ossicles in place. Figures 28 and 29 show us the situation.

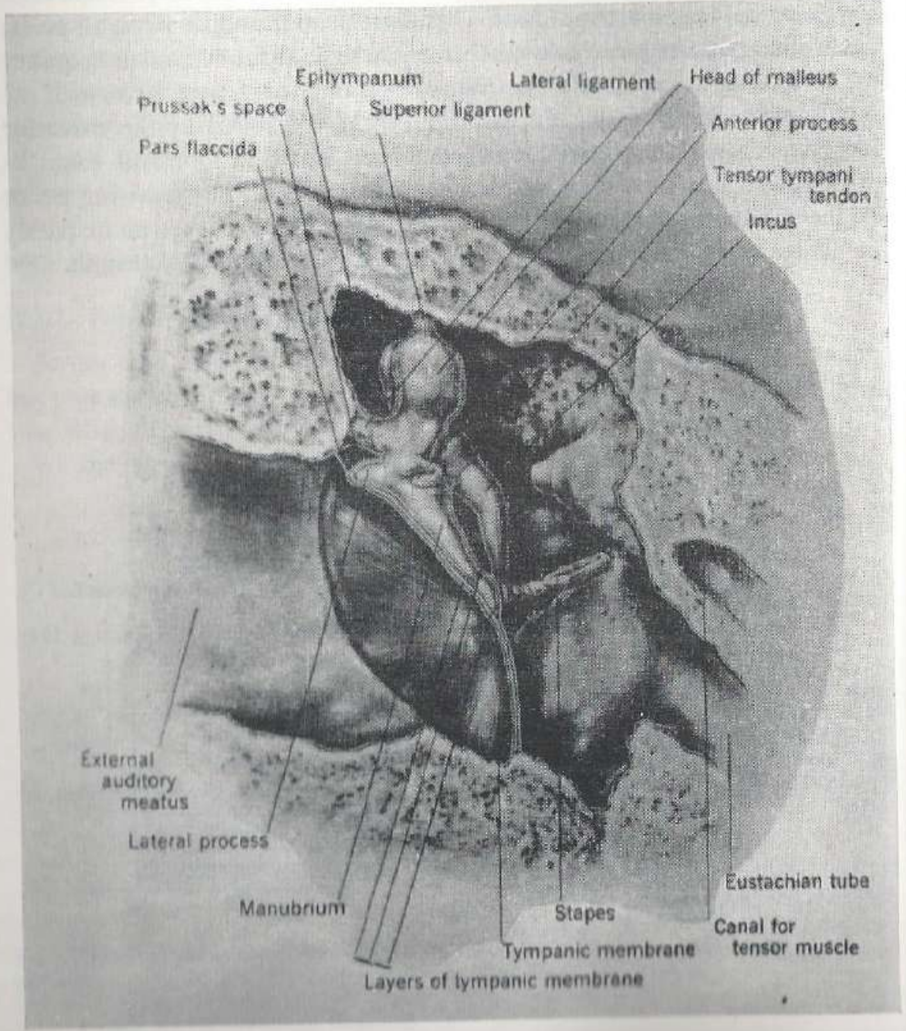


Fig. 28. The middle ear on the right side, seen from the front. The tensor tympani muscle and most of its tendon have been removed. From John B. Deaver, Surgical Anatomy of the Human Body, 1926, The Blakiston Company.

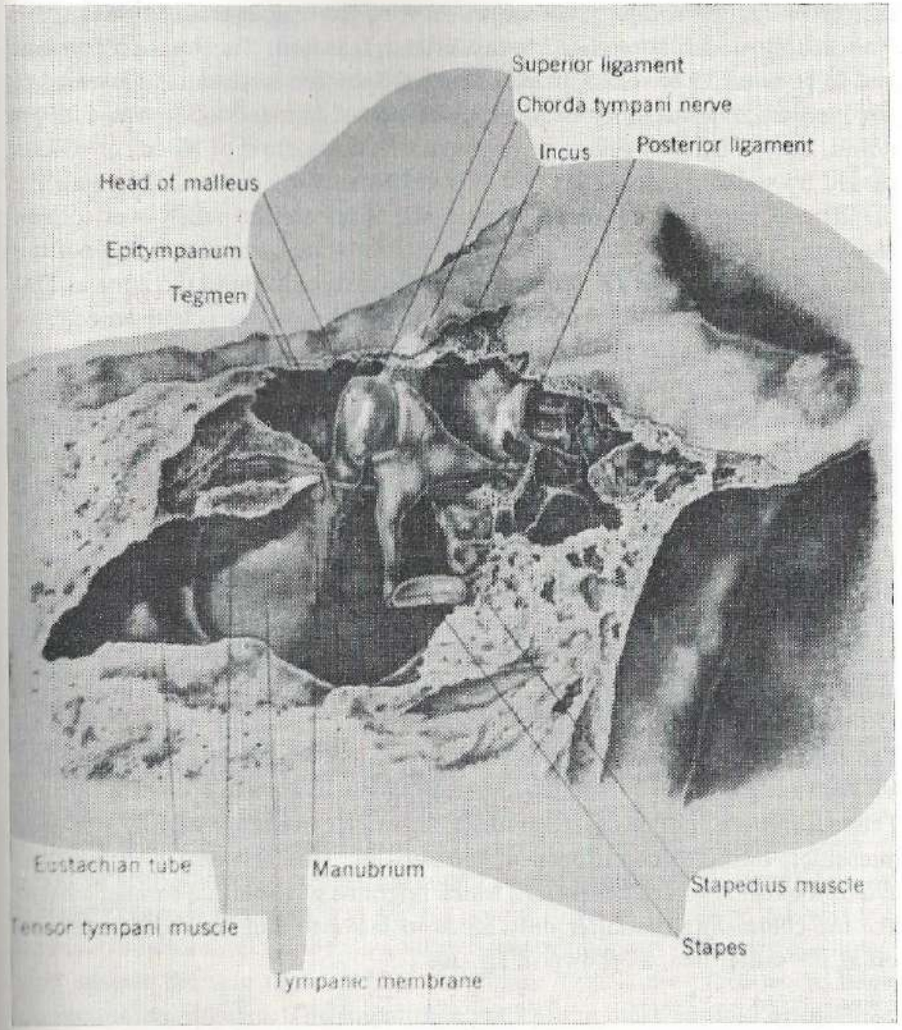


Fig. 29. The middle ear on the right side, seen from within. From John B. Deaver, Surgical Anatomy of the Human Body, 1926, The Blakiston Company.

Although it is dangerous, seen from a scientifical point of view, to search for a teleological reasoning in evolution, we may still ask ourselves what can be the reason for the complicated construction of the ossicle-chain? It was again Von Békésy [1]) who attempted to answer this question. The total mechanism had to be sensitive to sound which impinged upon the eardrum and insensitive to sound reaching the inner ear via another way of conduction, or to disturbing noises, caused by such things as yawning, breathing, flow of blood, or shocks caused by walking. Moreover, our own voice, reaching our hearing organ via the air and by bone conduction should not dominate too much over sounds reaching us from the outside. Measurements show that the contribution of the air-conducted sound to the loudness of our own voice is about the same as that of the bone-conducted sound. The latter, together with the sound pressure in the cavities around the vocal cords, makes our skeleton vibrate. The same can be said of the other noise sources mentioned above. The mass of the head, together with its connection to the body, and the situation of the inner ear in the petrous bone, reduce the noise transmission by bone conduction to the inner ear fluid to a minimum. The transmission of this sound to the tympanic membrane or middle-ear ossicles will be bad because of the soft connection of this system with its surroundings. Vibration of the ossicle chain caused by head shaking is kept to a minimum by the relative heavy masses of the hammer and anvil. On the contrary, conduction through the chain for sound caught by the ear, occurs by tilting of the ossicles about their centres of gravity so that their moment of inertia is minimal. The eardrum is a stiff cone joined to the handle of the hammer. It can tilt around its upper edge, taking the hammer with it. The connection between hammer and anvil is rather stiff, but the connection between anvil and stirrup is much looser, probably to serve as a shock absorber. The total system has one degree of freedom, which can change slightly at higher intensities, owing to contraction of the muscles. This one degree of freedom avoids the formation of undertones which might be possible in a simpler system like the columella. The latter only needs to move to and fro, but it can also tilt at the same time, as shown in fig. 30.

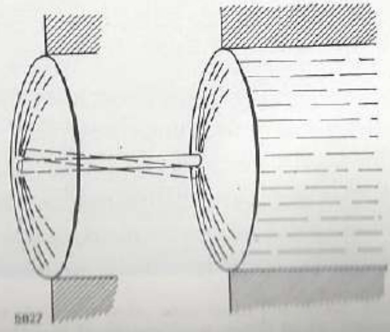


Fig. 30. The possible motion of the columella, giving subharmonics. After Von Békésy

The footplate of the stapes fills up nearly the whole oval window, so that the liquid in the inner ear cannot distend the membrane as shown in fig. 31, for that would mean a short-circuit. For high intensities the axis of rotation of the stapes is changed by the stapedius, resulting in a decrease of the amount of

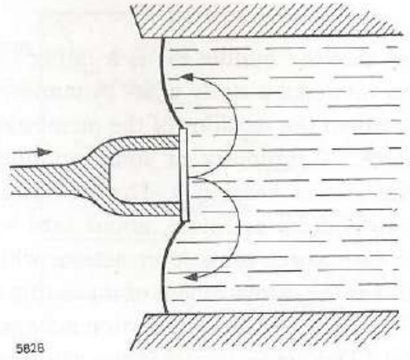


Fig. 31. The possible liquid flow if the stapes footplate were much smaller than the oval window. After Von Békésy.

fluid displaced, as can be seen in fig. 32. Contraction of the tensor tympani increases the stiffness of the eardrum, making the system less sensitive to bass tones, thus giving some protection against external noises, which often have a lot of energy at the lower frequencies, while the resonance frequency is increased making the system more sensitive to the more important middle frequencies. When animals prick their ears, this muscle always contracts also. Thus we may expect that this rather complicated construction of the middle-ear system is meant to give preference to external sound and to protect the inner ear against damage. There is a second way for the sound to reach the inner ear without too much troubles, i.e. via the mastoid, a rather porous part of the petrous bone, lying against the skin direct behind the pinna. That is the place where bone conductors are situated. The sound then reaches the inner ear mainly by three routes: as a result of inertial forces on the perilymphe and the middle-ear ossicles

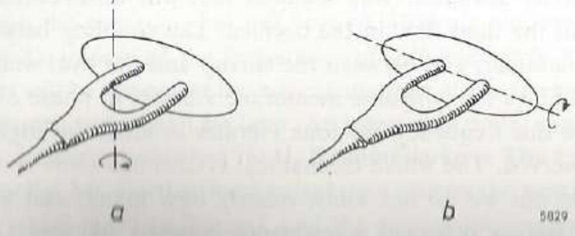


Fig. 32. The two possible axes of rotation of the stapes.
(*a*) for low intensities
(*b*) for high intensities.

due to vibration of the head as a whole (for low frequencies), by compression of the semicircular canals and the vestibulum (for high frequencies), and by magnification of the pressure in the auditory canal caused by motions of its walls (for low frequencies).

III.2. Dynamics

We have already seen that the middle ear is a rather complex system, and this appears again when we make a study of its dynamics. Many investigators have made assumptions about the motions of the membranes and ossicles, but they do not always agree. A summary of some opinions can be found in Kostelijk's review of theories of hearing [2]). The membranes and the ossicles do not so much move to and fro as rotate, about axes which are dependent on the intensity. So we can expect some lever action, which has indeed been found. Stuhlman found that the displacement of the eardrum is 1·3 times larger than that of the stapes. Another important question now arises. Do the ossicles form a stiff chain or not? Dahmann says that the whole chain is stiff for low amplitudes only, but at higher intensities the ossicles move with respect to each other. Von Békésy, however, believes that the malleo-incudial joint is stiff, but that the incudo-stapedial joint is soft. Stuhlman was the first to suggest that the malleo-incudial joint is soft at high intensities, and that the coupling ligament is nonlinear so that distorsion may arise here. Fumagalli has the same opinion, but he says, that the softness of the malleo-incudial joint exists only in man, but not in most animals, such as the rat or the guinea pig. The incudo-stapedial joint is never stiff, however.

Metz showed, that fixation of the stapes does not influence the input impedance of the system much, which is a proof of the soft connection between incus and stapes. This impedance is usually much higher at low frequencies in ears which suffer from otosclerosis, than in normal ears, which indicates that this sclerosis does not always restrict itself to the oval window only, but that other places are also attacked. Kobrak also believes that the nonlinear distorsion, which can be measured at intensities as low as 50 or 60 dB, is caused by the connecting ligament of the malleus and incus. This is denied however by Tonndorf who assumes that this distorsion is caused by nonlinearities in the fluid flow in the cochlea. The coupling between the eardrum and the hammer, and between the stirrup and the oval window, is very solid. Up to 2400 c/s the tympanic membrane vibrates in phase over its whole area, but above this frequency the cone vibrates in modes of higher order, as Von Békésy observed. The whole mechanical system has some resonances and anti-resonances, but we do not know exactly how many, and at which frequencies. Von Békésy observed a resonance between 700 and 1200 c/s, and Troeger found more than one in the 800-3000 c/s frequency band. Measurements of the impedance at the eardrum do not reveal the secret, for most of

these measurements have been done up to 2000 c/s and the results of different investigators differ considerably. Only during recent years has some agreement existed between different authors, e.g. Morton and Jones [3]), Zwislocki [4]) and Møller [5]). Figure 33 shows us the comparison between different results. Von Békésy [6]) gives us the mechanical "overall characteristic" of the system, i.e. the amplitude of the round window as function of the frequency with a constant pressure upon the eardrum, but not beyond 4000 c/s. In the same paper we can find measurements of the impedance of different parts of the inner ear, which results will be important for our calculations of the mechanical behaviour of the middle ear, as we shall see later. An interesting plate, comparing all these impedances, has been published by H. E. von Gierke in The Laryngoscope *68*, 347, 1958 (see fig. 34). Further mechanical data give us the area of the tympanic membrane, which is 0·5 to 0·6 cm^2, and the area of the oval window which is about 3 mm^2. So the area ratio is 17, according to Von Békésy, which means that the impedance ratio is $(1{\cdot}3 \times 17)^2 = 484$. Wever and Lawrence [7]), how-

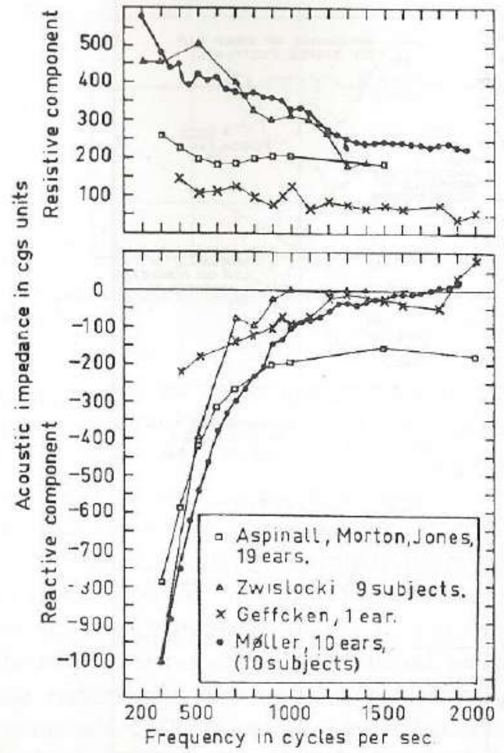


Fig. 33. The impedance at the eardrum obtained by four authors.
From A. Møller, J. acoust. Soc. Amer. 32, 250, 1960.

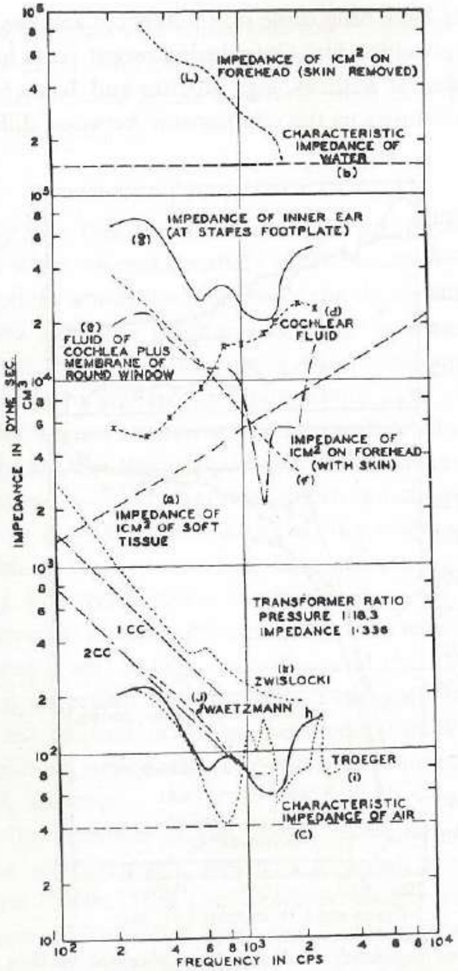


Fig. 34. Impedance values measured at various locations in the ear and on the body surface.
a-g see picture
h-k ear impedances measured at the tympanic membrane
h is the curve *g*, transformed by the middle ear.
From Von Gierke, The Laryngoscope **68**, 347, 1958.

ever, take the effective area of the eardrum smaller than its total area, resulting in an impedance ratio of 336. The masses of the ossicles are known, of course, but their moments of inertia, which are the important features for the dynamics, are unknown, except for a figure given by Frank and Broemser, who say that it is 25.10^{-4} g/cm^2 for the hammer-anvil combination.

As has been shown up to here, we have not much data on which to construct our model of the inner ear. We know some dimensions and impedances and an "overall-characteristic". Let us see what we can do with this.

III.3. The electrical model of the middle ear

With the data given by the anatomy and the physiology of the middle ear, together with conclusions drawn from measurements on the middle ear-cochlea combination, we came to the analogue circuit of fig. 35, which is similar to that of Zwislocki [4]).

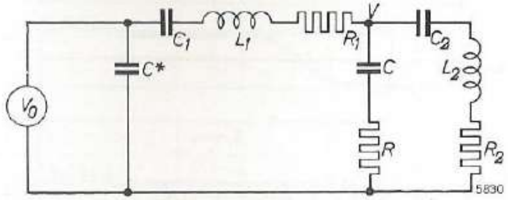


Fig. 35. The electrical analogue of the middle ear-cochlea combination seen from the tympanic membrane (see text).

We may assume, that the malleo-incudial joint is stiff, at least for low and medium intensities, so that malleus and incus form one unit, represented by L_1 and R_1. The stiffness of the tympanic membrane together with the middle-ear cavity has been divided into $1/C_1$, the part which is coupled with the hammer, and $1/C^*$, the part which is out of phase at the higher frequencies. The stiffness of the ligaments and the muscles connected to the hammer and anvil has been taken up in C_1, and the mass of the eardrum in L_1. Stapes, oval window, cochlea and round window are represented by C_2, L_2 and R_2, the compliance of the windows, the mass of stapes and inner-ear liquid, and the frictional damping in the scalae respectively. The transformer action has been neglected for simplicity, so the values of C_2, L_2 and R_2 have to be multiplied by the impedance ratio to get the real values. C and R depict the damped stiffness coupling between the anvil and the stirrup. Zwislocki [4]) was the first to suggest this analogue circuit. As will be shown, it is not so difficult to determine C_2, L_2 and R_2, but we can only make rough estimates of the other quantities, since the only data available are measurements of the input impedance of the system, and measurements of the "overall-characteristic", the volume displacement of the round window as function of the frequency, with a constant pressure on the eardrum.

Neglecting friction, we find for the input impedance

$$\mathrm{Imp} = \frac{1}{j\omega\left\{C^* + \dfrac{C_2+C-\omega^2 L_2C_2C}{1+\dfrac{C_2+C}{C_1}-\omega^2\left(L_2C_2+L_1C_2+L_1C+\dfrac{L_2C_2C}{C_1}\right)+\omega^4L_1L_2C_2C}\right\}}.$$

For low frequencies this becomes

$$\mathrm{Imp} = \frac{1}{j\omega\left\{C^* + \dfrac{C_1(C_2 + C)}{C_1 + C_2 + C}\right\}}\,.$$

The volume displacement of the oval window is represented by

$$x = \frac{i}{j\omega} = \frac{V}{j\omega\left(j\omega L_2 + \dfrac{1}{j\omega C_2}\right)} =$$

$$= \frac{C_2}{1 + \dfrac{C_2 + C}{C_1} - \omega^2\left(L_2C_2 + L_1C_2 + L_1C + \dfrac{L_2C_2C}{C_1}\right) + \omega^4 L_1L_2C_2C}\,V_0\,,$$

which gives for low frequencies

$$x = \frac{C_1C_2}{C_1 + C_2 + C}\,V_0\,.$$

We assume that the modulus of the volume displacement of the stapes is the same as the modulus of the volume displacement of the round window, which is justified by the fact that the inner ear is a closed system, filled with an incompressible liquid.

We will assume that:

the area of the eardrum is 0·5 cm^2,
the area of the oval window is 3 mm^2,
the area of the round window is 2 to 3 mm^2,
the area ratio is 18,
the velocity ratio is 1·3,
the impedance ratio is 484.

The effective mass, represented by L_2', the transformed L_2, is determined mainly by the moving liquid in the scalae. This mass is not entirely constant, as we have seen in the foregoing chapter, but for simplicity we will start by neglecting its variation.

The cross-section of the scalae is 1·2 mm^2, their length 35 mm and the density of the perilymphe 1 g/cc, so

$$L_2' = 2 \times 35 \times 1{\cdot}2.10^{-3} \times 1 = 85.10^{-3}\ \mathrm{g} = 85\ \mathrm{mg}\,,$$

or

$$\frac{85.10^{-3}}{3.10^{-2}}\,\frac{\mathrm{g}}{\mathrm{cm}^2}\,,\ \text{which is}\ \frac{85.10^{-3}}{9.10^{-4}} = 94\,\frac{\mathrm{g}}{\mathrm{cm}^4}\,.$$

Von Békésy 8) measured the impedances of different elements of the cochlea

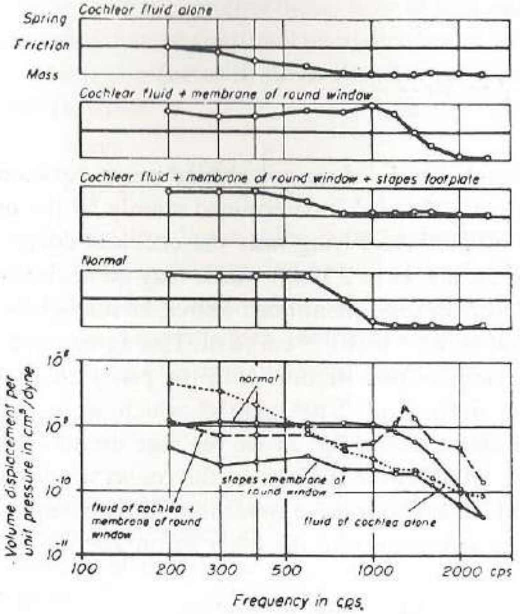


Fig. 36. Amplitude of vibration at the round window measured for a single ear as its parts were removed, one by one. The lower curves show the amplitude transmission for the normal ear, for the ear with drum removed, for the cochlea with round window alone, and for the fluid and the cochlear partition alone. The four upper curves show the corresponding phase angles between the pressure and the volume displacement near the round window. After G. von Békésy.

(see fig. 36) and found for the liquid motion alone that its volume displacement was

$$3{\cdot}1.10^{-10}\,\frac{\mathrm{cm}^5}{\mathrm{dyn}}\ \text{at}\ 1000\ \mathrm{c/s}\,,$$

which means that

$$\omega^2 L_2' = 3{\cdot}2.10^9\,\frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}^2}\ \text{at}\ 1000\ \mathrm{c/s}\,,$$

so

$$L_2' = \frac{3{\cdot}2.10^9}{4\pi^2 \times 10^6} = 80\,\frac{\mathrm{g}}{\mathrm{cm}^4}\,,$$

which is in good agreement with our results. From fig. 34 we read

$$\omega L_2' = 16.10^3\,\frac{\mathrm{g}}{\mathrm{cm}^2\mathrm{s}}\ \text{at}\ 1000\ \mathrm{c/s}\,,$$

giving

$$L_2' = \frac{16.10^3}{2\pi \times 10^3} = 2{\cdot}5\,\frac{\mathrm{g}}{\mathrm{cm}^2} = 83\,\frac{\mathrm{g}}{\mathrm{cm}^4}\,,$$

so that we may take

$$L_2' = 90 \frac{\mathrm{g}}{\mathrm{cm}^4}.$$

Von Békésy also found that L_2' does not change much between 100 c/s and 2500 c/s, so we see again that L_2' is determined mainly by the outer layers of the scalae and less by the layers lying near the cochlear duct.

The total mass of the stapes is 2·5 mg, which may be neglected here.

In the article by Von Békésy, mentioned above, he also gives the elasticity of the round window as 10^{-9} to 10^{-10} cm^5/dyn. This agrees with the fact that he measured a resonance of this window with the perilymphe at a frequency of 1400 c/s, giving a stiffness of 7.10^9 g/cm^{4}s^2 which is in agreement with the elasticity found above. From fig. 34 we see that the total stiffness of the inner-ear impedance, which is the stiffness of the round window plus the stiffness of the oval window, is about three times that of the round window alone, so that we can expect a resonance of the inner ear at about

$$\sqrt{3} \times 1400 \approx 2500 \text{ c/s}.$$

This resonance has also been measured by Von Békésy [6]), especially by means of phase measurements (fig. 36). Thus we may take

$$S_2' = 3 \times 7.10^9 = 2{\cdot}1.10^{10} \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}^2}.$$

The motion of the elements of the inner ear will be damped and again from the same phase-measurements of Von Békésy we find

$$\omega R_2' = S_2' \text{ for 800 c/s, giving}$$

$$R_2' = \frac{2{\cdot}1.10^{10}}{2\pi \times 800} = 4{\cdot}2.10^6 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}}.$$

Moreover the system stirrup-perilymphe-oval window seems to be critically damped, giving

$$R_2' \approx 1{\cdot}5 \sqrt{90 \times 2{\cdot}1.10^{10}} = 2{\cdot}1.10^6 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}^2}.$$

We have thus come to about the same result for the damping in two different ways.

From investigations of the unidirectional flow of liquid through the cochlea Von Békésy concluded that the frictional resistance to the flow of the perilymphe is 2.10^5 g/cm^{4}s which is a factor 10 lower than our R_2' found above. Zwislocki used $R_2' = 9000\ \Omega$, which is

$$\frac{9000}{3.10^{-2}} = 3.10^5 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}}.$$

We shall see later, that this latter value is better because the damping found above is too high to obtain the required overall-characteristic. Maybe, this d.c. measurement could be done more accurate than the others.

That does not take away the fact that this measured resistance does not agree with the calculated one. For frictional losses should give a resistance

$$\frac{8\pi l \eta}{S^2},$$

where l is the length of the canal,
S the (circular) cross-section,
η the viscosity of the liquid.

Here this would be

$$\frac{8\pi \times 2 \times 3{\cdot}5 \times 0{\cdot}02}{1{\cdot}4.10^{-4}} = 2{\cdot}4.10^4 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}}.$$

In the foregoing chapter we have seen that friction in the helicotrema gives

$$1{\cdot}1.10^4 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}},$$

so that now there is a factor 10 between the measured and calculated values. Is there any reason to assume that there is such a lot of friction in the vestibule or the semi-circular canals? It may be possible that Von Békésy measured at such high flow rates that the high value of the frictional resistance found by him is due to eddies. Seen from the eardrum the impedance of the inner ear has to be divided by the transformer factor so that we get

$$L_2 = \frac{90}{484} = 1{\cdot}8.10^{-1} \frac{\mathrm{g}}{\mathrm{cm}^4},$$

$$C_2 = \frac{484}{2{\cdot}1.10^{10}} = 2{\cdot}3.10^{-8} \frac{\mathrm{cm}^4\mathrm{s}^2}{\mathrm{g}},$$

$$R_2 = \frac{2.10^5}{484} = 4.10^2 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}},$$

but

$$R_2 = 600 \frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}}$$

gave a better overall-characteristic. The data from direct measurements on the inner ear are now exhausted. We can estimate values for the remaining elements of the circuit from other measurements. Figure 37 shows us the impedance of the total system as measured by Zwislocki [4]). He and Møller [5]), measure a value of 2800 g/cm^{4}s at 100 c/s giving

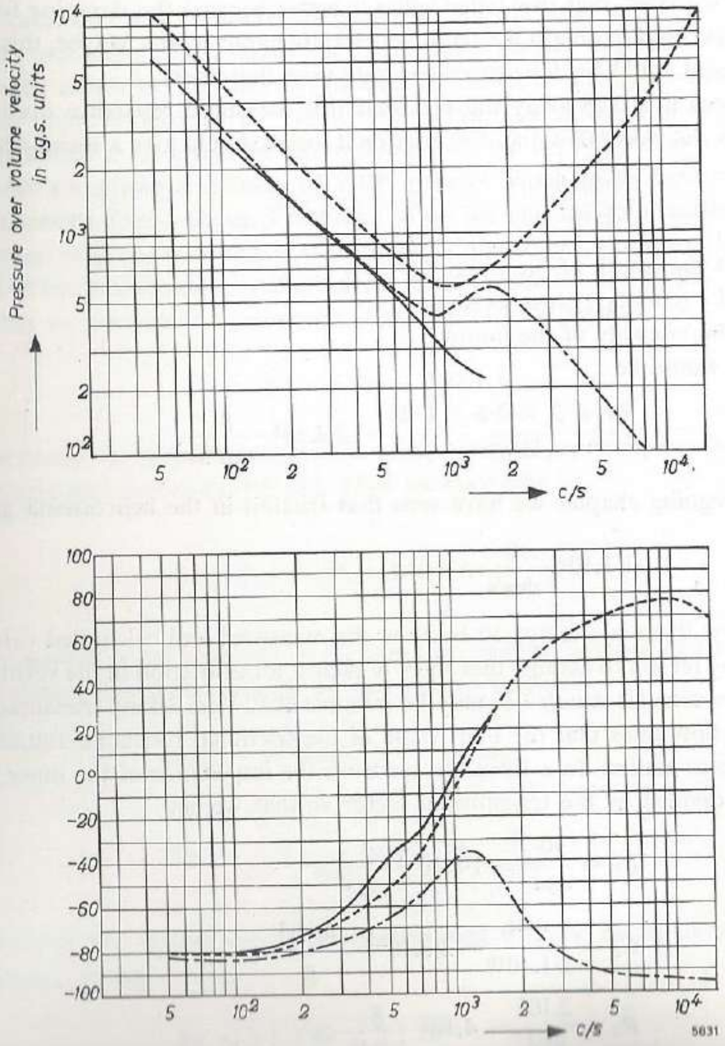


Fig. 37. The impedance at the eardrum in amplitude and phase.
——— measured by Zwislocki
— · — · — measured on our model
— — — — measured on our model without C^*.

$$\frac{1}{C^* + \dfrac{C_1(C_2 + C)}{C_1 + C_2 + C}} = 2\pi \times 100 \times 2800 = 1{\cdot}8.10^6 \, \frac{g}{cm^4s^2}\,.$$

Von Békésy [6]) gives the volume displacement ΔV of the round window at a pressure P at the eardrum of 1 dyn/cm^2 (see fig. 38):

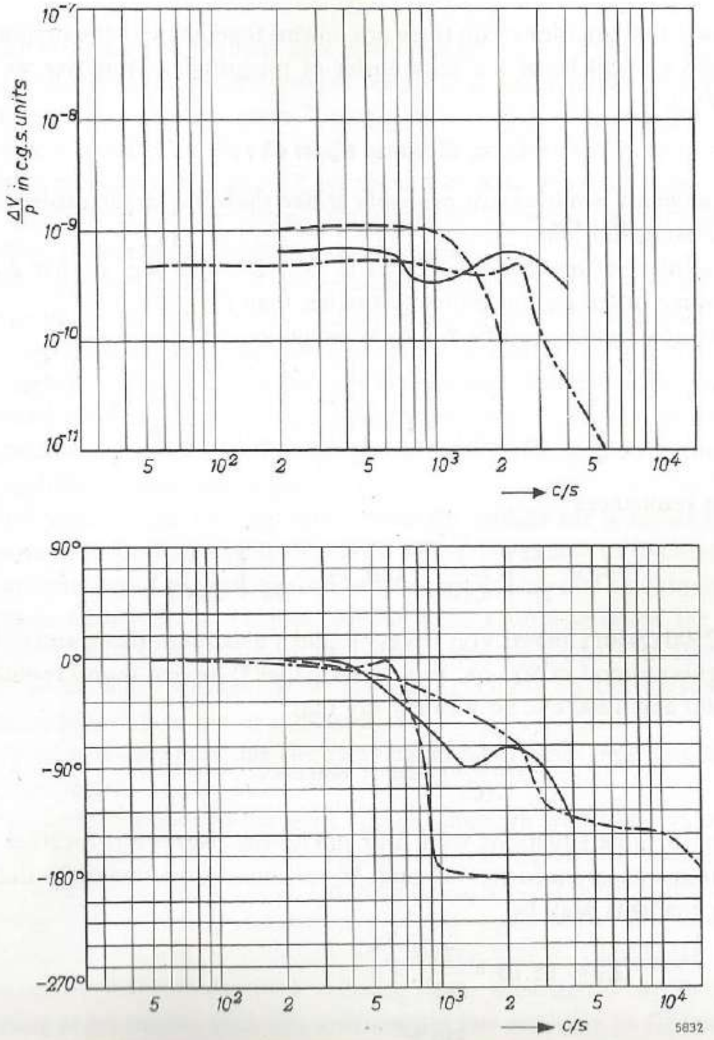


Fig. 38. The volume displacement of the stapes ΔV in amplitude and phase, caused by a pressure P on the eardrum.
——— } measured by Von Békésy
— — — }
— · — · — measured on our model.

$$\frac{\varDelta V}{P} = 5{\cdot}5.10^{-10}\,\frac{\mathrm{cm}^5}{\mathrm{dyn}}$$

at low frequencies.

After transformation we get

$$\frac{C_1 + C_2 + C}{C_1 C_2} = \frac{10^{10}}{5{\cdot}5} \times \frac{1}{22} = 8{\cdot}3.10^7\,\frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}^2}\,.$$

Here we have two equations with three unknowns, together with the supposition that C^* and C_1 will be of the same order of magnitude. Moreover we may expect that

$$C_2 \ll C \quad \text{and} \quad C_2 \ll C_1,$$

because the small windows are probably stiffer than the larger eardrum and the incudo-stapedial joint.

The total mass of malleus plus incus is $33 + 27 = 60$ mg, so that L_1 will be of the same order as, and probably smaller than L_2.

All these assumptions justify the approximation

$$x \approx \frac{C_2}{\dfrac{C}{C_1} - \omega^2\left(L_1 C + \dfrac{L_2 C_2 C}{C_1}\right) + \omega^4 L_1 L_2 C_2 C}\,V_0\,,$$

giving two resonances

$$\nu_1 = \frac{1}{2\pi}\sqrt{\frac{1}{L_1 C_1}} \quad \text{and} \quad \nu_2 = \frac{1}{2\pi}\sqrt{\frac{1}{L_2 C_2}}\,.$$

ν_2 will be 2500 c/s and indeed Von Békésy found a maximum there, and another in the neighbourhood of 800 c/s. In another paper [8]) he had found resonances between 800 and 1200 c/s. So we may say that

$$\frac{1}{L_1 C_1} = 2\pi \times 800\ \mathrm{c/s}\,.$$

Now we have three equations with four unknowns. Herewith, together with the measurements given in figs 37 and 38 we found experimentally that the remaining elements may be

$$L_1 = 65.10^{-3}\,\frac{\mathrm{g}}{\mathrm{cm}^4}\,,$$

$$C_1 = 6.10^{-7}\,\frac{\mathrm{cm}^4\mathrm{s}^2}{\mathrm{g}}\,,$$

$$R_1 = 500\,\frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}}\,,$$

$$C = 6{\cdot}8.10^{-7}\,\frac{\mathrm{cm}^4\mathrm{s}^2}{\mathrm{g}}\,,$$

$$R = 100\,\frac{\mathrm{g}}{\mathrm{cm}^4\,\mathrm{s}}\,,$$

$$C^* = 2.10^{-7}\,\frac{\mathrm{cm}^4\mathrm{s}^2}{\mathrm{g}}\,.$$

The total mass of malleus plus incus was $60/0{\cdot}5^2 = 240$ mg/cm^4, so that it may be possible that its moment of inertia is something like L_1 or perhaps still smaller. Wever and Lawrence [7]) give a value of 5.10^{-3} g/cm^4, but that seems to be very small. A smaller L_1 would give a larger C_1 in our circuit, and together with other values of C and C^* we should be able to satisfy again the data of the impedance and the overall characteristic as far as they are known now, so there is no reason to change our elements.

The impedance curve of the conducting part of the system has also been drawn in fig. 37. That means the input impedance of our circuit, if $C^* = 0$, which gives the result that this impedance is a mass instead of a stiffness in the higher frequency range, but we may assume that the breaking up of the eardrum-cone is a fact, so that we measure mainly the stiffness of the air in the middle-ear cavity together with the stiffness of the free part of the membrane in the higher frequency range.

The result of our investigations about the middle ear is rather meagre, but there are too few data available on this subject, to enable us to come to a closer approximation of the mechanism of this part of the ear. Looking at the combination middle ear — cochlea, we can raise a surmise about the correctness of our electrical model, whose properties agree very well with those found by Von Békésy and Zwislocki as is shown in fig. 37 and 38, but we shall deal with this combination in the next chapter.

Let us now compare our electrical model with other ones published during the last years.

Zwislocki [4]) comes to the same circuit, although with other values for some of the elements, which were concluded from impedance measurements on normal and pathological ears. He neglects L_2, and C_2 has a value of 2600.10^{-9} cm^{4}s^2/g, the remaining elements are of the same order as ours. From the fact that he measures a difference of a factor two in impedance for 100 c/s between normal ears and ears suffering from otosclerosis we may conclude, looking at his model, that this difference is due not only to C_2 becoming very small, corresponding to a fixation of the stapes, but also to a decrease in the other capacities, probably especially C, which means that in most cases the sclerosis does not limit itself to the oval window.

Völz [9]) gives an equivalent circuit with four parts, coupled by stiffness (fig. 39): *a*) the eardrum plus the hammer, *b*) the anvil, and *c*) the stapes together with *d*) the perilymphe. The pressure P_2 reaching the round window via the middle-ear cavity has been taken into account; the capacity parallel to the resistance of the perilymphe, which may depict the stiffness of stapes and inner-ear system, could better be connected in series with it. And where is the stiffness of the eardrum? In any case we see that the hammer-anvil connection is not stiff, both ossicles can move relative to each other, which gives rise to another resonance of the system.

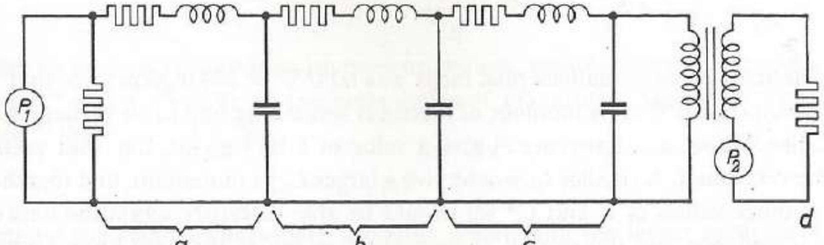


Fig. 39. The middle-ear model of Völz.

Nabelek [10]), who measured the impedance on the eardrum up to 7500 c/s, found two resonances and two anti-resonances. He says that above 2000 c/s the reactance and the resistance are nearly constant.

Wever and Lawrence [7]) worked with cats and found still more resonances and anti-resonances. They think that the impedance of the middle ear can be neglected as compared to the impedance of the inner ear, which we do not believe. Their analogue circuit is given in fig. 40, *a*) being the first part of the middle ear up to the stapes, *b*) being the stapes and all what is behind it. The impedance of this circuit will indeed give at least two resonances and anti-resonances.

Møller [11]) measured the impedance at the eardrum up to 2000 c/s; the eardrum was sometimes covered with a small layer of collodion, thus increasing its stiffness and damping, to see what effect this had on the impedance curve. He also studied the variation in impedance of the ear when the ear muscles are contracted. He constructed an equivalent network on the basis of these results (fig. 41). He considers the eardrum to be divided into two parts, one connected to the hammer, represented by L_1, C_1 and R_1, and an independent part represented by L_0, C_0 and R_0. The hammer is, according to Møller, rigidly coupled to the anvil, but the connection between the anvil and the stirrup is less stiff. He considers that the first two ossicles not only rotate, but also move to and fro, the latter motion being limited by the stiffness of the tensor tympani and the ligament. The moment of inertia is represented in the network by L_2, the mass by L_3, the stiffness and damping of the muscle and the ligament by C_3 and R_3. The stapes plus the inner ear are represented by C_4, L_4 and R_4, where C_4 is decreased by the contraction of the stapedius. C_5 represents the incudo-stapedial joint, but is mostly neglected by Møller. L_0 and C_0 resonate at 1800 c/s, L_1 and C_1 with L_3 and C_3 near 1200 c/s, and L_4 and C_4 near 800 c/s. For our model we assumed a frequency of 2500 c/s for the latter resonance.

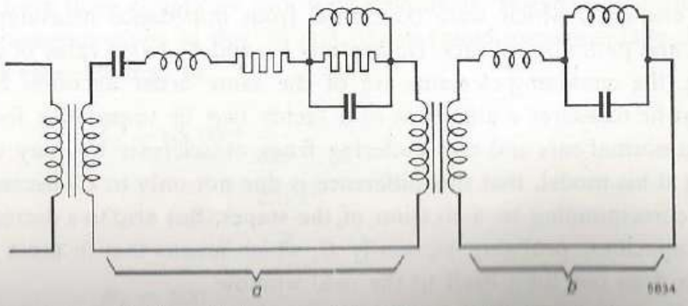


Fig. 40. The middle-ear model of Wever and Lawrence.

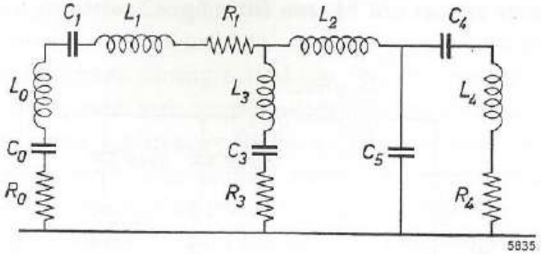


Fig. 41. The middle-ear model of Møller.

We may say, however, that the circuit given by Zwislocki and by us will give the best picture of the situation; perhaps other elements, such as the mass, friction and stiffness of the muscles and ligaments, should be added, giving rise to more resonances and anti-resonances. To build them in now would be too speculative, however. In any case we may say that for the low frequencies, the impedance at the eardrum will be a stiffness, and for the high frequencies the impedance of the sound-conducting part a mass. Between that the impedance will be more or less constant over some frequency range, depending on the number of resonances and anti-resonances and the damping of the system. In the same way we may assume that the "overall characteristic" will be fairly constant up to a certain frequency, whereafter it will fall by at least 12 to 24 dB/oct depending on the stiffness of the coupling by the incudo-stapedial joint. This tilt-point may be 2500 c/s or higher.

It is clear that the construction of the inner ear must give an impedance equivalent to that of an L_9-R_9-C_9 circuit. A satisfactory match between this impedance and the characteristic impedance of the air, which is a resistance, can only exist at and near the resonance-frequency of L_2 and C_2. If the middle-ear system acts as a good transformer we may expect some match between the air and the inner ear in the middle frequency range, since we have seen that the inner ear gives a resonance here. Let the part of the tympanic membrane vibrating in phase with the malleus be half the total area, then we find from fig. 37 that the impedance at the eardrum is about 150 g/cm²s, which is about four times the characteristic impedance of air. The matching is rather good here, although a part of the energy will still be reflected. However, even if the resonance of the eardrum — hammer — anvil system occured at a higher frequency, so that the dip in the impedance characteristic was deeper and a good matching occured between the air and the system, the total energy could not reach the inner ear, as can be seen from fig. 42, which is a rough approximation of the sound-conducting part of our original circuit near this dip, with the conversion from the mechanical system to the electrical model made on the following basis:

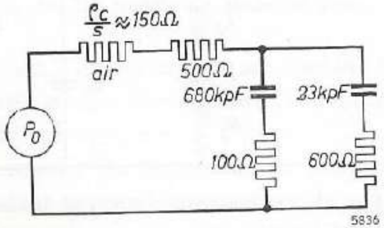


Fig. 42. Electrical analogue of the sound path through the air and through the sound conducting part of our ear, at frequencies near the dip in the impedance characteristic.

$$1\,\frac{\mathrm{g}}{\mathrm{cm}^4} = 1\ \mathrm{H}\,,$$

$$1\,\frac{\mathrm{g}}{\mathrm{cm}^4\mathrm{s}} = 1\ \Omega\,,$$

$$1\,\frac{\mathrm{cm}^4\mathrm{s}^2}{\mathrm{g}} = 1\ \mathrm{F}\,.$$

Here we see that, because of the short-circuiting by the incudo-stapedial joint, only a very small amount of energy is dissipated in the inner ear, so small that it forms another point of doubt for the rightness of our total circuit. Since we had more unknowns than equations while searching for the values of the network elements, it is possible that a better solution for these values can be found. This does not have much effect on the following of our theory, however. The energy reflected against the eardrum may cause resonance in the auditory

meatus. In our measurements and calculations we often start with the pressure on the eardrum. The difference between this pressure and the free field pressure has been measured already by Wiener and Ross [12]).

III.4. The artificial ear

The problem dealt with in this book is the construction of and experimenting with an electrical model of the human hearing organ, i.e. the working with an artificial ear. This term is never used for such a model, however, since it is already generally accepted to describe the well known acoustical couplers used in the measuring techniques of telephones. These artificial ears are simple coupling elements, having a twofold purpose. In the first place they have to form a load to the telephones which resembles as well as possible the situation in practice with the telephone on the ear. In the second place, if possible, a microphone situated in these artificial ears has to measure the same pressure as exists on the eardrum during actual use. We can distinguish two types of artificial ears, those used with large headphones, and those used with the small insert-type earphones, such as are found with hearing aids. An example of the first type is known as the 6-cc coupler, being a cylinder with a volume of 6 cc and a diameter of about 2 cm with a condenser microphone at its bottom. Below the resonance-frequencies of this coupler, which lie in the neighbourhood of or higher than 4000 c/s, this coupler can be represented by a capacity of 4300 kpF, which is due to the compliance of the air volume. The compliance of the condenser microphone is much smaller and can be neglected. Assuming that when it is placed on the real ear, the telephone has a cavity before it of about the same volume (including the compliance at the eardrum), the only differences remaining between the real and artificial ear are the difference in the softness of the walls and the difference in the shape of the cavities. That means that in the low-frequency range there may be a small difference between the two ears, and in the high-frequency range this difference becomes larger where the ear impedance seen at the eardrum is determined mainly by the compliance represented by C^* in our circuit. One of the most important demands made on an artificial ear is its reproduceability, so this simple 6-cc coupler will satisfy for frequencies up to 4000 c/s and its difference with the real ear will remain small, perhaps smaller than the difference between different specimen of that ear. The problem of the construction of a coupler for a larger bandwidth is still in study.

This can also be said of the 2-cc coupler, the artificial ear for the small earphones. These earphones are connected to earmoulds which can be inserted in the ear. The earphones have a small nozzle which fits in a hole of the earmould and is held in place by a small spring. The sound passes through a small hole in the earmould and then flows out into that part of the auditory meatus between an offshoot of the earmould, which serves to fit it in the ear, and the eardrum.

The acoustical pathway between the membranes of telephone and ear is thus firstly a little cavity before the telephone membrane, formed by the room between membrane and casing, to which sometimes a little cavity at the entrance of the earmould has to be added, secondly the tube through the earmould and thirdly the space between its offshoot and the eardrum. The artificial ear here consists of a tube of length 18 mm and diameter 3 mm, ending in a cylindrical cavity of volume 2 cc with a diameter of about 2 cm on whose bottom a condenser microphone is again situated. Thus the artificial ear represents here our hearing organ complete with the earmould. The tube corresponds to the hole in the earmould, the cavity represents the cavity between its offshoot and the eardrum plus the impedance at the eardrum. For frequencies lying below the resonance frequencies of the canal or vacity we can represent the artificial ear by an inductance L_0 and a capacitance C_0 as shown in fig. 43. For the real ear C_0 has to be replaced by C_e in parallel with Z_0, the impedance at the eardrum. For the 2-cc coupler,

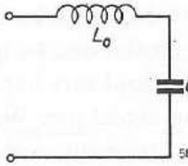


Fig. 43. Electrical analogue of the 2-cc coupler.

$$L_0 = 34.10^{-3}\,\frac{\text{g}}{\text{cm}^4},$$

$$C_0 = 1430.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}}.$$

For low frequencies we have seen (p. 71) that the impedance at the eardrum is a stiffness of

$$\frac{10^9}{550}\,\frac{\text{g}}{\text{cm}^4\text{s}^2},$$

corresponding to the stiffness of an air volume of 0·77 cc. If the total stiffness can be replaced by a volume of 2 cc, the space between earmould and eardrum would be 1·23 cc which seems rather large. The length of the part of the earmould that sticks in the auditory meatus is 10 to 15 mm. The length of the auditory meatus itself varies between 12·5 and 25 mm. Morton and Jones 3) take the length of the part of the meatus between earmould and eardrum as 15 mm, but a value of 10 mm or less seems better. Taking the cross-section of the eardrum as 0·5 cm², we find a free volume of 1 × 0·5 = 0·5 cc instead of 1·23 cc.

The total impedance behind the earmould can thus be depicted by an air volume of about 1·3 cc instead of 2 cc, the length of the hole in the earmoulds varies strongly, but in the modern types, which are as small as possible and where the telephone is situated as deep in the ear as possible, the average length is 15 mm rather than 18 mm. The average diameter is indeed about 3 mm.

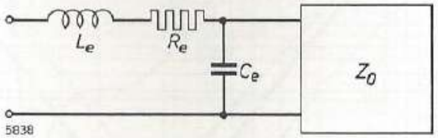


Fig. 44. Electrical analogue of the earmould in the ear.

For the real situation in the ear we get the equivalent circuit of fig. 44, with

$$L_e = 28.10^{-3}\,\frac{\text{g}}{\text{cm}^4},$$

$$R_e = 1{\cdot}4\,\frac{\text{g}}{\text{cm}^4\text{s}},$$

if we assume a viscous damping in the tube of the earmould, and

$$C_e = 340.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}}.$$

R_e can be neglected with respect to ωL_e.

The electrical models shown in figs 43 and 44 now can be used to estimate the difference in the impedance seen by the earphone connected to the 2-cc coupler or connected to the real ear. For Z_0 we took our electrical model of the middle ear, which represents more or less a stiffness in the low frequency range, and a mass and larger stiffness in the high frequency range, as we have seen in fig. 37. For low frequencies we have seen that the compliance of Z_0, which was 550.10^{-9} cm⁴s²/g, agrees very well with the impedance measurements mentioned earlier, so that our analogy is sufficient there. For the high frequencies there remains only a compliance $C^* = 200.10^{-9}$ cm⁴s²/g, which is short-circuiting the mass-like impedance parallel to it. As there still exists some doubt about this frequency range, it is not impossible that we make a fault here with our analogue of fig. 44, but the effect of this fault is decreased by, to a certain extent, C_e. As regards the impedance before the earphone this fault makes its appearance at frequencies where only L_e has an appreciable effect so that it does not make any difference if Z_0 is good or not. Figure 45 shows us the impedance measured at the entrance of the earmould tube for the model of the real ear, with and without C^*, and for the 2 cc-coupler. If we take

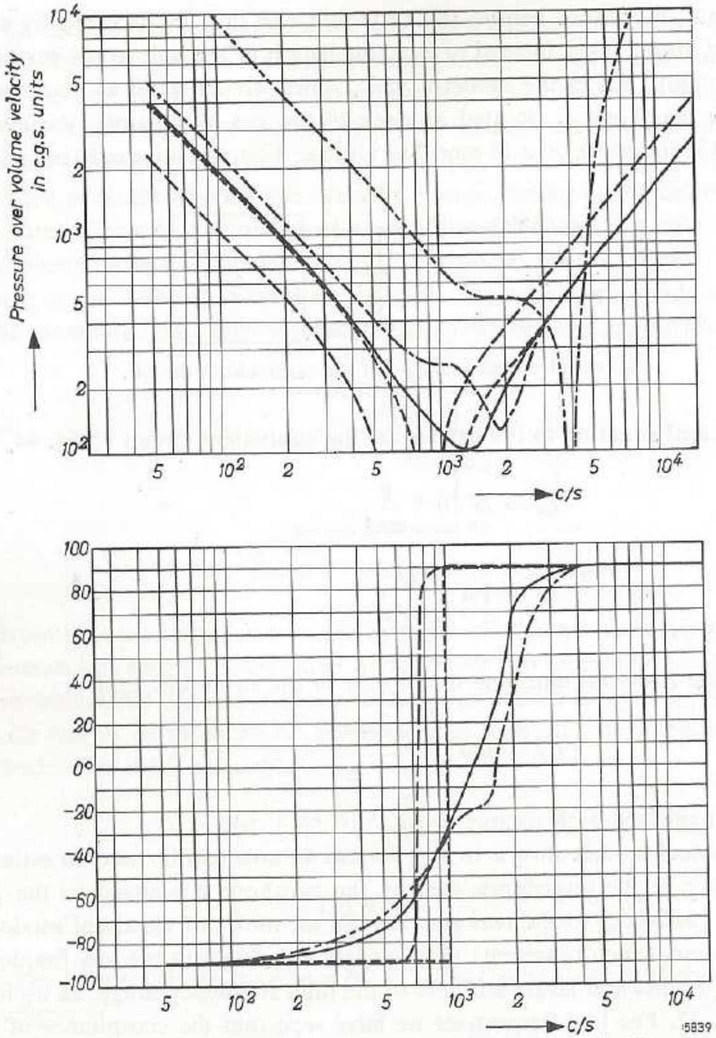


Fig. 45. The impedance at the entrance of the earmould tube.
——— measured on our electrical analogue of the ear + earmould
— · — · — measured on our electrical analogue without C^*
– – – – measured on our electrical analogue of the 2-cc coupler
- - - - - - - measured on our electrical analogue of the new coupler
— - - — - - $|Z|$ from fig. 47.

$$L_0 = 28.10^{-3}\,\frac{\text{g}}{\text{cm}^4} \text{ and } C_0 = 900.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}},$$

we have the model of an artificial ear which forms about the same load to the earphone as the real ear plus earmould.

The total circuit representing the combination earphone — earmould — ear is shown in fig. 46. L_m, R_m and C_m depict the mass, resistance and compliance of the earphone membrane, the last one decreased by the air volume between the rear of the membrane and the case. C' is the compliance of the air volume between the front of the membrane and the case, if necessary increased by the air volume in a cavity at the entrance of the earmould.

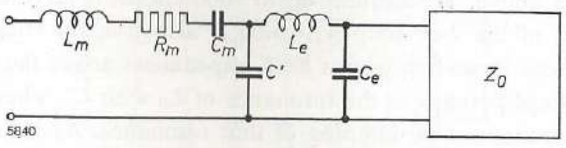


Fig. 46. The electrical analogue of the earphone - earmould - ear combination.

Reasonable values for an electro-magnetic earphone, which is mostly used with hearing aids, are

$$L_m = 65.10^{-3}\,\frac{\text{g}}{\text{cm}^4},$$

$$C_m = 170.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}},$$

$$R_m = 600\,\frac{\text{g}}{\text{cm}^4\text{s}},$$

$$C' = 60.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}},$$

which can be found by weighing the membrane to determine L_m, calculating C_m and R_m from the first resonance peak of the frequency characteristic (see below) and measuring the volume of air in front of the membrane, which gives C'. These values are of the same order of magnitude as those of the rest of the network of fig. 46, so we may expect that the results of measurements with this combination are dependent on the telephone used. This can best be seen if we transform the network of fig. 46 into that of fig. 47. Let us calculate

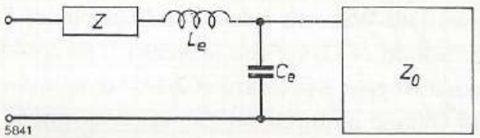


Fig. 47. Transformation of the network of fig. 46.

Z for the case of the model of the 2-cc coupler instead of that of the real ear.

$$|Z| = (1 - \omega^2 L_0 C')\sqrt{R_m{}^2 + \frac{1}{\omega^2 C_m{}^2}(1 - \omega^2 L_m C_m)^2},$$

if we neglect the slight damping in the tube of the artificial ear.

This is to be compared with

$$\frac{1}{\omega C_0}\,(1 - \omega^2 L_0 C_0)\,.$$

This function has also been drawn in fig. 45 for the values of the earphone-elements taken above. We see that up to 2000 c/s $|Z|$ is large compared with the impedance of the 2-cc coupler, which is also true for frequencies above 5000 c/s. Between those frequencies both impedances are of the same order of magnitude, except perhaps at the resonance of L_0 with C', when the situation depends on the amount of damping of that resonance. As we shall see later, this resonance causes the second peak in the frequency characteristics of earphones. Therefore, measurements made with the purpose of determining the difference between the real ear and the 2-cc coupler may give results which are dependent on the earphone used for it, and on the ears which were tested. People with otosclerosis have a higher stiffness in the low tones than people with normal ears. For example, we measured the pure-tone threshold of a number of people with normal hearing, with an electromagnetic earphone connected to the audiometer instead of its normal headphones. The calibration of the audiometer was corrected for this combination by recalibrating the scale when the earphone was placed upon the 2-cc coupler. The threshold level at a certain frequency was reached when the artificial ear gave the threshold pressure according to Sivian and White's data. As the audiograms of these people, measured with normal headphones, were known, the difference between their normal audiograms and those measured with the earphone and the recalibrated audiometer gave us the difference between ear and 2-cc coupler for that earphone. The result is shown as a dot-and-dash line in fig. 48. The same was done with a number of deaf people with different types of impairment. The average result is shown as a full line in fig. 48. The shadowed area indicates the spread in the latter measurement, which is due to the difference between the impedances of the patients' ears and to inaccuracies in the measuring method. Jonkhoff 13) measured the voltage across another earphone required to give the threshold impression. With the known audiograms of his test persons and with the normal threshold of Davis and Stevens (?) he could convert his results to the voltage needed to give a pressure of 2.10^{-4} dyn/cm^2 in a normal ear. He then measured the voltage required for the same earphone to give a pressure of 2.10^{-4} dyn/cm^2 in a 2-cc coupler. The difference between the two voltages gives the difference between the ear and the 2-cc coupler. He found a spread of ± 10 dB, depending on whether the earmoulds were polished (leakage?). His results are drawn as a dashed line in fig. 48. Measurements of this sort were right if they were done with an earphone with very small internal impedance or with a very high internal impedance, compared with the impedance at the entrance of earmould or artificial ear. And that on subjects with normal hearing

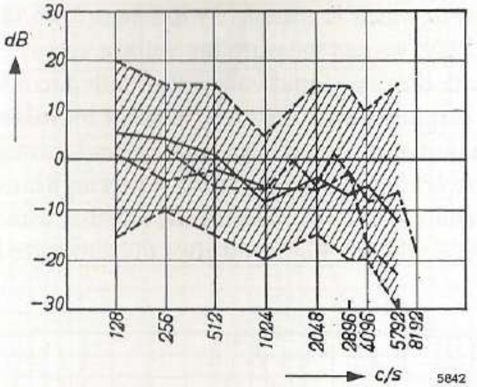


Fig. 48. The number of decibels that the artificial ear is more sensitive than the human ear.
— · — · — measured by us on normal people
———— measured by us on deaf people
- - - - - - - measured by Jonkhoff.
The shadowed area indicates the spread in the second measurement.

only. The latter has been done by Van Eijsbergen and Groen 14), who worked with a condenser telephone, but their results are most improbable, as we shall see later. We can use our electrical models to simulate both sets of conditions. We can measure the difference in pressure in the 2-cc coupler and on the eardrum, when a constant pressure is working on the membrane of an earphone,

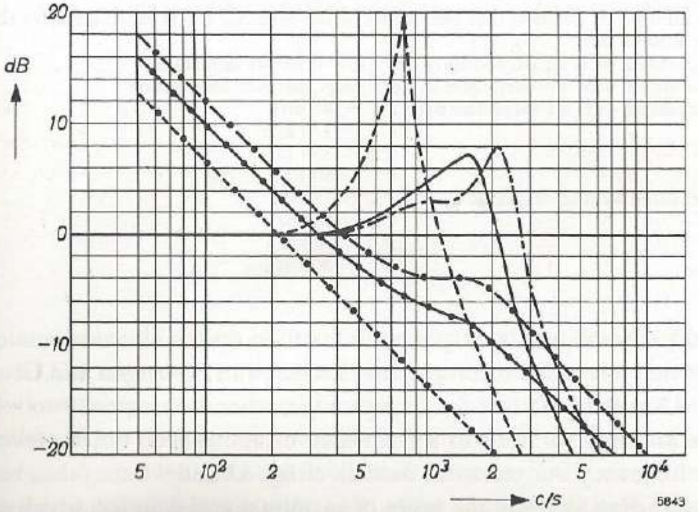


Fig. 49. The pressure on the tympanic membrane of our model of the ear.
———— with constant pressure at the entrance of the earmould
— · — · — the same for our model without C^*
·—·—·— with constant volume velocity of the air in the tube of the earmould
— , — , — the same for our model without C^*.
The pressure on the condenser microphone of our model of the 2-cc coupler
— — — — with constant pressure at the entrance
·-·-·-·-· with constant current through the tube.

which has an impedance which is completely different from that into which it is looking. That is to say, we can measure the voltage across C_0 in fig. 43 and across C_e in fig. 44, with the same input voltage for both circuits, corresponding to working with an earphone with very low internal impedance, and we can measure the same quantities if we send the same current through both circuits, which corresponds to working with an earphone of very high internal impedance. In fig. 49 we see the results of both measurements, together with that on a circuit like fig. 44 without C^* (see fig. 35). Figure 50 gives the difference between ear and artificial ear for both sorts of earphones, measured on the electrical analogues. Here we see that it is rather incomprehensible that Van Eijsbergen and Groen [14]) measured +20 dB in the low-frequency range, where we expect 0 to −4 dB. Our results are only valid up to a frequency of about 5000 c/s, however, for above that frequency our electrical models of fig. 43 and 44 are false, because there arise standing waves in the tubes of earmould and coupler, which can be seen in fig. 51 where we measured the ratio of the pressure on the condenser microphone to the input pressure of the 2-cc coupler, both on our model and on a real artificial ear.

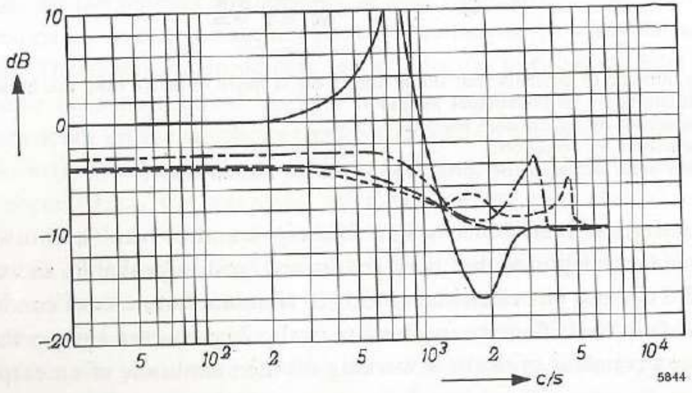


Fig. 50. The number of decibels that the model of the artificial ear is more sensitive than the model of the human ear.

———— measured with an earphone of very low internal impedance
— — — — measured with an earphone of very high internal impedance
— · — · — measured with an earphone with L_m = 65 mH
C_m = 170 kpF
R_m = 600 Ω
C' = 60 kpF
- - - - - - - measured with an earphone with L_m = 65 mH
C_m = 50 kpF
R_m = 600 Ω
C' = 30 kpF.

We measured the difference between the frequency characteristics with the earphone mentioned above and with a "broadband" earphone, with

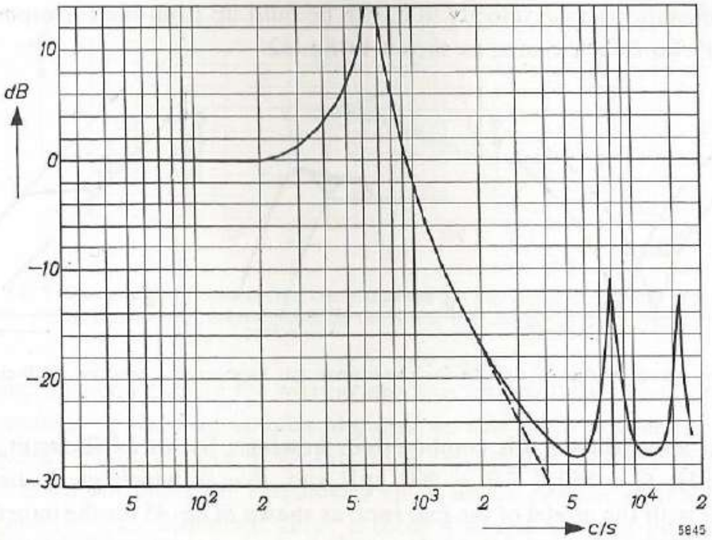


Fig. 51. The ratio of the pressure at the condenser microphone and at the entrance of the 2-cc coupler.

———— measured on a real coupler
— — — — measured on its electrical analogue.

$$L_m = 65.10^{-3}\,\frac{\text{g}}{\text{cm}^4},$$

$$C_m = 50.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}},$$

$$R_m = 600\,\frac{\text{g}}{\text{cm}^4\text{s}},$$

$$C' = 30.10^{-9}\,\frac{\text{cm}^4\text{s}^2}{\text{g}},$$

using our electrical models of the real and artificial ear. The results are drawn in fig. 50 and we see that they agree with our expectations: at low frequencies they follow the constant-current line, and also at high frequencies. In the middle range they follow neither the constant-current line nor the constant-voltage line.

The ear together with the earmould really form an LCR series circuit, whose C changes more or less abruptly, just where the ossicle chain becomes mass-controlled and the compliance of the inner-ear cavity remains, parallel to the cavity of the auditory meatus. This is shown very clearly in the measurements of figs 45 and 49, especially where we omitted C^*. We see that the impedance curve of the ear with the earmould as well as the curves representing the pressure at the eardrum with constant pressure at the entrance of the earmoulds

As has been shown by Metz and can be seen from our electrical analogue, the impedance of the inner ear cannot be felt at the eardrum. Measurements on our electrical model showed us that the impedance at the entrance measured without the last branch which depicts the inner ear, had risen a negligible amount below 1000 c/s and about 10% above 1000 c/s. Thus, the impedance at the eardrum is to a very good approximation a capacity with a series circuit parallel to it. Therefore, the circuit shown in fig. 56 is a more accurate representation of the earmould coupled with the ear; this corresponds to the artificial ear shown in fig. 57. The cavity of our first proposal has been split up into two cavities joined by a damped tube. From the second cavity to the outside we again find a release for the barometric fluctuations. We think, however, that the complexity of this construction outweighs the advantage that it may be somewhat more correct in the higher frequencies than our first proposal of very simple construction.

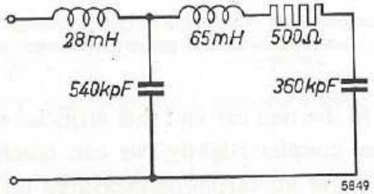


Fig. 56. Electrical analogue of the earmould in the ear (see text).

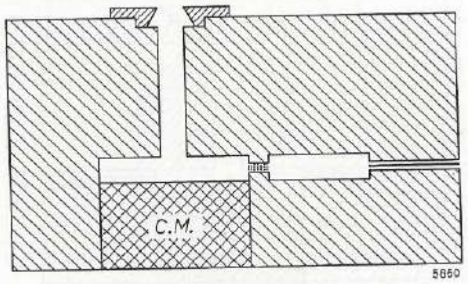


Fig. 57. Acoustical analogue of the earmould in the ear (see text).

It is easy to use our electrical model to estimate the influence of the dimensions of the earmould on the frequency characteristic of the earphone. From figs 43 and 46 we can calculate that the ratio between the pressure on the condenser-microphone membrane of the artificial ear and the pressure on the earphone membrane is

$$\frac{P}{P_0} = \frac{1}{1 + \dfrac{C_0 + C'}{C_m} - \omega^2 \left\{ L_0 C_0 + L_m (C_0 + C') + \dfrac{C_0 C' L_0}{C_m} \right\} + \omega^4 L_m L_0 C_0 C'},$$

if we neglect damping.
As

$$C' \ll C_0 \text{ and } L_0 < L_m$$

we find, to a first approximation,

$$\frac{P}{P_0} = \frac{C_m / C_0}{1 - \omega^2 \{ L_m C_m + L_0 C' \} + \omega^4 L_m C_m L_0 C'},$$

with resonances at

$$\omega_1 = \frac{1}{\sqrt{L_m C_m}} \text{ and } \omega_2 = \frac{1}{\sqrt{L_0 C'}}.$$

These two peaks, which are normally found in earphone characteristics, are caused by the membrane resonance and the resonance of the tube of the coupler with the cavity between the membrane and this tube.

The height of the first peak is given by

$$\frac{P}{P_0} \approx \frac{1}{\sqrt{\dfrac{L_0^2 C_0^2}{L_m^2 C_m^2} + \dfrac{R_m^2 C_0^2}{L_m C_m} \left(1 - \dfrac{L_0 C'}{L_m C_m}\right)^2}},$$

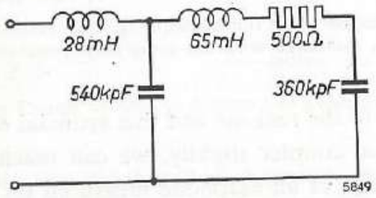
R_m being the damping of the membrane of the earphone. The height of the second peak is

$$\frac{P}{P_0} \approx \frac{1}{\sqrt{\left(\dfrac{C_0}{C'} + \dfrac{R_0 R_m C_0}{L_0}\right)^2 + \dfrac{R_0^2 C_0^2}{L_0 C'} \left(1 - \dfrac{L_m}{L_0}\right)^2}} \approx \frac{C'}{C_0},$$

as R_0, the damping in the tube of the artificial ear, is very small. We can use these formulae to give a qualitative prediction of the effect of changing the properties of the earmould or the earphone. We measured this effect, not on the model of the artificial ear, but on that of the ear with earmould, which will give practically the same results. The results are shown in fig. 58. The observed resonances occur at 1400 c/s and 4300 c/s, whereas with the formulae given above we calculated 1600 c/s and 3900 c/s. The same trend in the characteristics was found with a real earphone on a 2-cc coupler whose dimensions could be varied, and our results also agree with those of Güttner and Starke [16]).

The first resonance is practically independent of the loading of the membrane and is determined by L_m, R_m and C_m as can be seen in fig. 58 ($a - e$). The second peak is almost independent of the membrane properties, but L_0 and C'

As has been shown by Metz and can be seen from our electrical analogue, the impedance of the inner ear cannot be felt at the eardrum. Measurements on our electrical model showed us that the impedance at the entrance measured without the last branch which depicts the inner ear, had risen a negligible amount below 1000 c/s and about 10% above 1000 c/s. Thus, the impedance at the eardrum is to a very good approximation a capacity with a series circuit parallel to it. Therefore, the circuit shown in fig. 56 is a more accurate representation of the earmould coupled with the ear; this corresponds to the artificial ear shown in fig. 57. The cavity of our first proposal has been split up into two cavities joined by a damped tube. From the second cavity to the outside we again find a release for the barometric fluctuations. We think, however, that the complexity of this construction outweighs the advantage that it may be somewhat more correct in the higher frequencies than our first proposal of very simple construction.



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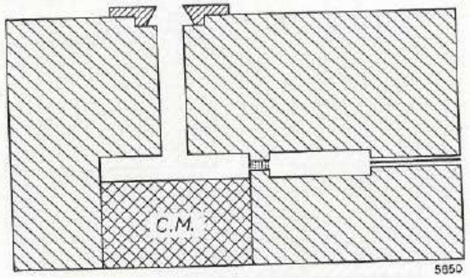

Fig. 57. Acoustical analogue of the earmould in the ear (see text).

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$$\frac{P}{P_0} = \frac{1}{1 + \frac{C_0 + C'}{C_m} - \omega^2 \left\{ L_0 C_0 + L_m (C_0 + C') + \frac{C_0 C' L_0}{C_m} \right\} + \omega^4 L_m L_0 C_0 C'},$$

if we neglect damping.
As

$$C' \ll C_0 \text{ and } L_0 < L_m$$

we find, to a first approximation,

$$\frac{P}{P_0} = \frac{C_m / C_0}{1 - \omega^2 \{ L_m C_m + L_0 C' \} + \omega^4 L_m C_m L_0 C'},$$

with resonances at

$$\omega_1 = \frac{1}{\sqrt{L_m C_m}} \text{ and } \omega_2 = \frac{1}{\sqrt{L_0 C'}}.$$

These two peaks, which are normally found in earphone characteristics, are caused by the membrane resonance and the resonance of the tube of the coupler with the cavity between the membrane and this tube.

The height of the first peak is given by

$$\frac{P}{P_0} \approx \frac{1}{\sqrt{\frac{L_0^2 C_0^2}{L_m^2 C_m^2} + \frac{R_m^2 C_0^2}{L_m C_m} \left(1 - \frac{L_0 C'}{L_m C_m}\right)^2}},$$

R_m being the damping of the membrane of the earphone. The height of the second peak is

$$\frac{P}{P_0} \approx \frac{1}{\sqrt{\left(\frac{C_0}{C'} + \frac{R_0 R_m C_0}{L_0}\right)^2 + \frac{R_0^2 C_0^2}{L_0 C'} \left(1 - \frac{L_m}{L_0}\right)^2}} \approx \frac{C'}{C_0},$$

as R_0, the damping in the tube of the artificial ear, is very small. We can use these formulae to give a qualitative prediction of the effect of changing the properties of the earmould or the earphone. We measured this effect, not on the model of the artificial ear, but on that of the ear with earmould, which will give practically the same results. The results are shown in fig. 58. The observed resonances occur at 1400 c/s and 4300 c/s, whereas with the formulae given above we calculated 1600 c/s and 3900 c/s. The same trend in the characteristics was found with a real earphone on a 2-cc coupler whose dimensions could be varied, and our results also agree with those of Güttner and Starke [16]).

The first resonance is practically independent of the loading of the membrane and is determined by L_m, R_m and C_m as can be seen in fig. 58 ($a - e$). The second peak is almost independent of the membrane properties, but L_0 and C'

have some effect on it, as can also be seen in fig. 58 (*a* – *e*). The volume of the cavity in the auditory meatus only influences the sensitivity, as is shown in fig. 58 (*f*).

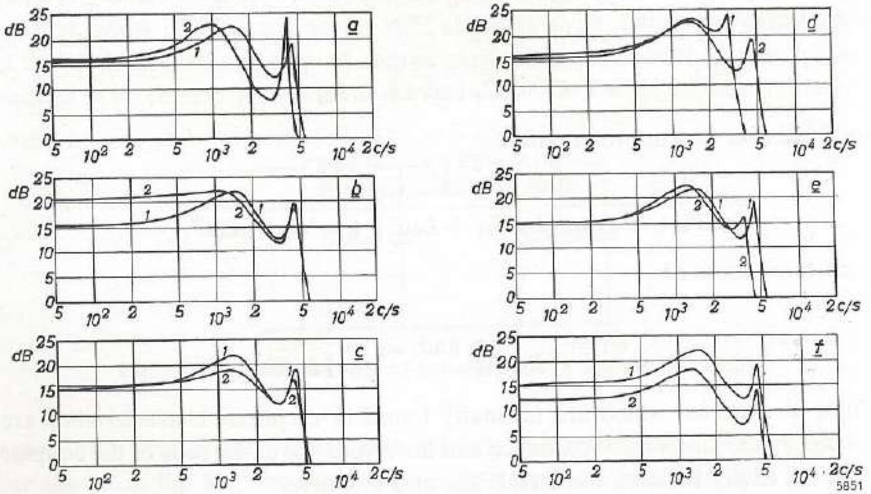

Fig. 58. The influence of the shape and size of the earmould upon the frequency characteristic of earphones measured with constant force on the earphone membrane.
(*a*) the mass of the membrane of the earphone in 2) was 2·5 times as high as in 1).
(*b*) the stiffness of the membrane of the earphone in 2) was 2·2 times smaller than in 1).
(*c*) the damping of the membrane of the earphone in 2) was 1·7 times higher than in 1).
(*d*) the cavity between the membrane of the earphone and the entrance of the tube in the earmould was 2·7 times larger in 1) than in 2).
(*e*) the length of the tube in the earmould in 2) was 1·7 times larger than in 1).
(*f*) the cavity between earmould and eardrum in 2) was 2·2 times larger than in 1).

To get a broad spectrum the tube in the earmould must be as short as possible and not too narrow. The cavity between the tip of the earmould and the eardrum has to be small, in order to keep the pressure on the eardrum as high as possible, although a large change in this volume gives only a few decibels change in the pressure at the eardrum. That means that the earphone has to be situated deep in the ear, which moreover tends to make it less visible. The total volume of the cavity between the membrane of the earphone and the entrance to the tube of the earmould has to be such that the second peak has a frequency which is not too low, but also not too far from the first resonance, since then it is too isolated, and the dip between the peaks is too deep. The earmould has to fit closely into the auditory meatus, as leakage would give a loss of low tones and a chance of oscillation.

Reviewing the results obtained in this chapter, we must conclude that there is still some doubt about the mechanical behaviour of the middle ear. The data available from direct mechanical measurements are too scanty and often contradictory. Maybe the system consists of more than two units coupled

together, but we do not believe that the joint between malleus and incus is soft, except at high intensities where the behaviour of the whole system is changed, since then it tilts around other axes, owing to pure mechanical causes and contraction of the middle-ear muscles. And what is the influence of those muscles and the ligaments on the frequency characteristic? Perhaps the impedance ratio we have taken is rather high, bearing in mind that the eardrum consists of a part coupled to the hammer and a part which can vibrate separately, but that will not change the overall picture. Let us hope that in the future more investigations will be done on the physics of the middle-ear system.

Nevertheless we were able to make some predictions about artificial ears, and to propose a new earphone-coupler which is more in agreement with the facts than the one used nowadays.

The study of the middle-ear-cochlea combination, with which we shall deal in the next chapter, will provide some further indications about the correctness of our middle-ear model.

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IV. THE MIDDLE EAR - INNER EAR COMBINATION

IV.1. The pure-tone threshold

It might be said that we were already working with the middle ear - inner ear combination in the previous chapter, since the last branch of our middle-ear circuit depicted the inner ear. All the investigations, whose results were used in the design of our circuit, were done outside the inner ear, however. Now we will include this inner ear itself in the system, so that we can use the results of the measurements of the electrical phenomena in the cochlea, i.e. the cochlear potentials, probably a sort of microphonic effect of the hair cells, and the action potentials, voltage pulses which run along the nerve fibres.

These phenomena are the most important data to be got from the cochlea, as measuring the mechanical behaviour is very difficult and, as far as we know, Von Békésy's curves are the only direct mechanical data obtained from the cochlea. Nowadays, the measurement of the electrical phenomena with small electrodes near or in the cochlea or the cochlear nerve, is less difficult and a lot of deductions can be made from measurements of this sort. We can connect our cochlear model directly parallel to the 600 Ω resistance of the last branch of the middle ear model, since the impedance of the cochlear model is about 5000 Ω. The measured results as a function of frequency are analogous to those measured in the real ear but the absolute values have to be transformed before comparisons can be made.

One of the most important problems involving the mechanical behaviour of the middle ear and the inner ear (and the properties of the nervous system) is that of the pure-tone threshold. Let us see what we can find about it in the literature.

Tumarkin, cited by Kostelijk, says that the shape of the threshold is mainly determined by the mechanical system, and not by the nervous one.

Fowler [1]) believes that the threshold curve can already be measured in the cochlear microphonics and on the higher nervous levels. These data were taken from Davis and Stevens [2]), who state that the threshold of the cochlear potentials in guinea pigs is parallel to the subjective human pure-tone threshold. The latter authors posit that the displacement of the eardrum at threshold pressures is the same function of frequency as the particle displacement of the free air at threshold pressures. That would mean that they have the same type of impedance, which is resistive for the air. We cannot believe that. The same conclusion can be drawn from Wilska's supposition that the plot of the amplitude of the eardrum at the hearing threshold against frequency, raised 6 dB/oct., has the same shape as our threshold curve. That means that the velocity curve of the eardrum is parallel to the threshold pressure curve, which again means that the impedance at the eardrum is a resistance. Modern measurements showed other results, as we have already seen.

The threshold curve for the cochlear microphonics and for the action potentials of the primary neurons should be parallel to our subjective threshold curve, according to Davis and Stevens, indicating that this curve is determined mechanically, if at least the electrical phenomena are proportional to e.g. the maximum displacement of the basilar membrane, which we already assumed in chapter II. This is not certain, however, because the measured action potentials are dependent on the situation of the electrodes. Wever and Lawrence [3]) give the pressure needed at the eardrum to give cochlear microphonics of 10 μV at each frequency in cats. Up to 1000 c/s this pressure curve is parallel to the subjective threshold but above this frequency the pressure needed is higher than expected from the subjective threshold.

Tasaki [4]) showed by means of animal experiments that the intensity, needed to give a constant cochlear microphonics in the basal turn of the cochlea, decreased only 10 dB from 500 to 8000 c/s. This is strongly dependent on the experimental conditions, however, as this author points out. And does a measurement at one point give a good idea of the real values at the different points along the cochlea? Does this result indicate a more or less constant "overall-characteristic" of the middle ear? In the same paper we find the sound pressure needed to give a constant output at different frequencies in a certain nerve fibre. The form of fig. 25 would lead to expect a rather flat curve up to a certain frequency, and a sharp rise thereafter, if the middle ear "overall-characteristic" were flat. Tasaki finds no horizontal part in this curve, however, but the tilting point is present. In another issue of the same journal [5]) this author gives the stimulation threshold curve of one fibre at different frequencies. Giving vertically the sound intensity at the ear in dB, and horizontally the frequency on a linear scale, he finds a curve consisting of two straight parts with a minimum between them.

It thus appears that the measurements which have been made on the cochlea are not much help in deducing the frequency characteristic of the mechanical system. Assuming that the cochlear microphonics at a certain frequency, and measured at the position of maximum displacement of the basilar membrane, are proportional to this displacement, and assuming that the activity in the neurons is caused by this microphonics, both the thresholds for the cochlear microphonics and for the action potentials should be parallel to each other and should correspond to a simple function (e.g. linear) of the amplitude curve of the maxima at the basilar membrane. Then, together with the results of the authors mentioned above we could draw conclusions about the mechanical behaviour of the system. But there is too little agreement between these investigators to permit this. Let us see what we can add ourselves to it.

We can ask ourselves: what precisely is the threshold sensation? In hearing as well as in the other sensory perceptions the threshold level is not one steady level below which we do not perceive and above which we do. There are levels we never perceive and there are levels we always perceive and between them there is a small range where we sometimes perceive and sometimes not. Perception is a matter of chance. In the small range of intensities of the stimulus between "never" and "every time" perception there are intensities we perceive only a certain amount of the total number of times they are offered. We can plot the percentage of times we perceived against the corresponding intensities and we find a curve like that of fig. 59. The intensity I_0 at which the chance of perception is 50 % is called the threshold intensity.

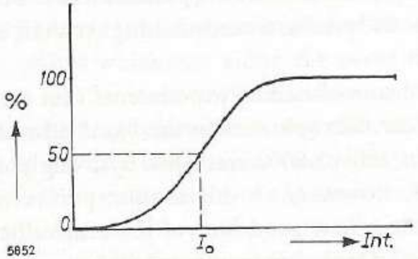


Fig. 59. The probability that a pure tone is heard, as function of intensity. The intensity I_0 is defined as the threshold-intensity.

It is impossible to give exactly the same stimulus twice, because some noise is added to each signal. A certain value of the stimulus is needed to give perception, i.e. a reaction to the stimulus, but this value is also not absolutely constant but depends on the state of the perceiving organ. Here too we have fluctuations. That is the reason why there is always a range of stimulus intensities which may or may not give perception. We may say that to have perception the stimulus must make itself felt above the noise; every threshold is determined by a noise source (see also 7)).

We can point out different noise sources on the acoustical pathway. In the first place there is the Brownian motion of the air and liquid molecules and the sound of the blood flowing, breathing etc. Then we have the noise source at the entrance of the nervous system: the state of the receptors, which determines whether they will react to a given stimulus. This state may be dependent on the food supply of the receptor and its previous history. The latter source is distinguished from the first one in that the acoustical noises cannot give a totally different stimulus at two neighbouring points of the cochlear partition, so that two neighbouring receptors can react in the same way to this source. The latter noise however can give a totally different behaviour of neighbouring nerve fibres. Since the spontaneous discharges cannot be detected in the more central regions, we believe that a coincidence system operates in the pathway to the central organ, so that the influence of the second source is another one than that of the first one. The acoustical noise can reach the central organ, the second noise only indirectly.

There may be a third noise source, situated more centrally where the signals from both ears meet and can interact. It is not impossible that this third noise source is the most important one in determining the hearing threshold, because the shape of the probability curve for binaural hearing seems to be the same as for monaural hearing, which means that we are dealing with the same probability function. The signals from the two ears seem to add before the last noise source. As the noise sources may be frequency dependent, it is not impossible that there are frequency ranges in which one of the other sources is more important. In that case every ear should have its own source determining its threshold. The probability function for binaural hearing would then be different from that for monaural hearing, if both ears are alike. If the latter is a function $K(I)$ of intensity, K being the chance that a tone with intensity I is heard, then the chance that a tone is not heard with both ears is

$$(1-K)\,(1-K),$$

so the chance that it is heard by one or both ears is

$$1-(1-K)^2 = 2K - K^2.$$

The probability function $K(I)$ has been drawn in fig. 60 for speech intelligibility in this case, not for pure tones. The straight lines give $K(I)$, the dashed lines give the functions $2K - K^2$. Here we see that the two probability functions have

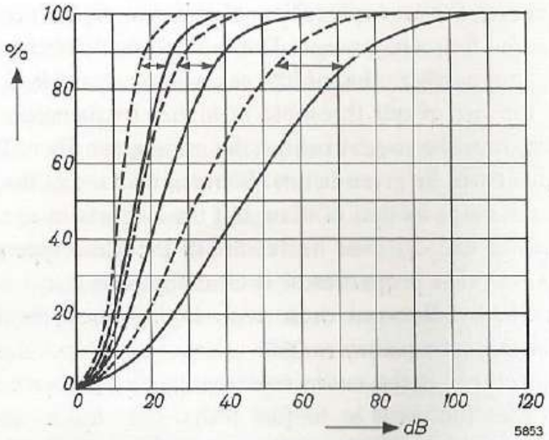


Fig. 60. The comparison of the function $K(I)$ (full lines) and $2K(I) - K^2(I)$ (dashed lines).

different shapes. In reality it is found that the binaural speech audiogram for normal ears had the same shape as the monaural one, indicating the importance of the central noise source. The difference between the two curves, however, is not 6 dB but 3 dB (Groen 6)). Somewhere the information is integrated over a certain time, the total amount of energy per second arriving in the central organ is important. This is supported by the fact that the threshold for pulses becomes lower when the time between the pulses is filled up with subliminal tones, while this threshold remains the same when the pulses become longer but less intensive 7). It was a good idea of Groen's to use the difference between the monaural and binaural speech audiograms of deaf people to detect if their defect is cochlear or more central.

If e.g. the noise source at the eardrum were the most important, its noise would pass the mechanical filter of the middle ear and get the same linear distorsion as the stimulating tones. If a source behind the filter were the main source, the stimulating tone would have a frequency characteristic which compensated for that filter. If that noise source were flat the pure-tone threshold would have the shape of the mirror image of the curve of fig. 38, if we assume that a constant displacement of the stapes at different frequencies, giving constant amplitudes at the maxima of the cochlear partition, also gives constant reactions of the receptors. One look at fig. 38, however, shows us that the mirror image of this curve has nothing in common with the shape of our pure-tone threshold. Other investigators, e.g. Von Békésy 8) and Zwislocki 9) have also tried to explain this threshold mechanically, but without success. In any case we know that the frequency characteristic of the mechanical system is flat for low and medium frequencies. Our noise source, which may have a thermal origin, will not have such high enough intensities at low frequencies to explain our bad hearing of low tones. The only remaining possibility is to search the properties of the nerves for an explanation of this rise of the threshold from the medium to the low frequency range. The fall of our filter characteristic in the high frequency range, where the middle ear is mass controlled, will mainly be responsible for the rise of our threshold at higher frequencies. This means that the noise source must be sought behind the middle-ear filter. The justification for this statement will be given below. Some animals, e.g. the bat, have a threshold of the same shape as that of man, but the rise sets in at much higher frequencies than in our ear. As their nerves are of the same type as ours, but their middle ears have other properties, it is clear that this rise is for the main part caused mechanically. Between those two sloping lines, the threshold is rather flat in the medium-frequency range.

The pure-tone threshold is the curve representing the pressure to be given to pure tones in order for them to be just heard over the noise mentioned above; we are thus dealing with the well known phenomena of masking of pure tones by noises, which have been considered by several investigators. One of the facts revealed by this research is the existence of the so called "critical bandwidth". Fletcher 10), inter al., found, that if a band of noise had an intensity (power per c/s) just sufficient to mask a given pure tone, it was not necessary to raise the intensity of the noise, while making the band narrower and narrower, to keep this tone masked. It seems as if only a small part of the noise band did the work and the rest had no effect. If, however, the bandwidth came below a certain limit, called the critical bandwidth, it was necessary to raise the noise intensity to mask the tone. It appeared that the total noise power within the critical band had to be the same as the power of the maskee tone. It is just if our ear in this case can only pay attention to a small region around the tone. The power in the noise band lying outside the critical band does not have any effect.

If I_m is the intensity of the maskee tone, and I_f the intensity per cycle of the noise, then we can write

$$(\Delta f)_c = \frac{I_m}{I_f} = 10^{\frac{K}{10}},$$

where $(\Delta f)_c$ is the critical bandwidth and K the difference in decibels between I_m and I_f. Fletcher calls K the critical bandwidth in decibels.

It may be expected that there is a certain relation between this critical bandwidth and the minimum audible frequency-shift Δf. And indeed, it was shown by Fletcher that

$$(\Delta f)_c = 20\,\Delta f.$$

This Δf turns out to be constant (3 c/s), up to about 2000 c/s, and increases above this frequency to a value of about a twentieth of a semitone. That means that Δf at 10000 c/s is about ten times Δf at 1000 c/s. This corresponds to the measurements of K, giving a value of about 19 dB up to 2000 c/s, and increasing to about 29 dB at 10000 c/s. So there is an agreement between the increase of ten times in Δf and the increase of 10 dB in K, which has been overlooked by most investigators.

It is clear that the pure-tone pressures, forming together our pure-tone threshold, will also be masked by the power of the still unknown noise sources in their critical bands only. Below 2000 c/s the critical bandwidth is constant and if the amplitude of the cochlear partition determines the stimulus, the pressure at the eardrum must be constant in the lower frequency range, in order to dominate over the noise. Looking to fig. 61, we see that Sivian and White's measurements made in 1922 are still in agreement with more modern measurements taken from the British Standards, so that we shall go on using Sivian and White's data. The difference between these results and those of e.g. Fletcher is to be found in the difference in measuring methods, as has been stated by Fletcher himself. We see from fig. 62 that from about 1000 c/s to the lower frequencies the threshold is rising by 12 dB/oct.

We know that, in general, the greater the stimulus, the higher the number of pulses per second travelling along the nerve-fibres, and the greater the sensation. We may thus expect the same behaviour with the auditory nerve. There is some synchronism between the stimulus and the pulse firing up to about

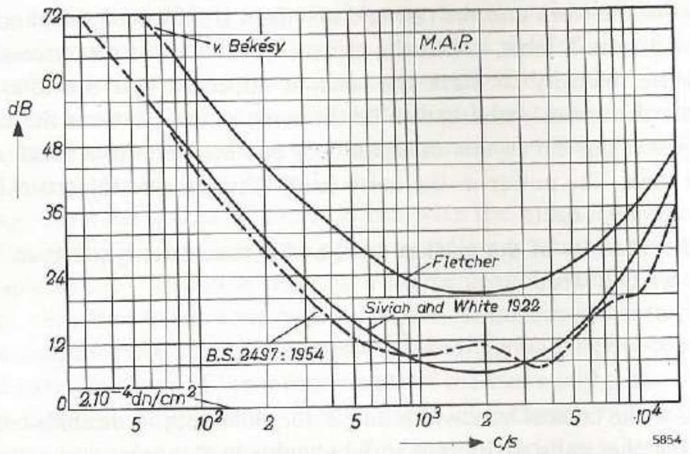


Fig. 61. Comparison of the minimum-audible-pressure curves of Sivian and White, Fletcher, Von Békésy (for low tones only)and the British Standard curve.

1000 c/s. That means, that the total number of pulses fired per second by a couple of fibres will be not only proportional to the amplitude of the stimulus but also to the frequency. That means that in this low-frequency region the pressure has to be proportional to $1/\omega$ to give a constant sensation. We still have to account for another 6 dB/oct. It is easy to say that this can be found in the frequency characteristic of our noise source. Another reason may be the pressure distribution along the cochlear partition. If the pressure on the cochlear partition rather than the displacement were the stimulus for the hair cell activity, and if we imagine for a moment that the middle-ear characteristic is flat, the pressure at the eardrum must be proportional to $1/\omega$ over the whole frequency range to a first approximation to give a constant pressure on the partition at its maxima, because of the changing impedance along the partition. At the present state of our knowledge, however, we must say that we do not know the exact reason for this second 6 dB/oct. and leave at that. The threshold curve can thus be represented to a first approximation by three straight lines, one falling by 12 dB/oct. up to about 1000 c/s, and the second horizontal or falling by only 6 dB/oct. in order to have the nerve actions dominating over the noise source. Above a certain frequency the mechanical behaviour of the middle ear makes a rise of the eardrum pressure necessary, in order to keep the displacement function of the stapes unchanged, which may be needed if the noise source is situated in the inner ear or more central. This rise will be 24 dB/oct. if the displacement characteristic were flat from 1000 c/s, or 18 dB/oct. if this displacement characteristic was falling 6 dB/oct., for we have seen in the foregoing chapter (fig. 38) that the middle ear "overall characteristic" is flat up to a certain frequency and falls 24 dB/oct. behind. Figure 62 shows the Sivian and White threshold curve *a*) and the corresponding curve calculated for a constant critical bandwidth *b*). The 12-dB/oct. drop is a very good approximation to this curve in the low-frequency region (we started from the Sivian and White curve at 100 c/s) and both cases for the situation above 1000 c/s have been drawn in. Here we see that the tilting point, which we took as 2500 c/s in chapter III, is probably at a higher frequency, perhaps near 4000 c/s to 5000 c/s or even near 8000 c/s. Von Békésy's measurements (fig. 38) also suggest this conclusion.

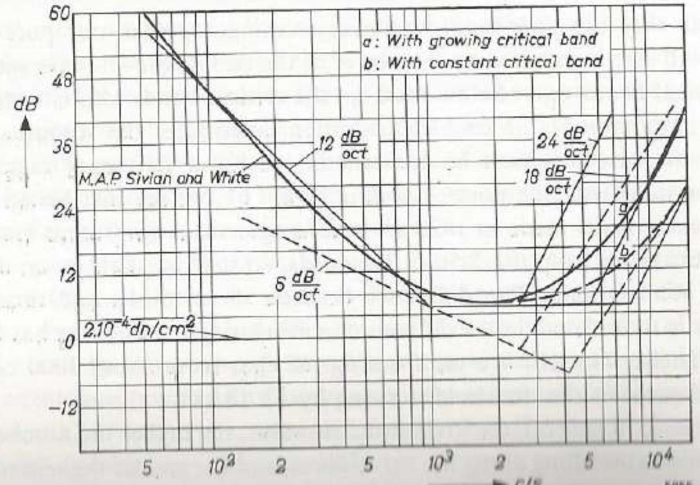


Fig. 62. Sivian and White's threshold curve together with some theoretical propositions (see text).

Consideration of the damage caused by very loud sounds also supports this shift of the tilting point to higher frequencies. The inner ear is protected by the contraction of the middle-ear muscles in the low-frequency range, and by the inertia of the middle ear at high frequencies, but in the medium frequency range it is not protected at all.

It has been found that very loud sounds damage that part of the organ of Corti which corresponds to 4000-6000 c/s (c^5-dip), which suggests that the tilting point of the middle-ear filter is situated around 4000 c/s.

De Vries [11]) calculated that the pure-tone threshold at 1500 c/s would be determined by the noise of the mechanical system middle ear - inner ear. He calculated the noise caused by the real part of the impedance at the eardrum in a bandwidth of 300 c/s. In the first place we do not understand why one should take such a large bandwidth and in the second place we believe that modern measurements have shown that the threshold power is larger than 20.10^{-12} erg/s, which was the value taken by De Vries. The bandwidth needed in the light of these modern measurements is so large as to be ridiculous as we will now show.

The pressure on the eardrum to give a just audible tone of 1500 c/s is about

$$p = 4.10^{-4}\ \frac{\text{dyn}}{\text{cm}^2}\,.$$

The impedance at the eardrum at the same frequency is practically resistive being

$$Z = 250\ \frac{\text{g}}{\text{cm}^4\text{s}}\,,$$

so that

$$\frac{p^2}{Z} = \frac{16.10^{-8}}{250} = 64.10^{-11}\ \frac{\text{g/cm}^2}{\text{s}^3} = 64.10^{-11}\ \frac{\text{erg}}{\text{s}}\,.$$

The noise pressure caused by Z can be calculated from

$$p^2 = 4\,kT\,Z\,\mathrm{d}\nu,$$

where k is Boltzmann's constant,
T the absolute temperature,
$\mathrm{d}\nu$ the bandwidth,
giving

$$16.10^{-8} = 4 \times 1{\cdot}38.10^{-16} \times 310 \times 250 \times \mathrm{d}\nu.$$

This equation gives $\mathrm{d}\nu = 4000$ c/s as the bandwidth needed for the noise of Z to reach the threshold power.

It would seem more reasonable to consider the noise caused in the critical bandwidth, which is about 60 c/s near 1500 c/s; this gives a noise power

$$4\,kT\,\mathrm{d}\nu = 4 \times 1{\cdot}38.10^{-16} \times 310 \times 60 \approx 10^{-11}\ \text{erg/s}$$

and an equivalent noise pressure at the eardrum

$$p = \sqrt{4\,kT\,Z\ \mathrm{d}\nu} = \sqrt{4 \times 1{\cdot}38.10^{-16} \times 310 \times 250 \times 60} \approx 5.10^{-5}\ \text{dyn/cm}^2,$$

which is much lower than the threshold pressure.

Moreover, the monaural pure-tone-threshold pressure is measured with a headphone, so that the noise source is loaded with the compliance of the air-volume in the ear between the eardrum and the headphone. This volume is about 3 cc, giving an impedance of about

$$50\ \frac{\text{g}}{\text{cm}^4\text{s}}$$

at 1500 c/s which is much lower than Z, so that the equivalent pressure of the noise caused by the mechanical damping of the system will be still lower than calculated above.

From assumptions about the evolution of the cochlea, and from phenomena associated with nerve deafness (see below), it might be concluded that the pure-tone threshold is determined by the hair cells or more central. That means that the threshold sound must contain more high frequencies in order to compensate for the influence of the middle-ear filter and overcome the noise.

Man and cat have the same pure-tone threshold in the low-frequency range [12]) In the middle-frequency range the cat's ear is 10 to 20 dB more sensitive than ours, and the upper limit of frequencies heard by the cat is much higher than for man. The cat's difference limen for frequency Δf is constant up to about 1000 c/s, above which frequency $\Delta f/f$ is constant, just as in man. From the similarity of the threshold for low tones and the behaviour of this difference limen as a function of frequency, we may conclude that the cat's nerves have the same properties as ours. So the difference in the upper-frequency limit will be caused by different properties of the middle ears. The hair cell density is in man about 40% larger than in cat, which may be the reason that $\Delta f/f$ is in cat three times greater than in man. It is impossible to say, however, why the threshold for medium frequencies is about 10 dB lower in cat than in man.

In any case we may be sure that the shape of the pure-tone threshold is determined by nervous processes in the low-frequency region up to about 1000 c/s and is determined mainly by the mechanics of the middle ear in the middle and high-frequency regions, where the effect of the increasing critical bandwidth forces to still higher pressures. The "overall frequency characteristic" of the middle-ear system will be rather flat up to 4000 c/s or 5000 c/s, above which frequency it will fall by 24 dB/oct.

The input impedance of the cochlear partition, 5000 Ω, is large compared with R_2 of fig. 35, 600 Ω, so we connected the two models directly in parallel with each other, the voltage across R_2 being the input voltage for our cochlear filter, and measured the output of a number of taps as a function of frequency with constant voltage at the entrance of the middle ear, representing a constant pressure at the eardrum. The result is shown in fig. 63, where the frequency which has its maximum at the tap considered is indicated. We see that up to about the 1000-c/s tap the indicated frequency does indeed give the highest output. But for "higher" taps the frequency giving the highest output is determined by the middle-ear model, and remains constant at 2500 c/s. On the curve of the 3240-c/s tap we see still a faint indication of a maximum at the rated frequency.

Many phenomena indicate that there is some synchronism between the signal and the pulse firing of the nerves up to about 1000 c/s, or even 4000 c/s, but above this frequency the pulse rate of the nerves has nothing to do with the periodicity of the signal. So it was commonly accepted that place detection occurs for the higher frequencies, which give rather well defined places of maximum displacement on the basilar membrane. For single pure tones this may be possible, but what about complex sounds? From fig. 63 we see that at the 6800-c/s tap a tone of 2500 c/s has a much larger displacement than a tone of

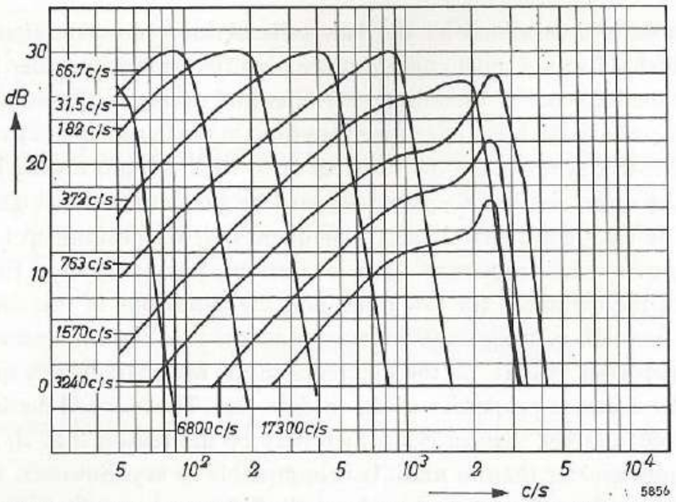


Fig. 63. The frequency characteristic of some taps, indicated by their peak frequency from chapter II, measured with the combined middle-ear and inner-ear models with constant pressure at the eardrum.

6800 c/s. This low tone will completely mask the high tone if only place detection operates. A white noise in a band between 2000 c/s and 16000 c/s will sound like a 2500-c/s tone, since the 2500-c/s tap has the highest output. The higher taps have nothing to do in place detection. But even if the tilt frequency of the middle ear was not 2500 c/s but 5000 c/s or still higher the problem remains, and is only displaced. If the "overall characteristic" of the middle ear were flat, this problem would not exist. Also, if L_2 and R_2 of fig. 35 were not constant but varied with frequency, being large for low frequencies and small for high frequencies, because the moving part of the cochlear partition is smaller for high tones than for low tones, the resonance frequency of 2500 c/s would not be constant, but rise for the higher tones. It would then be possible that each frequency had its own point of maximum displacement, allowing place detection. However, one of the most important results of our theory in the chapters II and III was that only a small part of the liquid in the cochlea co-operated with the partition, so that seen from the stapes the impedance of the cochlea, L_2 and R_2, remains constant. Moreover, Von Békésy [13]) measured constant values for these quantities between 200 c/s and 2500 c/s. We do hear difference between low-tone and high-tone noises. Is place detection nonsense then? We have to leave this problem here, not being able to add one sensible remark to it.

The study of the middle-ear - cochlea combination has not brought us the solution of our problems. On the contrary, it added another one to the row. In any case we may expect that the "overall characteristic" of the middle ear is flat, but drops above a certain frequency by 12 to 24 dB/oct. This frequency will be higher than the 2500 c/s from the foregoing chapter, may be about 4000 c/s.

The problem of the matching of the impedances between air and inner ear via the middle ear still remains. We see from fig. 35 that the impedance of the cochlear branch is always higher than the impedance of the coupling branch. In the region where the total impedance at the eardrum approximates to the characteristic impedance of the air we calculate

	impedance coupling branch	impedance cochlear branch
1000 c/s	350 Ω	8700 Ω
2000 c/s	225 Ω	6300 Ω
3000 c/s	180 Ω	6200 Ω

So the coupling branch is a short circuit for the cochlea. Is that a form of protection? It has been known for some time that the power needed for the electrical phenomena in the cochlea and the nerves is provided chemically via the blood and the cochlear fluids so that the acoustical power is not needed for it. It is therefore sufficient that the stimulus of the receiving organ caused by the lowest sounds to be heard is high enough to overcome the inner noise sources, and we know that this is so. That there is some matching between the air and the ear in the middle-frequency range may be caused by the demand that no frequency may dominate over the others, just as we have seen in chapter II. That means that in the region where the wavelength in air is comparable with the length of the external auditory meatus, there must be as small a reflection against the eardrum as possible. The experiments of Wiener and Ross [14]) show that this is in fact so.

Many investigators have struggled with the problem of the matching between air and inner ear. We have to be careful with their calculations sometimes. Wever and Lawrence [3]) for example, calculate the mismatch by calculating the impedance transformation in units of pressure per volume velocity, and applying this to the characteristic impedances of the air and the inner-ear liquid, which are given as pressure per velocity. Moreover, the inner-ear impedance is not only determined by the characteristic impedance of the liquid. We have seen from the calculations on our models of the middle ear and the cochlear partition that only a very small amount of the sound energy caught by our ear is dissipated in the cochlear partition. It would be very interesting to see if this agrees with reality, and a knowledge of the "overall characteristic" of the middle ear, the displacement of the stapes as function of the frequency with a constant pressure at the eardrum, will be indispensible for further calculations and measurements on this question. Now we are only able to go on with the simple filter mentioned above, giving the characteristic as a flat line with a 24-dB/oct. drop above a certain frequency.

IV.2. Experiments with complex sounds

IV.2.1. *A spectroscope*

For pure tones the calculations and measurements on our models were rather simple, but for other sounds the calculations become too complex and the tap by tap measurements too laborious. However, the models have been built in order to be able to study the mechanical behaviour of our hearing organ with complex sounds. We therefore built a spectroscope with which we can make the output of all the taps visible on a television screen at the same time.

The output of 96 taps (8 octaves) is amplified in order to be able to rectify the output signals over a 40 dB range. After rectification the signal is smoothed by a capacity C parallel to a resistance R. An electronic switch selects each capacity once in 20 ms, and the signal, obtained in this way can be amplified linearly or logarithmically and made visible by television techniques (see fig. 64). The RC-time of the smoothing filter has been chosen as 20 ms, because quicker changes do not occur in the natural sounds. Moreover, with smaller RC-times, the low-frequency limit to which the ripple over the smoothed signal can be neglected is shifted to higher frequencies. With $RC = 20$ ms the ripple is already about 40 % at 100 c/s. That means that at the 100-c/s tap, the image-dot can be up to 40 % too low if the electronic switch is synchronized with 100 c/s, and otherwise it moves up and down. Finally, changes quicker than once in 20 ms cannot be seen on the screen. The electronic switch consists of 96 electronic gates which are opened one by one by a ring counter, consisting of 96 flip-flops coupled together and driven by a multivibrator via diodes, so that only one couple is switching per period, which is a rather

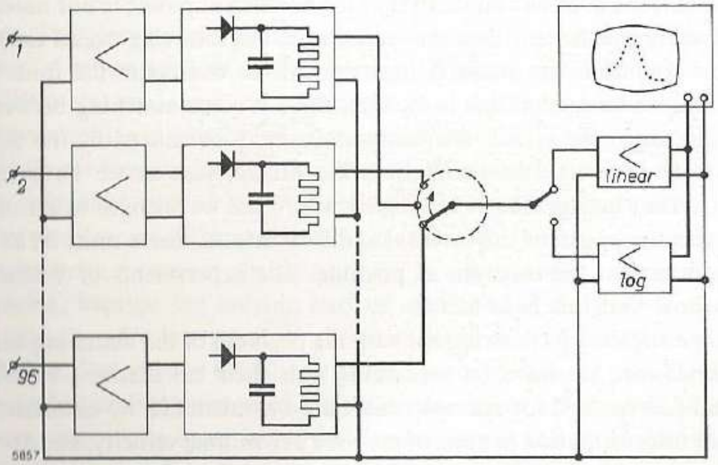


Fig. 64. Block diagram of the spectroscope.

common circuitry. The deflection-coils of the picture tube were turned through 90° so that the picture lines are traced vertically, proceeding from left to right. The unmodulated picture is suppressed. When the voltage of the line oscillator reaches a value proportional to the output voltage of the tap in question, a small spot of light appears on the screen. Only one dot is visible from every line and the height of this dot corresponds to the output voltage of the tap. The displacement curve of the cochlear partition is thus plotted as a series of dots. This is in fact the envelope of the displacement curve during time and not the displacement curve itself, because that would have demanded far more complex techniques. We will call this envelope the "cochlear spectrum".

We think that the behaviour of the envelope is more important than the sequence of momentary values of the displacement; the only additional information for a pure tone given in the latter case is the phase at each tap. For we know that, apart from special cases such as interference and binaural hearing phenomena, phase is not very important for hearing. Of course, we do hear phase changes but mostly as a second-order effect.

This spectroscope also allows the original signal at each tap to be made visible on an oscilloscope. With 96 switches we can switch off each of the 96 taps separately to see at which place in the curve it was situated or to see at which place in the curve we are seeing the original signal. We will now describe some experiments which were made with the aid of this spectroscope.

IV.2.1.1. *Masking of a pure tone by a pure tone*

We started the study of masking with tones giving maxima in the middle of the cochlear partition where the middle ear does not influence the frequency characteristic of the signals, i.e. we were working in the frequency range up to about 4000 c/s where sounds of different frequencies give the same maximum amplitudes of the partition if their pressures on the eardrum are the same.

For simplicity the pictures were photographed from an oscilloscope connected in parallel with the television-set, mentioned above.

It was found that the cochlear spectrum for a maskee tone of 1200 c/s together with a just audible tone of any frequency between 400 and 3200 c/s could not be distinguished from the envelope for the 1200-c/s tone alone, as may be seen in fig. 65, for just audible tones of 800 and 1600 c/s. The three curves are displaced with respect to each other so that they can be compared more easily.

The signal at the tap where 1200 c/s has its maximum was found to be a sine wave of 1200 c/s, slightly modified by the just audible tone; the difference was too small to show up in a photograph, however. With a just audible tone of 3200 c/s, the tap corresponding to this frequency gives a signal with a periodicity of 1200 c/s formed by the summation of a 1200-c/s sine wave and a 3200-c/s sine wave. This can be seen in fig. 66, while fig. 67 gives the signal produced

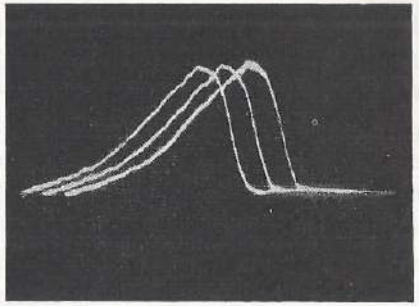


Fig. 65. From left to right; the cochlear spectra for a pure tone of 1200 c/s, the same tone of 1200 c/s together with a just audible tone of 800 c/s, and the same tone of 1200 c/s together with a just audible tone of 1600 c/s.

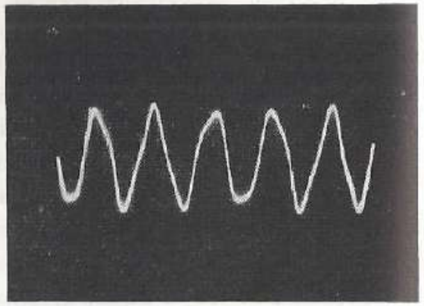


Fig. 66. The signal produced at the 3200-c/s tap by a tone of 3200 c/s just not masked by a tone of 1200 /s.

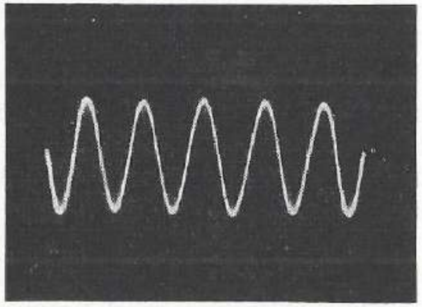


Fig. 67. The signal produced at the 800-c/s tap by a tone of 800 c/s just not masked by a tone of 1200 c/s.

at the 800-c/s tap by a 1200-c/s masker tone with a just audible tone of 800 c/s. Here we expected the summation of a sine wave of 800 c/s and one of 1200 c/s, but the influence of 800 c/s can hardly be seen, although the amplitude of the 1200-c/s signal must have decreased seriously at the 800-c/s tap. Here too, the periodicity is that of a 1200-c/s tone. Figures 68 and 69 show similar results for just audible tones of 4800 c/s and 6000 c/s, also for the case where the middle-ear filter is omitted. It may be seen that the middle ear considerably reduces the effect of the high frequencies.

Figure 65 shows clearly that place discrimination on the cochlear partition is not much use for distinguishing a just audible tone from the masker tone. However, the influence of the just audible tone can be found in the signal at different points along the length of the basilar membrane (figs 66-69), although sometimes not very distinctly, especially for just audible tones of high frequencies (figs 68 and 69 with middle-ear filter). Anyhow, the main periodicity measured on the taps is that of the masker tone, and it seems probable that the influence

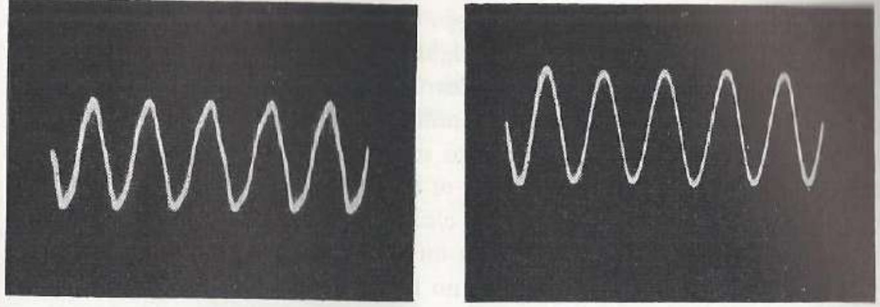


Fig. 68. The signal produced at the 4800-c/s tap by a tone of 4800 c/s just not masked by a tone of 1200 c/s. At the left without, and at the right with the total signal passing the middle ear filter.

of the maskee tone has to be found by a correlation measurement between neighbouring taps, which cannot be done by the hair cells. We may expect this in the synapses in the trapezoid body or higher, but cannot give any suggestion how these correlation measurements will take place. We know that a tone can be masked more easily by a lower tone than by a higher one, which seems to have some connection with the fact that the envelope curves on the cochlear partition for low tones overlap those for higher tones, but the intensity difference between a masker tone and a tone which is just not masked is so large that in both cases the envelope of the masker tone overlaps the other one. The hair cells react only to one of the two excursions of the basilar membrane. In the curve of fig. 67, where the maskee tone is lower than the masker tone, the upper half (or the lower one) looks like an amplitude-modulated signal. This might be the reason why the lower tone is easier to detect than the higher one; it can be seen from figs 68 and 69 that where the maskee tone is higher than the masker tone, it only influences the shape of the masker tone. However, if this should be true, why do not we hear a tone of 400 c/s in the cases of figs 66

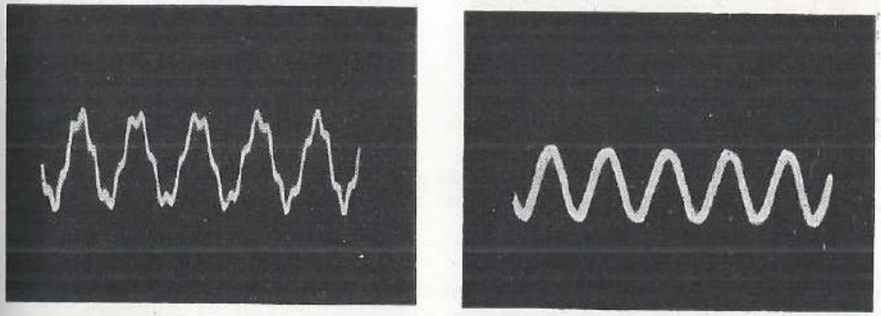


Fig. 69. As fig. 68, at the 6000-c/s tap with a tone of 6000 c/s.

and 67? The periodicity seen in the tops of the signal is 400 c/s. Here a place-correlation measurement between neighbouring taps seems to be indicated. The travelling waves along the cochlear partition will cause the maxima on different phases of the masker tone at different places of the basilar membrane, at any given moment. Comparing two such places, we will be able to detect the difference between a maskee tone of 800 c/s and a maskee tone of 400 c/s together with a masker tone of 1200 c/s. In general, measuring the zeroes of the signal at different taps also gives information about the influence of the just audible tone; but this would be no help in distinguishing between e.g. a pure tone and the same pure tone together with one of its odd harmonics, if the amplitude and phase of the latter have certain values.

IV.2.1.2. *Complex sounds consisting of two pure tones of the same intensity*

To study the behaviour of the combination of two pure tones of the same physical strength we took one with a constant frequency of 3000 c/s and another one with a lower frequency. Supposition of 2500 c/s on 3000 c/s gives a single-side band modulation of 2750 c/s with 500 c/s as can be seen in fig. 70, which shows the displacement function at the tap where 3000 c/s has its maximum and the amplitude curve at the cochlear partition, which is the same as that for a single pure tone which is modulated. Since the frequency with which the cochlear partition is scanned is much lower than the modulation frequency, we record different phases of the modulation at different points of the picture, resulting in the bump which can be seen on the left-hand portion of the curve. If the modulation frequency is not an exact multiple of the scanning frequency this bump moves along the curve, producing a ripple. We hear a grating sound, which becomes a beat if the second frequency approaches 3000 c/s. Whenever a beat can be heard, evidence for it can be found in the displacement function

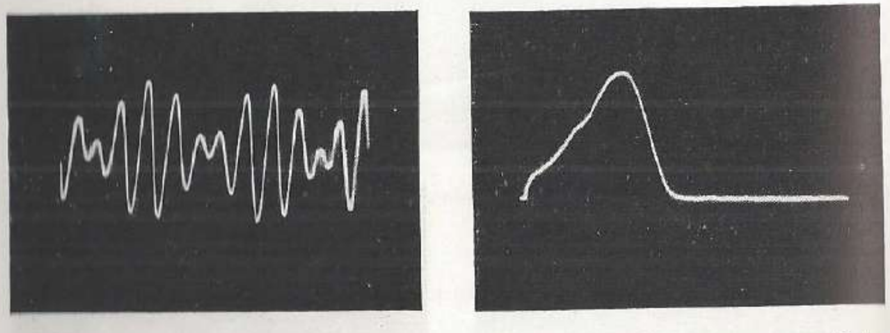


Fig. 70. The signal at the 3000-c/s tap and the cochlear spectrum for two pure tones of the same intensity and with frequencies of 2500 c/s and 3000 c/s.

at tap 3000 c/s as well as in the envelope of the cochlear partition. Figure 71 shows the signal at the 3000-c/s tap for the combination of a tone of about 1500 c/s with one of 3000 c/s in two different phase differences. The second tone was chosen slightly different from 1500 c/s so that the influence of this tone at the 3000-c/s tap can be seen as a beat. As the lower frequencies overlap the higher frequencies on the cochlear partition, it may be expected that both signals can be seen at tap 3000 c/s. The higher frequencies, however, have much less influence on low-frequency taps, and the effect of a tone at the tap where the tone one octave lower has its maximum is imperceptible. This is demonstrated in fig. 72 which was taken from the 1500-c/s tap under the same conditions as fig. 71. Figure 73 shows the envelopes of the cochlear partition, corresponding to two different times, superimposed on each other. The beat is seen only where 3000 c/s has its maximum. This beat can also be heard, which shows that beats between two tones differing by about an octave are quite natural and have nothing to do with beats between overtones due to

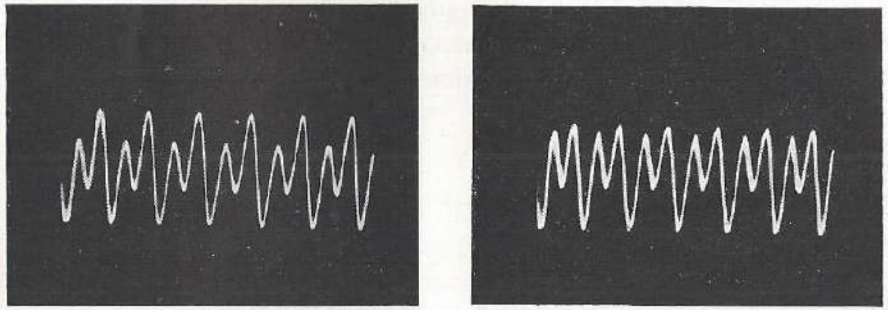


Fig. 71. The signal at the 3000-c/s tap for a tone of 3000 c/s together with a tone of about 1500 c/s of the same intensity, at two different times.

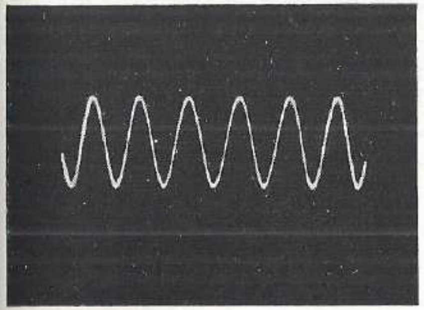


Fig. 72. As fig. 71, at the 1500-c/s tap.

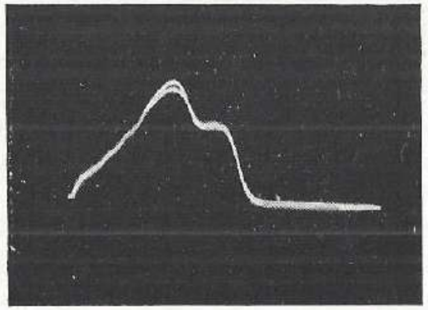


Fig. 73. The cochlear spectra corresponding to fig. 71, superimposed one on the other.

distortion, as has been supposed by some investigators. If the two tones differ by more than one octave the two maxima on the cochlear partition are separated by a minimum. This one-octave difference is also the limit beyond which the high frequency cannot be detected in the signal at the tap where the lower frequency has its maximum; and the octave also forms the limit above which the two tones can be heard apart. Figure 74 shows the cochlear spectrum and the signal at the 3000-c/s tap for the combination of 3000 c/s and 750 c/s. It is clear that there is no sign of modulation here anymore.

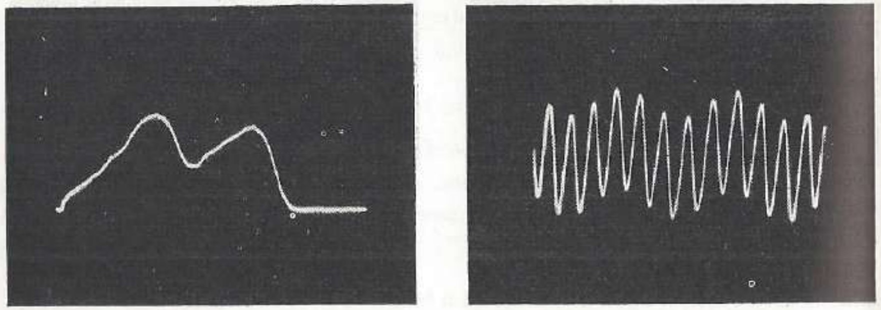


Fig. 74. The cochlear spectrum and the signal at the 3000-c/s tap for a tone of 3000 c/s with a tone of 750 c/s of the same intensity.

Place detection could be used in these latter cases, especially for persons with a linear ear in the sense of Enkel[16] (see IV.3) and so could place and time correlation measurements, perhaps especially for persons with an ear of the polar type in the sense of Enkel, as can be seen in fig. 74. The lowest of the tones can then be detected very easily at its own tap. If the tones are closer together, these correlation measurements grow in importance and enable us to hear the beats of mistuned octaves (figs 71 and 73), which are not caused by difference tones formed by distortion. It is impossible to say if place-detection is still possible for two tones with a small difference (fig. 70), although the highest tone can be distinguished on the back of the lower one. In any case we do not hear both tones separately, unless we possess a highly trained ear. Correlation measurement is again possible (fig. 70) but we do not know why the ability to distinguish both sounds separately stops below a certain value of the frequency difference, when we hear only one rough sound. This may be related to the type of correlation measurements, by which the signals are detected.

IV.2.1.3. *Noise*

For studying noise we triggered the oscilloscope once, and synchronized its timebase with the scanning of the cochlear partition so that we see one scanning of this partition or the displacement at one tap during 20 msec. Figure 75(*a*) shows the cochlear spectrum during a white-noise signal, the middle-ear cut-off being omitted from the circuit. Figure 75(*b*) gives the envelope for the same noise filtered out below 1000 c/s and fig. 75(*c*) that for white noise filtered out above 1000 c/s. It can be seen clearly that for noise without low frequencies the apical part of the partition remains

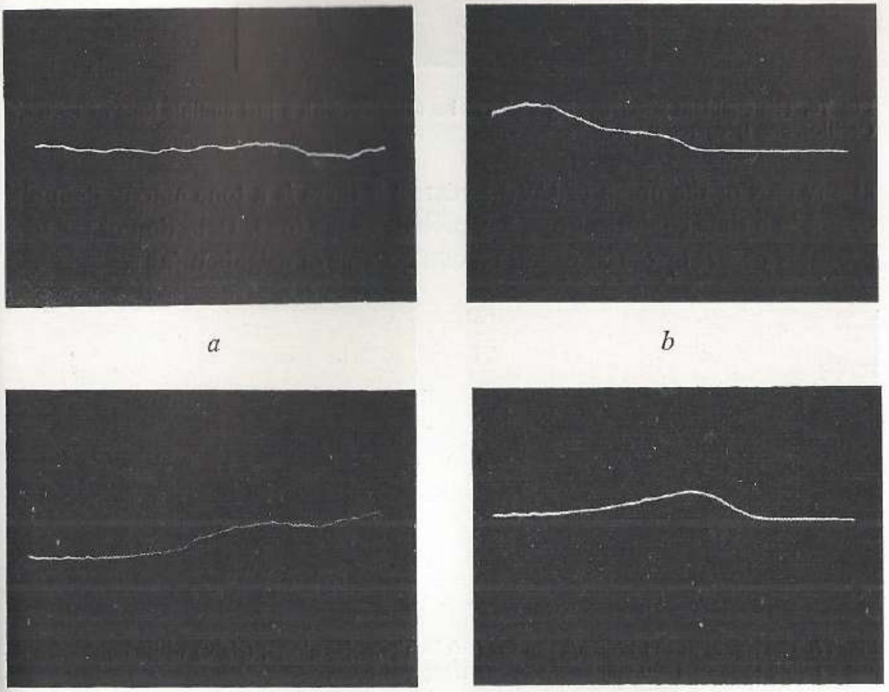


Fig. 75. The cochlear spectrum for white noise:
(*a*) total band
(*b*) above 1000 c/s
(*c*) below 1000 c/s
(*d*) between 500 c/s and 1000 c/s.
Oscilloscope triggered once.

in rest. Figure 75(*d*) gives the cochlear spectrum for the part of the noise in the band between 500 c/s and 1000 c/s. Figure 76 gives the envelope for a wide-band white noise together with a tone of 1200 c/s which is just not masked by the noise, and fig. 77 shows the signal at the 1200-c/s tap, at the left with the white noise alone, at the right with the white noise together with the just audible 1200-c/s tone.

It is impossible to detect the 1200-c/s tone among the noise from the cochlear spectrum or from the signal at one tap, i.e. it is impossible for one receptor

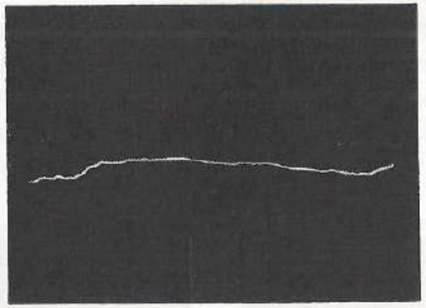


Fig. 76. The cochlear spectrum for white noise together with a just audible tone of 1200 c/s. Oscilloscope triggered once.

at any part of the organ of Corti to detect if there is a tone among the noise or not in a time equivalent to a few periods of the tone. Detection of the tone probably occurs by the co-operation of a number of neighbouring sense organs in some correlation measurement, as has been suggested by Licklider, among others. If a number of sense organs can do this in a short time, it seems reasonable that one sense organ can do the same in a longer time. We therefore repeated the experiment of fig. 77 (the time base being synchronized with 1200 c/s) but instead of triggering the time base of the oscilloscope once, we choose an exposure time of about five seconds. Figure 78 shows that the difference between the noise alone and the noise with the tone can be seen surprisingly well.

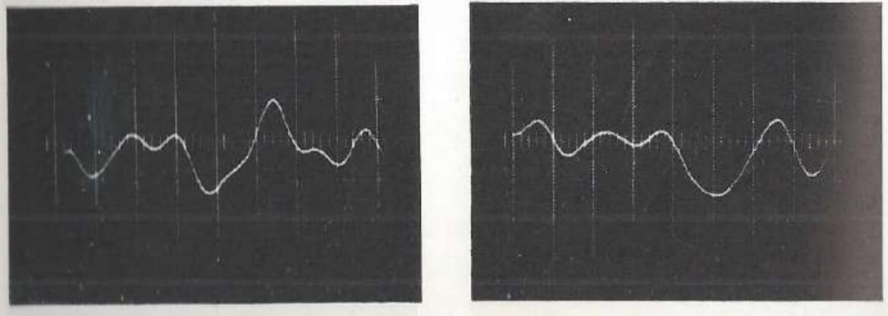


Fig. 77. The signal at the 1200-c/s tap for (left)white noise alone; (right) white noise with a just audible tone of 1200 c/s. Oscilloscope triggered once.

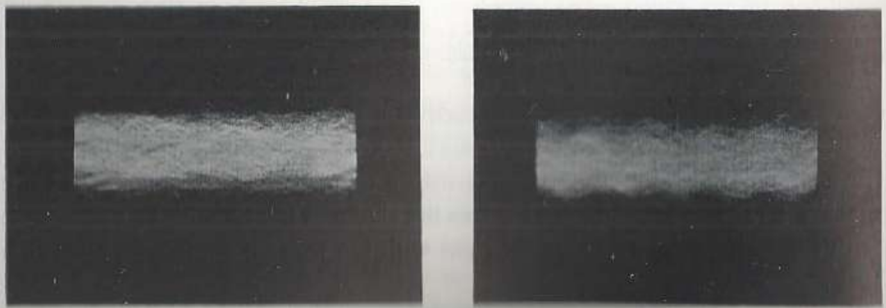


Fig. 78. As fig. 77. Time exposure.

IV.2.1.4. *Square-waves*

It is known that the dominant pitch of a sound containing a number of harmonics is determined by the first harmonic, even if this harmonic is completely missing. It was previously thought that the ear actually produced the first harmonic by non-linear distortion, but it has now been proved that the pitch information is actually carried in the higher harmonics. The part of a tone composed of the higher harmonics is known as the residue. In order to study how the information contained in the residue is conveyed to the brain, we took a 400-c/s symmetrical square wave. Figure 79(*a*) shows us the cochlear spectrum, with a flat middle-ear filter. Figure 79(*b*) gives us the signal at the tap where a frequency of 400 c/s gives its maximum

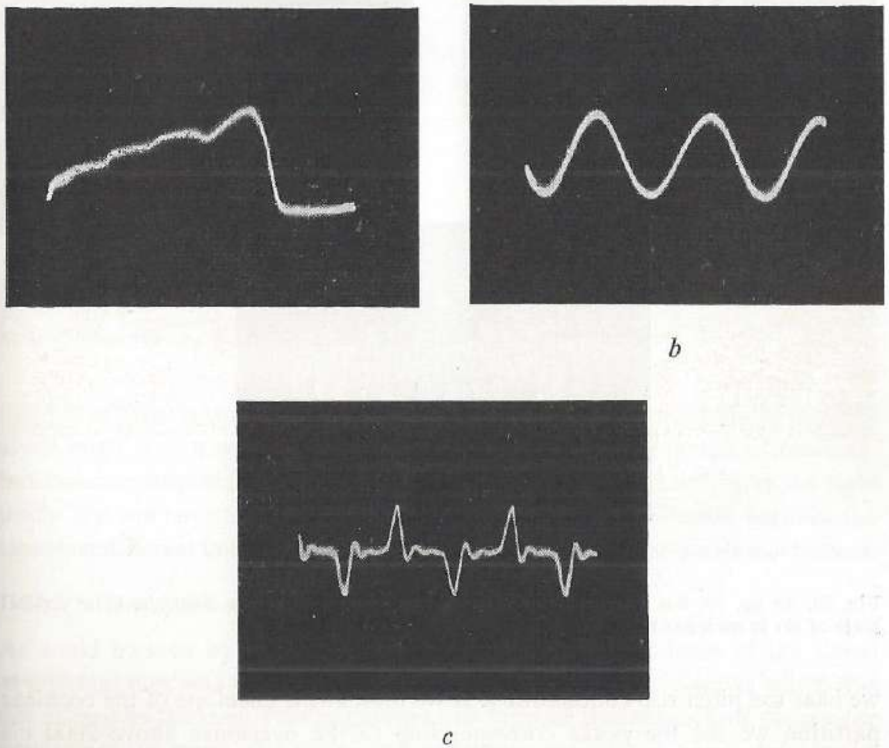


Fig. 79. (*a*) The cochlear spectrum; (*b*) the signal at the 400-c/s tap; (*c*) the signal at the 2400-c/s tap for a symmetrical square-wave of periodicity 400 c/s.

and fig. 79(*c*) does the same for the 2400-c/s tap. Figure 80 shows the corresponding curves for the same square-wave with all the frequencies below 2000 c/s filtered out. We see that at the 400-c/s tap only the noise of the apparatus remained. If we increase the periodicity of the square-wave, and listen to it after it has been through the high-pass filter, we hear the pitch rise continuously. If we look at the envelope of the cochlear partition we see the peaks corresponding to the overtones above 2000 c/s moving to the left as the periodicity is increased, and the envelope of the partition getting narrower, until the next lowest overtone comes into the picture. This happens visually in a rather discontinuous manner, although we hear a smooth glissando. Figure 81 gives the cochlear spectrum and the signal at the 2400-c/s tap for a square-wave of 600 c/s which has been through the same high-pass filter.

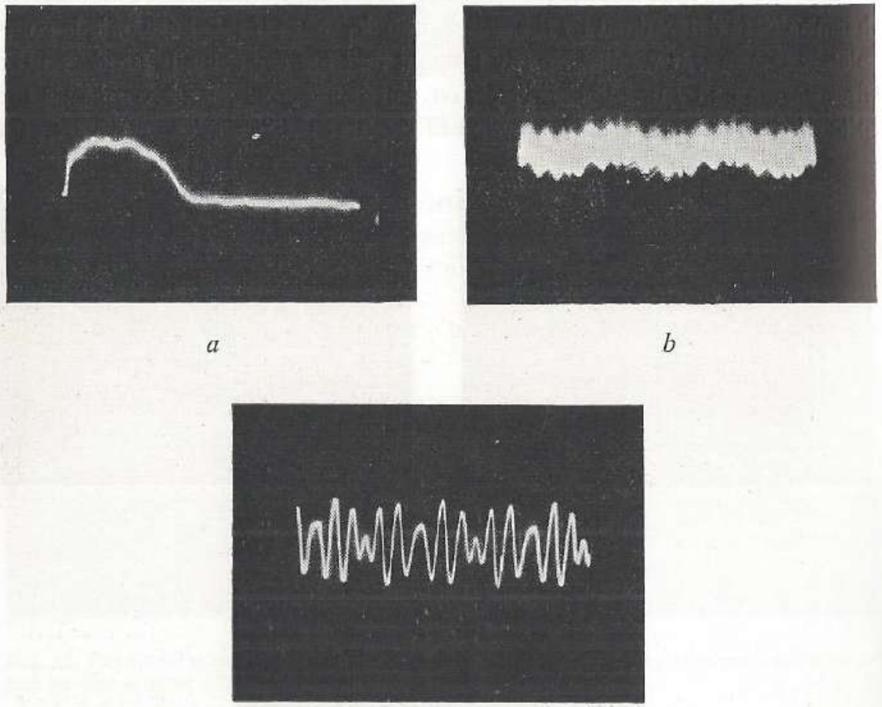

a *b* *c*

Fig. 80. As fig. 79, but without components with frequencies below 2000 c/s. (The vertical scale of (*b*) is enlarged.)

It is clear that the pitch of a square can be determined from the envelope of the cochlear partition as well as from correlation measurements, because, especially where the fundamental has its maximum, the periodicity is clearly visible, The difference between the shapes of the envelope for the square-wave and for the fundamental alone may be responsible for the difference in timbre and experiments with speech sounds also suggest that timbre is connected with the shape of the envelope curve. The filtered square-wave retains its pitch, which is not caused by difference tones because only noise can be found at the tap of the fundamental (fig. 80). The periodicity again can be detected by correlation measurements, however. The periodicity seen in a signal is always that of the highest common factor of its components. Measuring this periodicity alone might give a wrong pitch, as we have seen in the paragraph of masking, but the comparison of the signal at different places will certainly give the right pitch. We will have to do more experiments about the correlation between the signals at different taps before we can draw any conclusions about its mechanism.

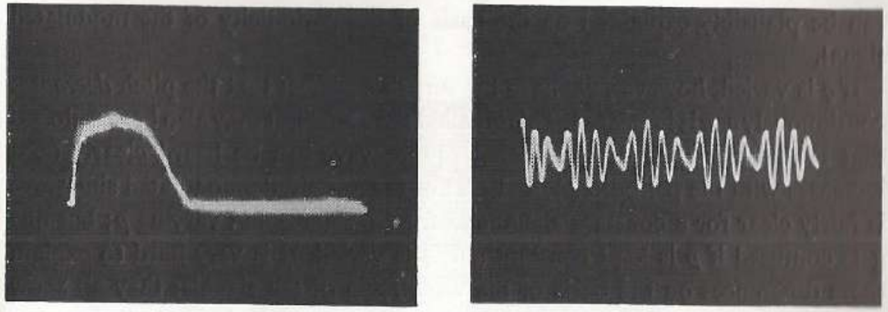

a *b*

Fig. 81. (*a*) The cochlear spectrum and (*b*) the signal at the 2400-c/s tap for a square-wave of periodicity 600 c/s with all the frequencies below 2000 c/s filtered out.

IV.2.1.5. *Amplitude modulation*

As could be seen by studying the square-waves, the periodicity of the signal at different taps was the same as the periodicity of the square-wave, which was not altered by filtering. This might make us suppose that this is how the residue determines the pitch of a sound. An amplitude-modulated signal can also be composed of components with a high frequency and still have a low periodicity, and has often been used to study the residue, e.g. by Schouten 17) and De Boer 18). Let us consider the signal

$$(1 + \cos 2\pi qt) \cos 2\pi pt = \tfrac{1}{2} \cos 2\pi(p + q)t + \cos 2\pi pt + \tfrac{1}{2} \cos 2\pi(p - q)t.$$

When $p = nq$ (where n is an integer > 2) we hear a sound with a pitch like that of a pure tone of frequency q c/s owing to the residue. If p is increased we hear a gradual increase in pitch, with a sharp drop back to the original pitch at $p = (n+1)q$. For example if $p = 2000$ c/s and $q = 200$ c/s we hear something like the pitch of a pure tone of 200 c/s. Increasing p gives an increasing pitch up to $p = 2200$ c/s where some people hear the pitch of 200 c/s and some hear a higher pitch in the neighbourhood of 225 c/s. This is called the p effect. For some people the p effect takes a rather different form: the pitch increases as p is raised from nq to $(n+\frac{1}{2})q$, then falls to a lower pitch than the original, and then increases again to the original pitch at $p = (n+1)q$. The precise nature of the p effect depends on the way in which the experiment is carried out as well as on the person who is listening. However, all these effects can be plausibly explained on the basis of the periodicity of the modulated signal.

If q is varied, however, we have the surprising effect that the pitch *decreases* continuously as q is increased. This is called the q effect. It may also be mentioned that the residue tone of the filtered square-wave can be heard clearly (and increases with the periodicity), and that of the amplitude-modulated sine-wave is fairly clear for a constant signal and for constant q and varying p; but one gets confused if p is kept constant and q is varied. It is very hard to explain these differences on the basis of the wave form of the signals: they all show a clear periodicity, and the only difference between them is, that all the components of the square-wave signal will increase in frequency with increasing periodicity, and all the components of the modulated signal will increase in frequency with increasing p, but with increasing q the carrier frequency remains constant, the frequency of the summation tone increases, while that of the difference tone decreases.

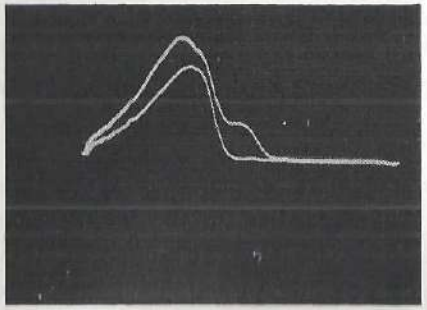
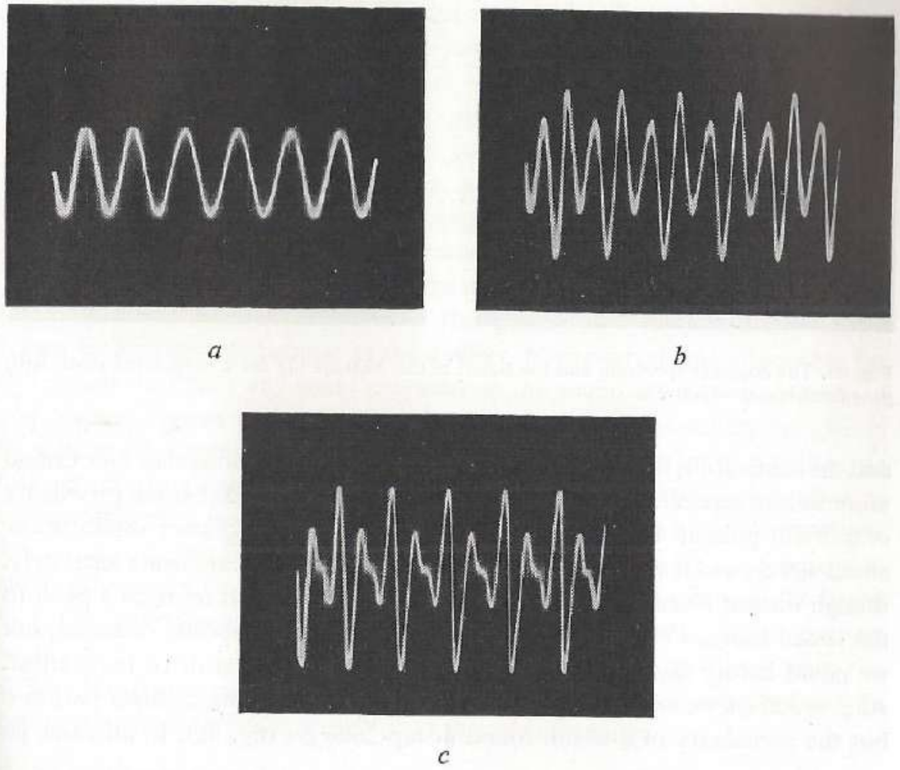


Fig. 82. The cochlear spectrum for a pure tone of 2000 c/s amplitude modulated 100% with a pure tone of 1000 c/s, compared with that for the unmodulated pure tone of 2000 c/s.

Let us see what happens in our model when q is varied. We started with a large value of q, where it is known that no residue tone can be heard. Figure 82 shows us the envelope of the cochlear partition for a 100% amplitude-modulated signal with $p = 2000$ c/s and $q = 1000$ c/s, compared with the unmodulated signal of 2000 c/s. Figures 83(*a*), (*b*), (*c*) show the signal at the 1000-c/s, 2000-c/s and 3000-c/s taps respectively. Changing the frequency of q a little bit gives beats of the same type as described in IV.2.1.2. These can be seen in fig. 84, which gives two different phases of the signal at tap 2000 c/s. We decreased q continuously from 1000 c/s to 500 c/s and heard the difference tone increase



a

b

c

Fig. 83. The signals (*a*) at tap 1000 c/s, (*b*) at tap 2000 c/s, (*c*) at tap 3000 c/s for the same signal as for fig. 82.

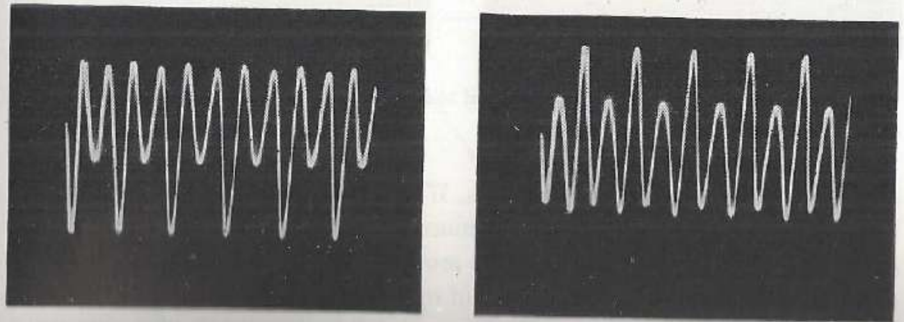


Fig. 84. The signals at the 2000-c/s tap for a modulated signal with $p = 2000$ c/s, $q \approx 1000$ c/s, at two different times.

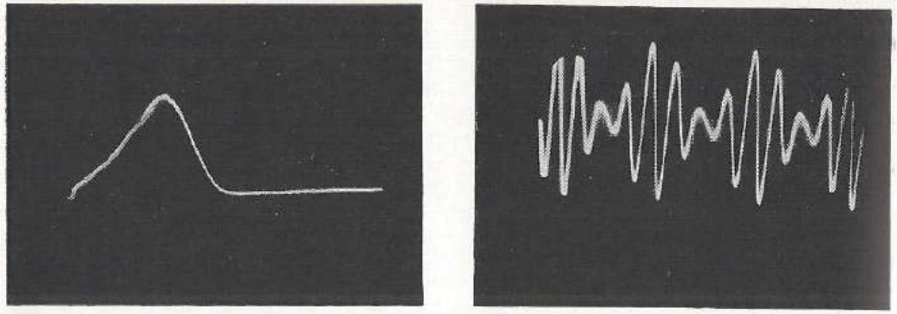


Fig. 85. The cochlear spectrum and the signal at the 2000-c/s tap for a modulated signal with $p = 2000$ c/s, $q = 500$ c/s.

and the summation tone decrease. Below about 800 c/s the difference tone can no more be seen separately on the cochlear partition (see fig. 85) but the periodicity of q is still present. If q is decreased further, we heard a grating sound below about 400 c/s and it was difficult to distinguish the three components separately, though trained listeners were able to do so. It was difficult to asign a pitch to the sound heard. Changing q changed the pitch in the opposite direction, but we could hardly say if this was due to the difference tone or to the q effect. At $q = 200$ c/s we see mainly the envelope of 2000 c/s at the cochlear partition but the periodicity of q is still found at tap 2000 c/s (fig. 86). In all cases no signal could be seen at the taps q c/s. If p was modulated by a square-wave instead of a sine-wave it was even more difficult to hear the residue tone, especially when the periodicity of the modulating signal was varied, although this periodicity could be seen clearly in the signals at the individual taps.

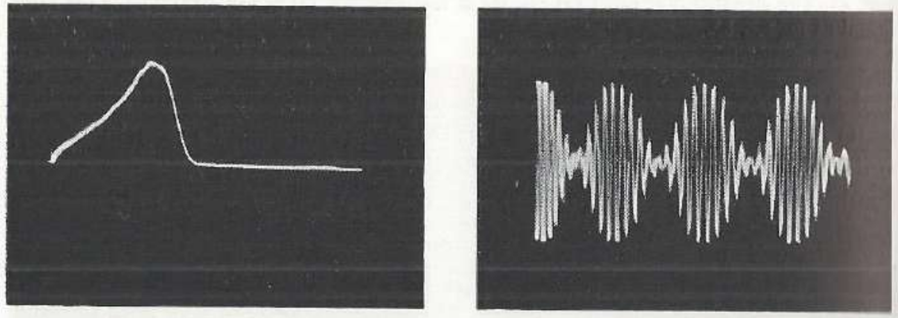


Fig. 86. The cochlear spectrum and the signal at the 2000-c/s tap for a modulated signal with $p = 2000$ c/s, $q = 200$ c/s.

If the carrier frequency and the modulation frequency of a sine wave modulated with a sine wave differ by less than an octave, the three Fourier

components can be heard separately and can be seen separated on the cochlear partition. Moreover, correlation measurements will detect them as well as any beats (figs 82, 83, 84). If the carrier frequency is about four or more times higher than the modulation frequency, place measurements will not be able to detect the components. With constant sounds we hear a rather sharp timbre with a tonal character, and, of course, we conclude that this tonal character is caused by the periodicity in the signal as it can be found on the basilar membrane and can be detected by correlation measurements (figs 85 and 86). This conclusion is sustained if we change the carrier frequency. But if we change the modulation frequency the idea of the measurement of periodicity can no longer be maintained, because of the q effect. Moreover, it was impossible for the author, to detect any tonal character in the sound when q was decreased continuously from a high value, in spite of the fact that periodicity can clearly be seen in the signal. Perhaps this depends on the experiment or whether the test person has a linear or a polar ear. The changes of q may give confusion, because different components of the signal are changing into different directions while changing the periodicity of other residue signals causes components to change frequency into the same direction. The theory that pitch can be heard by correlation measurements giving the periodicity of a signal, which gives an explanation of most hearing phenomena, seems not to be able to explain the q effect. Further investigations with the aid of our model will have to be made before we can get a better insight into this phenomenon.

IV.2.1.6. *Speech sounds*

Other sounds having a tonal character due to the residue can be found

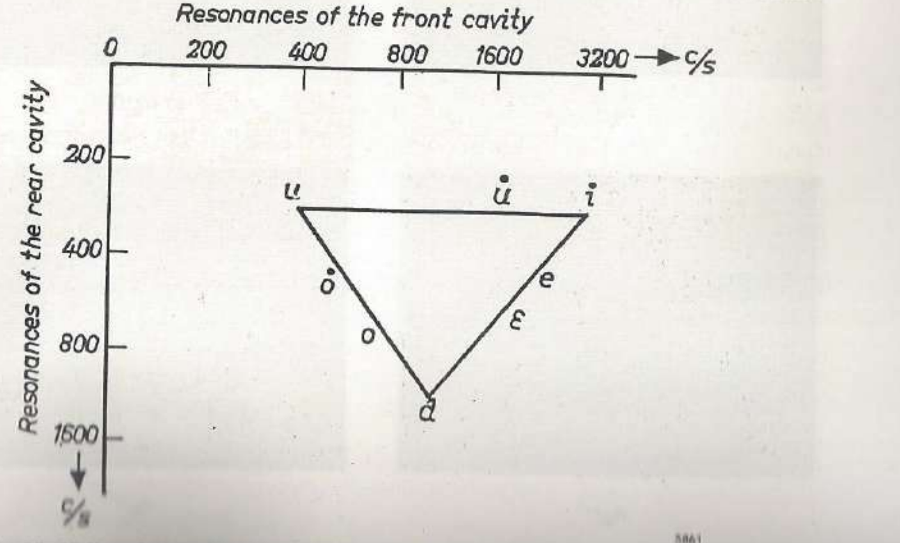
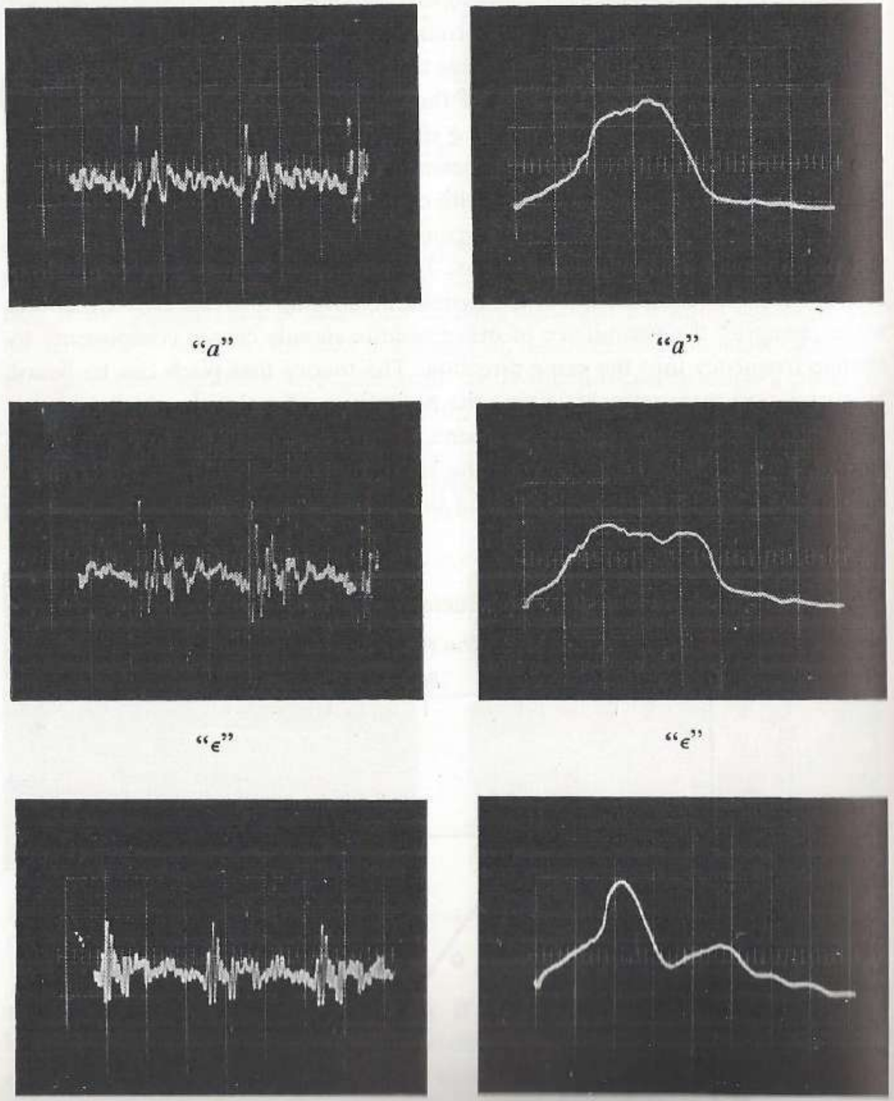


Fig. 87. Hellwag's triangle in a coördinate system indicating the main formants.

among the speech sounds, because their fundamentals are usually very faint or even missing, as in telephony. This pitch is quite clear, although sometimes it may be difficult to conclude in which octave the tone is. Since we can only study more or less stationary signals we will restrict ourselves to some Dutch vowels, taking *a, ε, e, i, ü, u, ö, o* in that order, because they are arranged in this sequence in Hellwag's triangle (fig. 87). All the speech sounds shown in this chapter have been studied assuming that the middle-ear filter has no cut-off. These vowels were spoken by a male voice with a pitch of about 100 c/s. Figure 88 shows the oscillograms of these sounds together with their cochlear spectra. We see that the fundamental is hardly visible in most cases. The first overtone

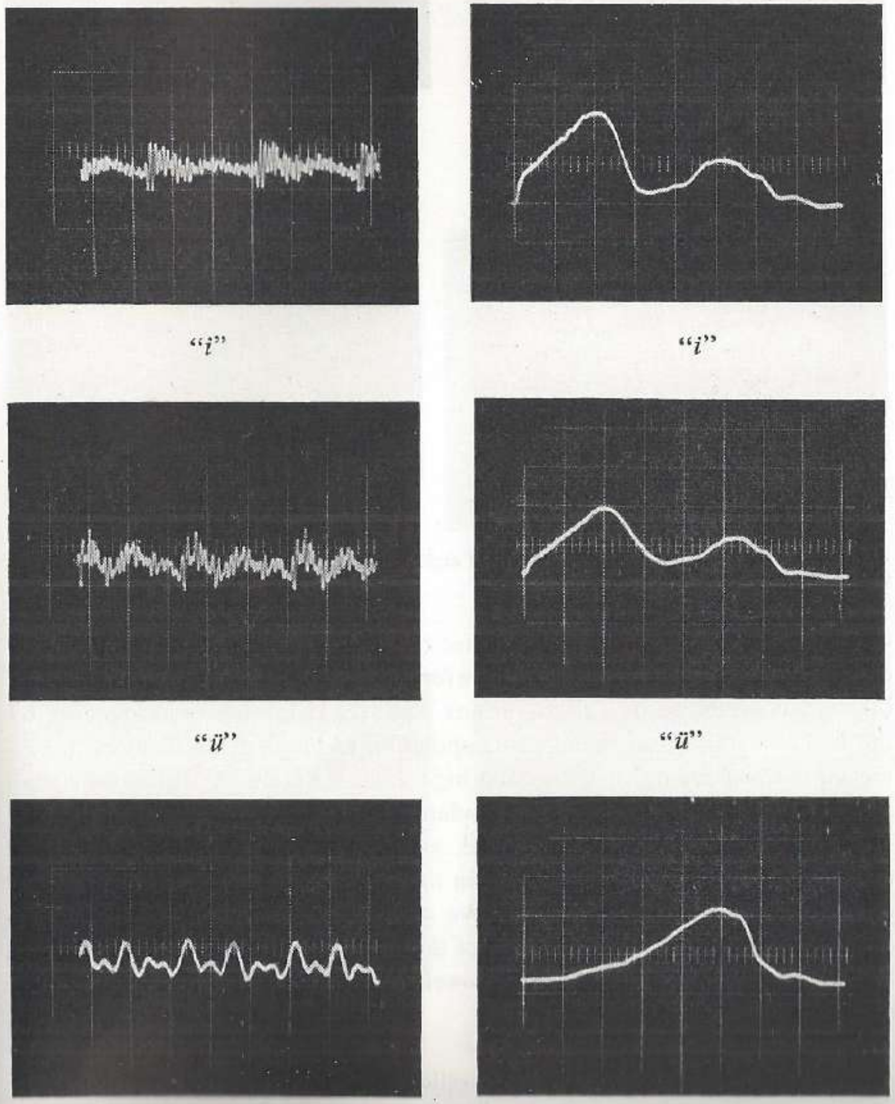


"*a*" "*a*"

"*ε*" "*ε*"

"*e*" "*e*"

Fig. 88. Oscillograms and cochlear spectra of eight Dutch vowels spoken by one male speaker with a pitch of about 100 c/s.

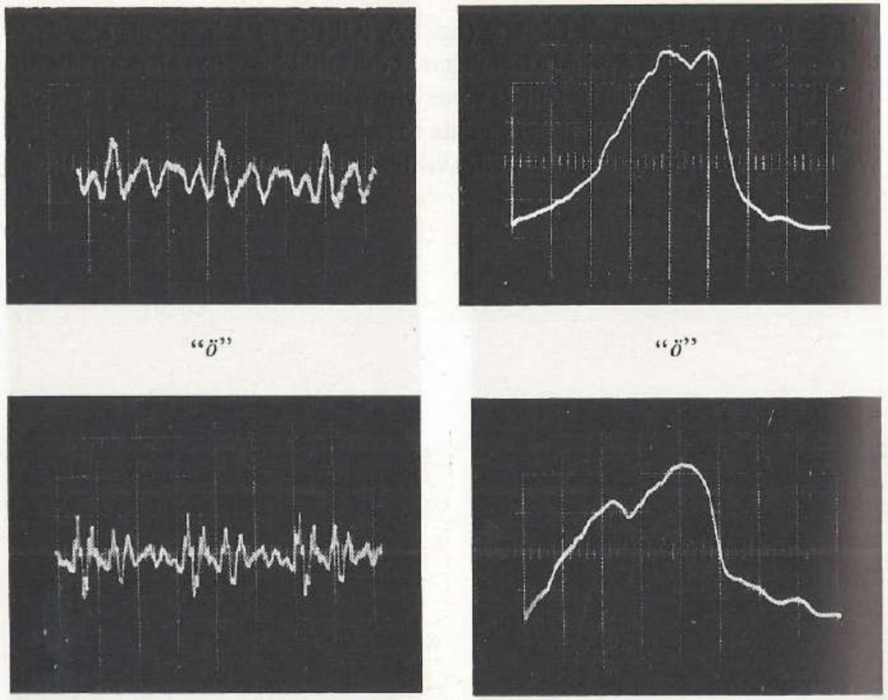


"*i*" "*i*"

"*ü*" "*ü*"

"*u*" "*u*"

Fig. 88. Oscillograms and cochlear spectra of eight Dutch vowels spoken by one male speaker with a pitch of about 100 c/s.



"ö" "ö"

"o" "o"

Fig. 88. Oscillograms and cochlear spectra of eight Dutch vowels spoken by one male speaker with a pitch of about 100 c/s.

can sometimes be seen, but the higher overtones are far more pronounced, combined in one or two clearly visible formants. Figure 89(*a*), (*b*), (*c*) shows us the signals produced by "*a*" at various taps: (*a*) at the tap corresponding to the fundamental, (*b*) at the tap corresponding to the first big formant, (*c*) at the tap corresponding to the second big formant. Figure 89(*d*) gives the signal produced by "*e*" at the tap of the fundamental, (*e*) gives the signal at the tap of the first big formant of this vowel, and (*f*) the signal at the second big formant. The ratio of the amplitudes in the latter figure have been changed in order to make the pictures clearer. We see that the periodicity of the signal can be found at all the taps. Because of the analysis made by the inner ear, the high-frequency information of the vowels can be seen clearly in the higher formants.

What happens if a vowel is sung?

A male voice sung the "*i*" and the oscillograms as well as the corresponding envelope curves on the cochlear partition can be seen in the next figure. Figure 90(*a*) gives the "*i*" sung with a periodicity of (*a*) 100 c/s (*G*), (*b*) 123 c/s (*B*), (*c*) 147 c/s (*d*), (*d*) 196 c/s (*g*), (*e*) 247 c/s (*b*), (*f*) 294 c/s (*d'*), and (*g*) 392 c/s (*g'*).

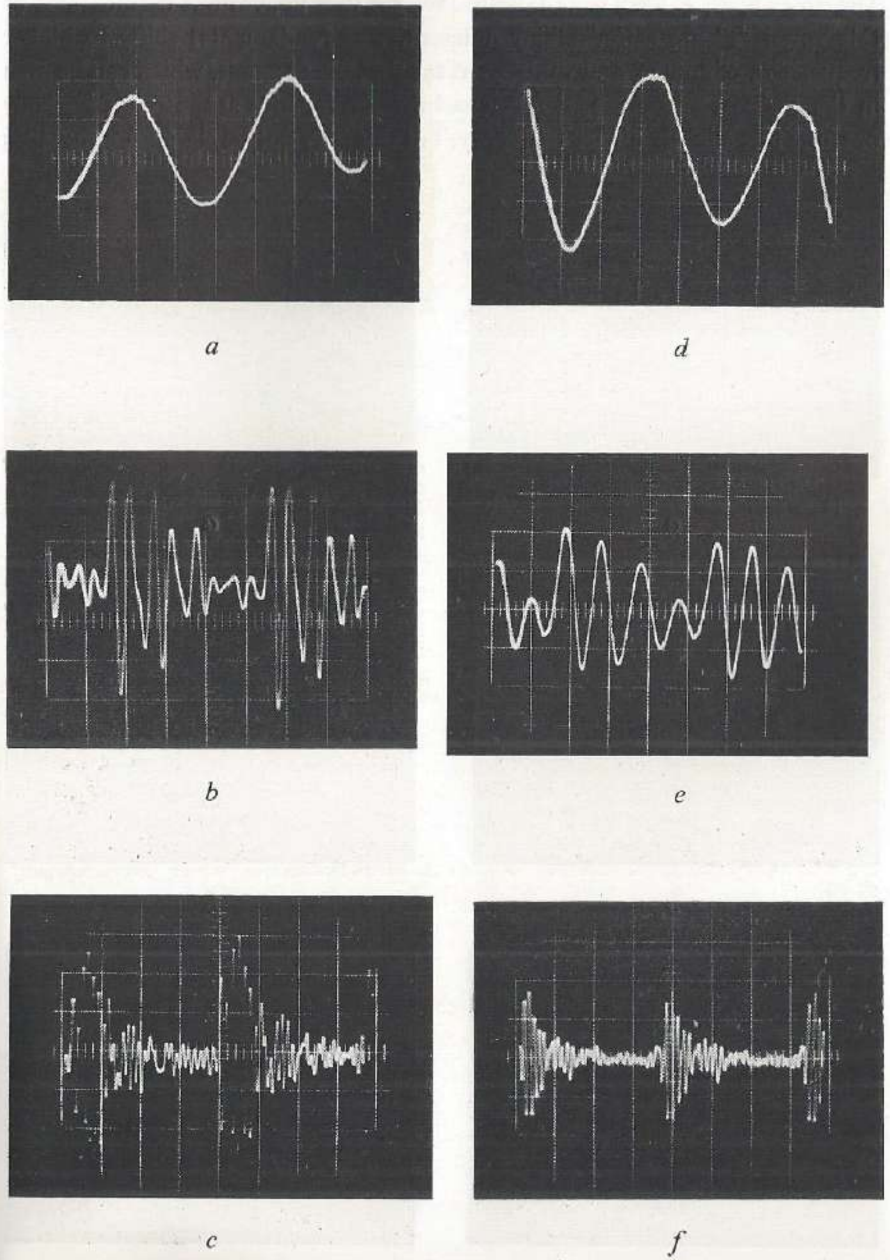
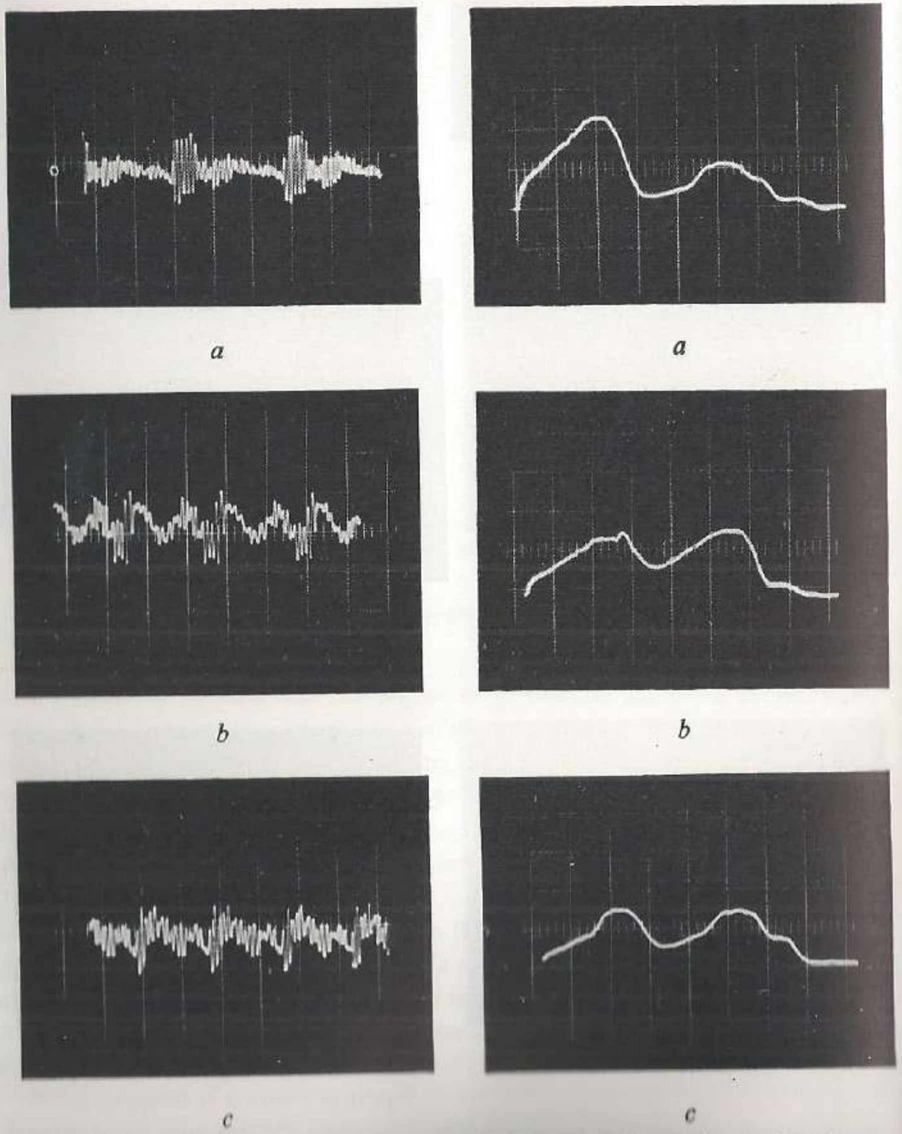


Fig. 89. Signals found at different taps for the vowel "*a*".
(*a*) At the tap corresponding to its fundamental
(*b*) at the tap corresponding to its first big formant
(*c*) at the tap corresponding to its second big formant.
(*d*), (*e*), (*f*), as (*a*), (*b*), (*c*) for the vowel "*e*".

The notes *b*, *d'*, *g'* were sung falsetto. We see that the various oscillograms of this vowel "*i*" are astonishingly different. The fundamental shifts to higher frequencies, of course, and vanishes in the first big formant, which can be seen in the cochlear spectra. This formant, however, remains at the same frequency or shifts to a slightly higher frequency, but this may not be significant, because

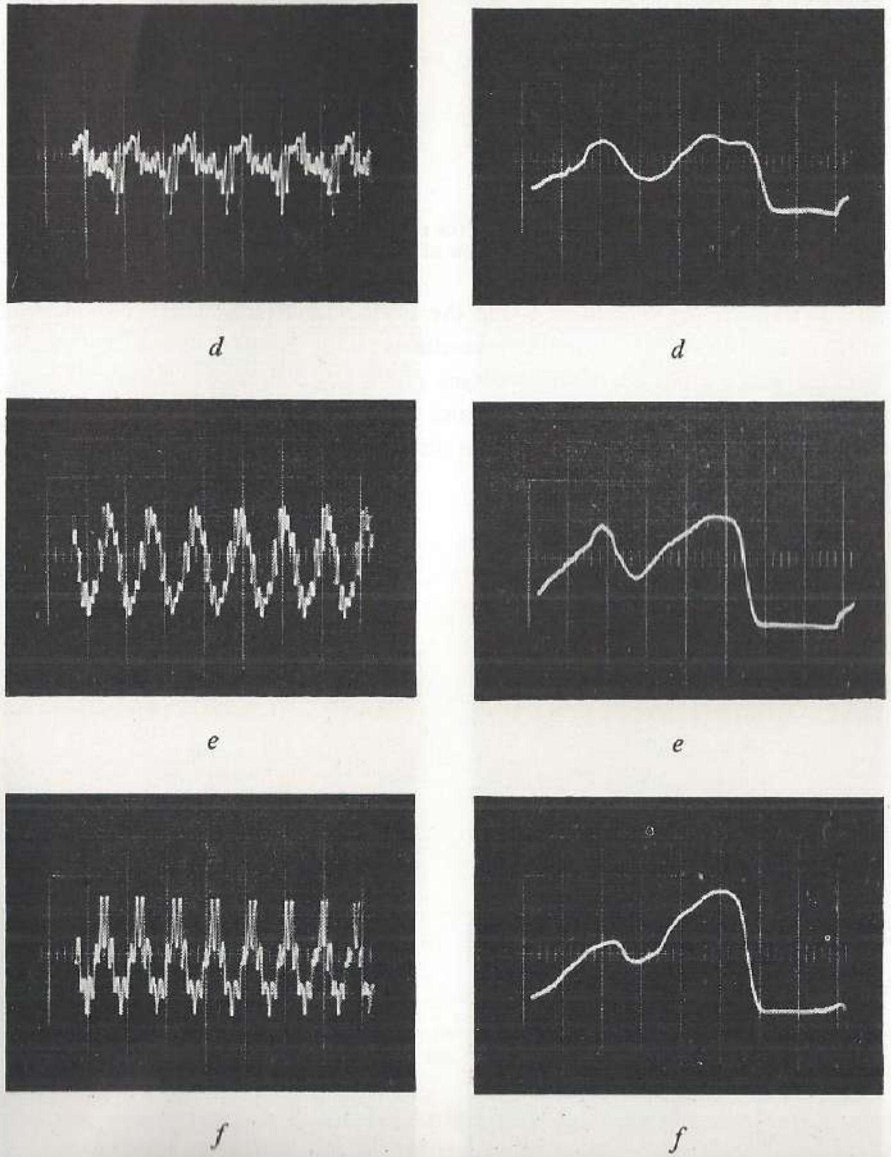

a *a*

b *b*

c *c*

Fig. 90. Oscillograms and cochlear spectra for the vowel "*i*" sung by a male voice.
(*a*) with a pitch of 100 c/s — *G*
(*b*) with a pitch of 123 c/s — *B*
(*c*) with a pitch of 147 c/s — *d*

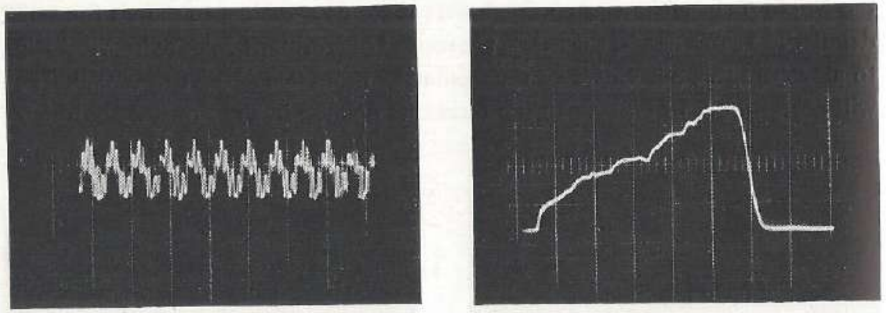
the whole picture changes so much that it seems senseless to search for small details. The same can be said from the second big formant. We are here referring to areas of large amplitude of the basilar membrane as "big formants". They will correspond, of course, to the formants defined in the Fourier analysis of


d *d*

e *e*

f *f*

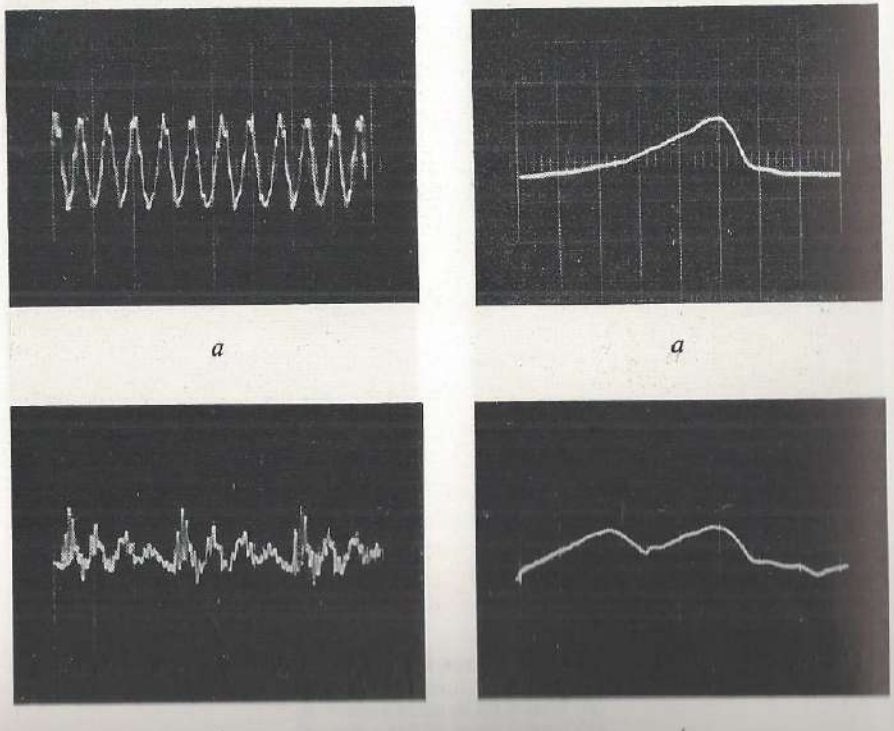
Fig. 90. Oscillograms and cochlear spectra for the vowel "*i*" sung by a male voice.
(*d*) with a pitch of 196 c/s — *g*
(*e*) with a pitch of 247 c/s — *b*
(*f*) with a pitch of 294 c/s — *d'*



g *g*

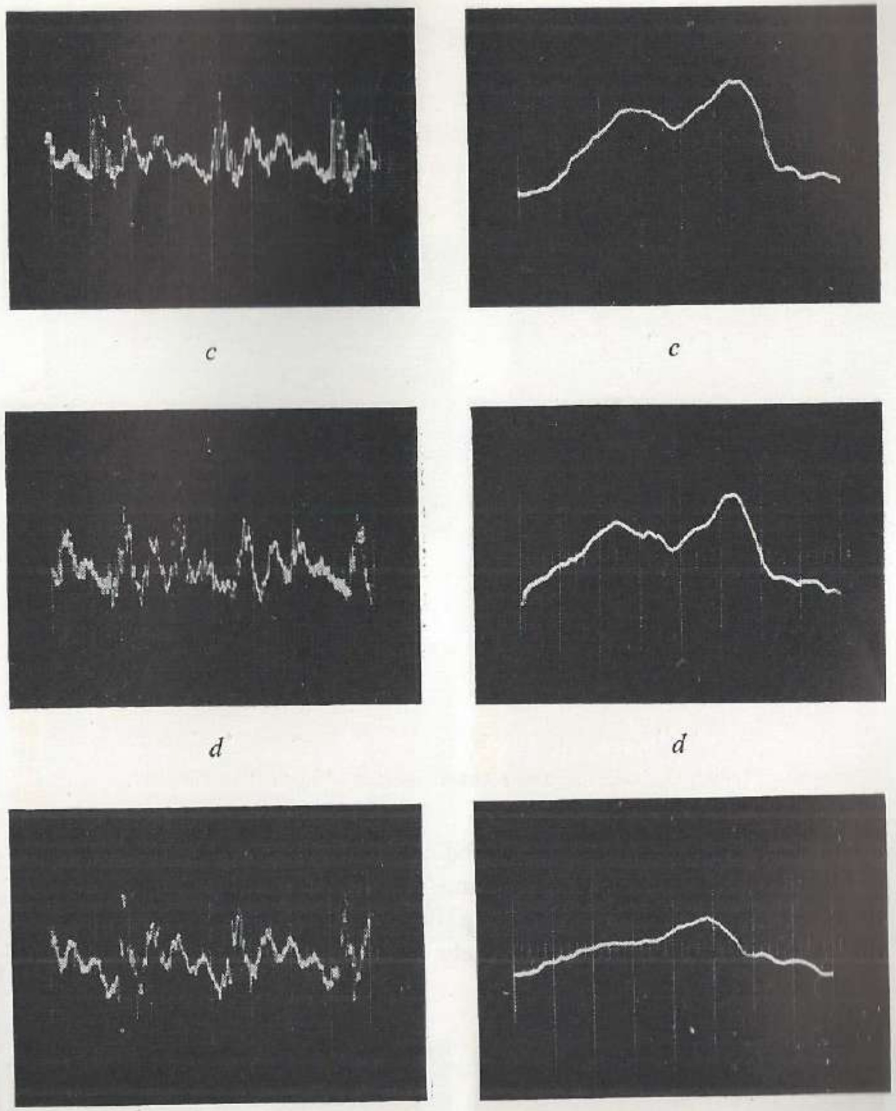
Fig. 90. Oscillograms and cochlear spectra for the vowel "*i*" sung by a male voice. (*g*) with a pitch of 392 c/s — *g*′.

speech sounds. Another filter giving the Fourier analysis, will perhaps reveal more of the behaviour of the formants during singing, but it seems improbable that the exact situation of the formant plays any role in vowel recognition. Moreover, if we look at the shape and broadness of these formants on the cochlear partition we again see large differences from note to note.



a *a*

b *b*



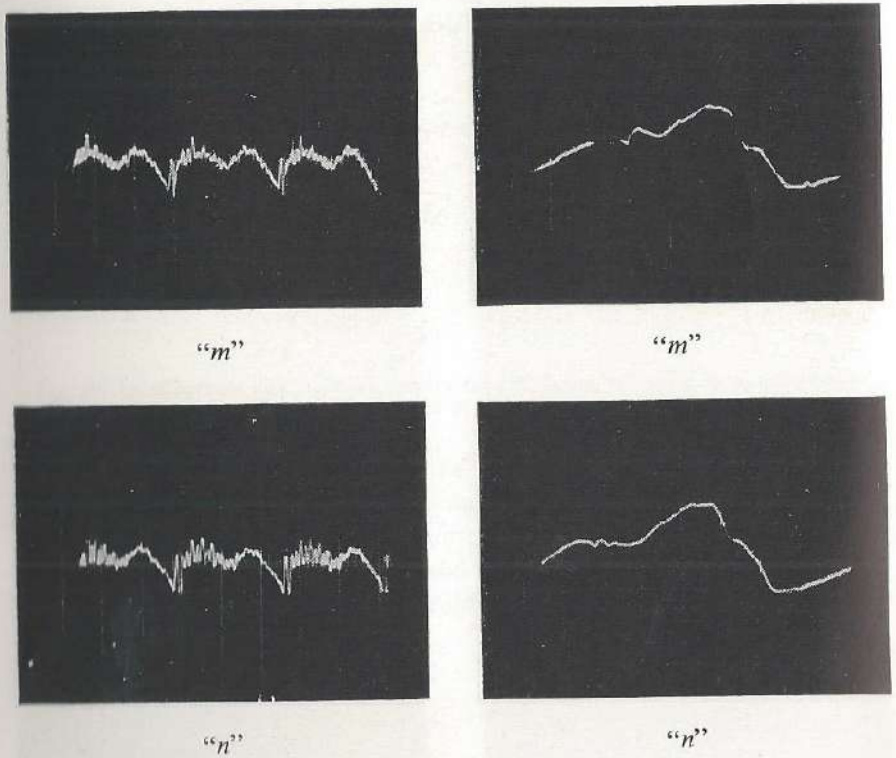
c *c*

d *d*

e *e*

Fig. 91. Oscillograms and cochlear spectra for the vowel "*e*" spoken by five different male speakers. The first one with a pitch of 200 c/s, the others with a pitch of 100 c/s.

The oscillograms and the cochlear spectra for the vowel "*e*" spoken with a fundamental of 100 c/s by five different male speakers are shown in fig. 91. Figure 92 gives an "*m*" and "*n*" spoken by a male speaker with a periodicity of 100 c/s. Both the oscillograms and the cochlear spectra show only slight differences. The cochlear spectra of an "*s*" and an "*f*" spoken by the same



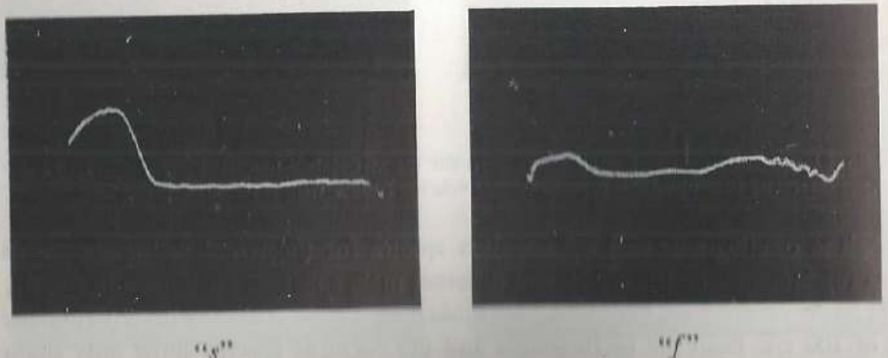
"*m*" "*m*"

"*n*" "*n*"

Fig. 92. Oscillograms and cochlear spectra of an "*m*" and an "*n*".

speaker are shown in fig. 93. It will be seen that the "*f*" has more low tones.

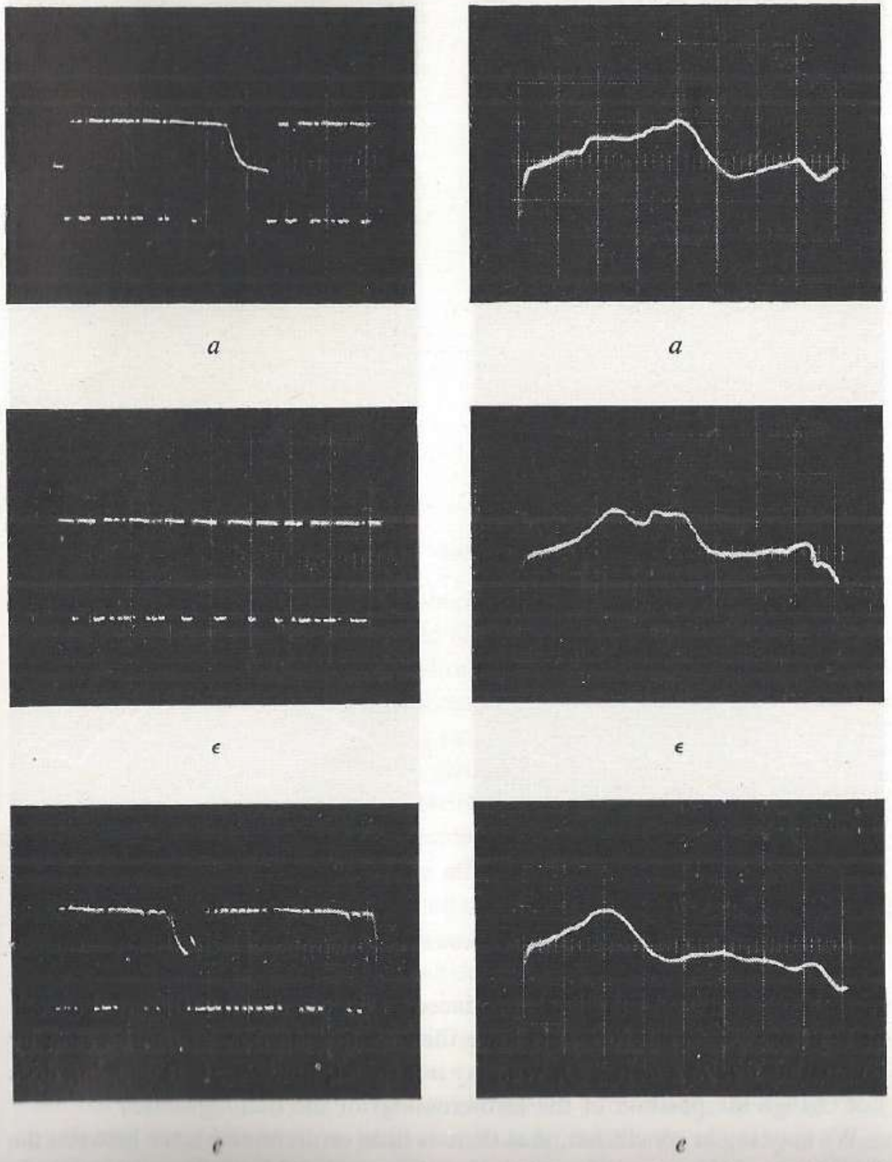
Licklider and Pollack [15]) did some experiments on the intelligibility of distorted speech and found, among other things, that speech which was differentiated and afterwards infinitely clipped retained an intelligibility of



"*s*" "*f*"

Fig. 93. Cochlear spectra of an "*s*" (left) and an "*f*" (right).

97·9%. Figure 94 shows the oscillograms and the envelopes of the cochlear partition for the vowels *a*, *ε*, *e*, *i*, *ü*, *u*, *ö*, *o* spoken by a male speaker, which have been treated in this fashion. The resemblance of these envelopes with those of the undistorted speech, especially as regards the formants, is rather surprising, although the distorted speech has more overtones, of course. The

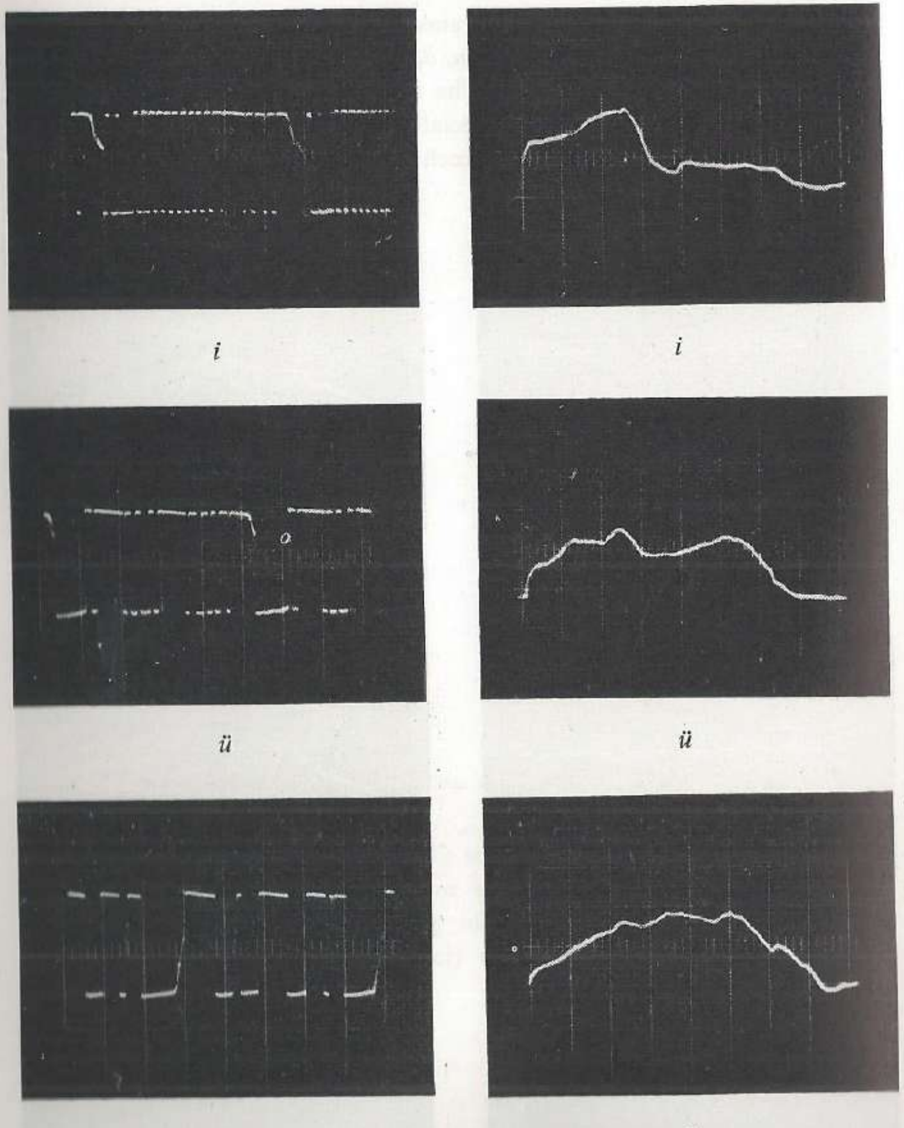


a *a*

ε *ε*

e *e*

Fig. 94. Oscillograms and cochlear spectra of vowels which have been differentiated ond clipped.



i *i*

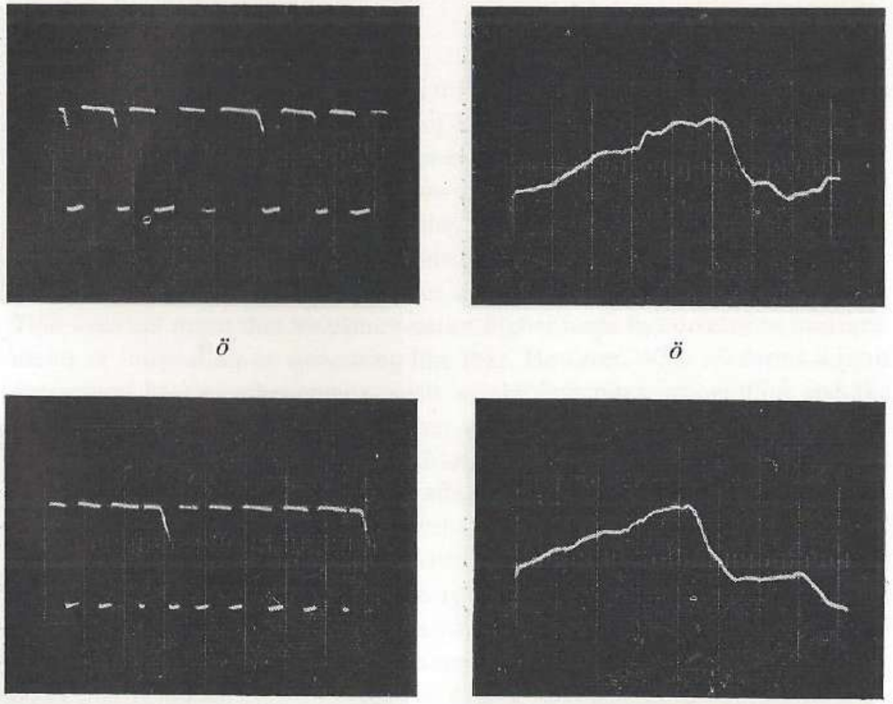
ü *ü*

u *u*

Fig. 94. Oscillograms and cochlear spectra of vowels which have been differentiated and clipped.

resemblance between the signals produced by distorted and undistorted speech at the taps where the formants have their centre, is poor, as can be seen by comparing fig. 95 and fig. 89. We may not forget, however, that clipping does not change the position of the zero-crossings of the oscillograms.

We may say in conclusion, that there is little or no resemblance between the oscillograms of one vowel spoken by different speakers, or even sung by the



ö *ö*

o *o*

Fig. 94. Oscillograms and cochlear spectra of vowels which have been differentiated and clipped.

same person at different pitches, or between the oscillograms of normal and distorted speech. The same can be said of the signals at the taps of the cochlear partition corresponding to high amplitudes. On the other hand, the cochlear spectra of one vowel obtained in different ways look like each other, although the relative intensity of the formants can vary considerably.

Two formants are usually clearly visible in the envelope curves of speech sounds on the cochlear partition. Hellwag's triangle can be related to two frequency scales, one giving the resonance frequencies of the rear cavity in our mouth and the throat cavity, and the other giving the resonance frequency of the front cavity in our mouth near the teeth, which is usually smaller (fig. 87). The change of these formant frequencies of the successive vowels in Hellwag's triangle can be clearly seen in the cochlear spectra.

The great differences between the oscillograms of the same vowel spoken by different speakers, or sung with different pitches or clipped, make it pretty certain that speech recognition does not take place directly from the displacement curves at any given tap. The time difference between the zeroes of those signals may carry information, but we see from fig. 94 that the clipping of speech destroys a lot of the high frequency information. Moreover, a considerable

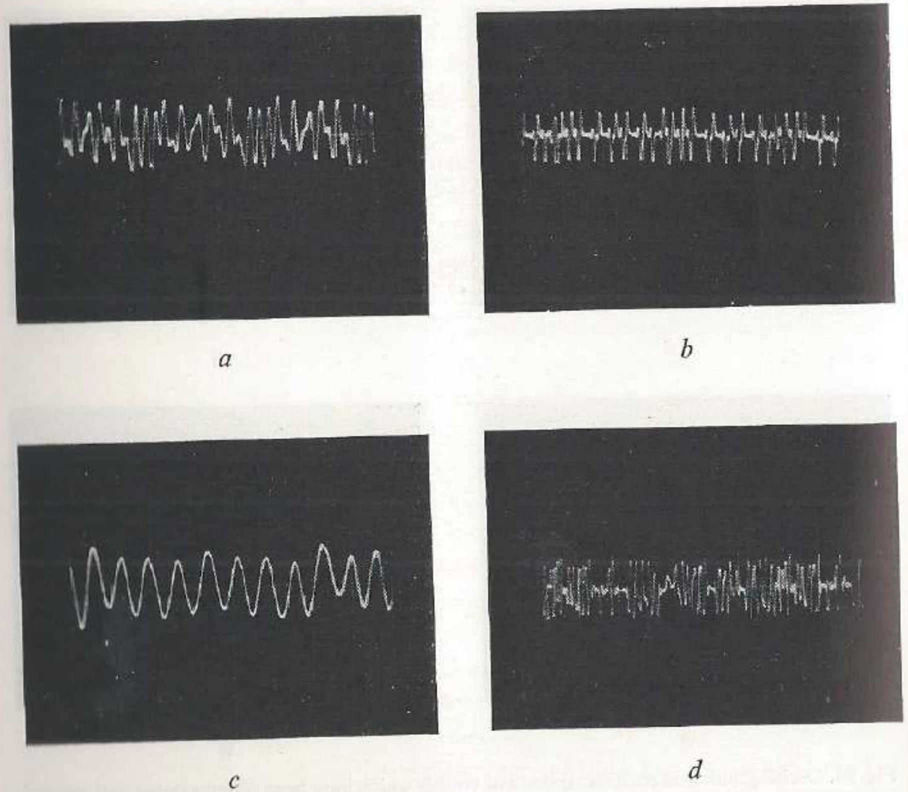


Fig. 95. The signals due to the vowel "*a*" differentiated and clipped,
(*a*) at the tap corresponding to its first big formant
(*b*) at the tap corresponding to its second big formant
(*c*) and (*d*) as (*a*) and (*b*) for the vowel "*e*".

phase change between the components of a signal can hardly be heard, although it causes a large change in the pattern of zeroes. On the other hand, the resemblance between the cochlear spectra for the same vowel produced in these different manners, suggests that the recognition of vowels is a question of timbre, and possibly occurs by place detection. The latter is supported by the fact that we can understand whispered speech, which has the same formants as normal speech. Each vowel has something characteristic in its envelope curve on the cochlear partition. It is well known, and can be seen in the figures that they overlap each other, but the combination with the neighbouring speech sounds doubtless aids us in understanding the right word. The fricatives may also be recognised from their formants (fig. 93). It was difficult to study the plosives with our model. The recognition of these sounds might take place by the type of onset or offset they form for the longer sounds coming after or before.

IV.3. Pitch and timbre

On the basis of the above evidence, it may plausibly be assumed that we hear pitch by measuring the periodicity of a signal or the time interval between marked points by a time-correlation method, probably combined with a place-correlation method, because of the low maximum pulse rate in one nerve, the irregular pulse succession, and because the periodicity at any one place may give the wrong pitch. The synchronism between the signal and the pulse succession in a group of nerve fibres ceases at frequencies above 4000 c/s. That does not mean that we cannot detect higher tones by correlation measurements or integration or something like that. However, 4000 c/s forms a limit for several hearing phenomena, such as absolute pitch recognition and the pitch of musical instruments, so that we may conclude that periodicity is important and simplifies pitch recognition. The only phenomenon which cannot be explained in this context is the *q* effect for residue tones.

Timbre, the typical characteristic of a sound, may be recognised by place detection. Although the cochlear partition is a rough filter, different sounds with different timbres had their own typical cochlear spectra. It appears not to be necessary for the place of formants to be absolutely defined. Vowels from different dialects have their own characters but can be recognized by the listener. The place detection may be refined by different mechanisms. In the first place, we must not forget that the envelope curves we measured are those of the whole cochlear partition. At least for higher frequencies, the different parts of the cochlear partition do not vibrate in phase, the different types of hair cells are sensitive to different motions of the basilar membrane, and some selectivity magnification seems to take place in higher neurons, giving a frequency-place relation in the auditory nerve. This funnel action or selectivity magnification has been mentioned by Von Békésy [19]) and by Franssen [20]) although it may be less effective than is supposed by the latter. Franssen showed that it was easy for the explanation of some directional-hearing phenomena to have place shifts corresponding to frequency shifts. He succeeded in constructing an electronic model for this selectivity magnification and showed that this same circuit could also be used in a modified form for recognizing the direction from which a sound is coming and for stereophonic listening. Place correlation and time integration measurements were indispensable for this circuit.

A pure tone may thus be recognized by periodicity as well as place detection. That suggests that a pure tone also has a timbre, and indeed low tones sound like an "*u*", and high tones more like an "*i*", as was already mentioned by Lachmund in 1921 [21]). The selectivity magnification will, of course, take time. That means that the beginning and end of the signal are measured everywhere in the nerve and on the cortex. This is very important, for they carry a lot of information, especially about the direction from which a sound is reaching our both ears.

It seems plausible on geometrical grounds that place detection uses the inner hair cells (see figs 3 and 96), although we know that they play a role in loudness detection at least for higher intensities. The combination of outer hair cells along the spiral fibres may be important for the place-correlation measurements, although it seems more probable that these measurements occur in the higher synapses. The long spiral fibres with their many connections to the outer hair cells may be used in loudness detection 22). But we may not say that the inner hair cells, from which only one or two are connected to a radial fibre, are used only for pitch recognition and the outer ones only for loudness recognition, for it appears probable that both types play a role in both functions. This may be related to the fact, that there are two types of outer and two types of inner hair cells 23).

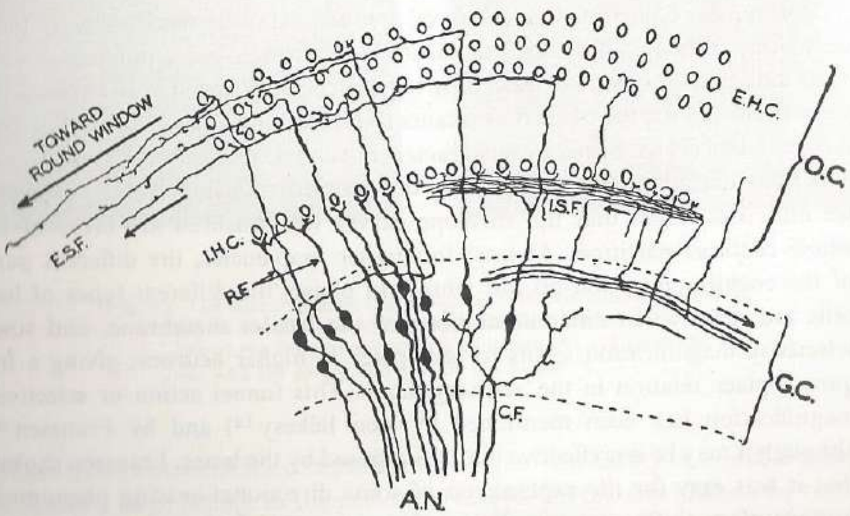


Fig. 96. Diagram of innervation of the organ of Corti.
(O.C.) Organ of Corti; (E.H.C.) external hair cells; (E.S.F.) external spiral fibres, each innervating many external hair cells; (I.S.F.) internal spiral fibres, of unknown function; (I.H.C.) internal hair cells; (R.F.) radial fibres, each innervating one or two internal hair cells; (G.C.) ganglion of Corti; arrows show the direction of the fibres away from their cell bodies; (C.F.) centrifugal fibres of unknown function; (A.N.) auditory nerve.
After Lorente de Nó.

Is place detection absolutely necessary? People with an absolute pitch may be divided into two categories 16): the linear type, who can analyse chords and distinguish musical intervals, with an error not exceeding a semi-tone, and the polar type, who cannot analyse chords and who never make errors of a tone or a semi-tone in a musical interval, but of an octave or a fifth. We might assume that the first type uses a place mechanism and the second type a frequency mechanism. But above 4000 c/s, where no synchronism between the signal and the nerve pulses is possible, absolute pitch seems to be non-existent. Also the residue tone can no longer be heard when the frequency of the components is near or above 4000 c/s 29). Moreover, no one wants musical instruments having a fundamental higher than 4000 c/s. For most of the instruments this tone is the limit. It seems plausible that linear ears recognize pitch by place detection, while polar ears do it from the periodicity. The parrot can distinguish speech sounds, but it seems improbable that place detection plays a large role in its hearing mechanism with a cochlea only 3 mm long. It seems plausible to suppose that our cochlea has been shaped accomodate to a larger number of receptors, so that our detection possibilities could be magnified, and that our ears then learned to use the resulting relation between frequency and place, to refine our perception.

IV.4. Loudness and nerve-deafness

Not much is known about loudness detection. Since our ear can stand amplitudes of up to 10^6 times those at threshold level, some compression is probably used in the detecting mechanism. A considerable compression is already provided by the middle-ear muscles, without which the dynamic range of our ear is only 30 to 40 dB 24). The interaction of the outer hair cells connected to one spiral fibre may also cause some automatic volume control by inhibition 22). For very low intensities the number of nerve pulses is so small that the chance of interactions is very small too, so that the variation in loudness for a certain variation in amplitude is much larger than for high intensities. This is also true of amplifiers with an automatic volume control: all feedback mechanisms used for this purpose must be non-linear systems. The fact that ears with cochlear lesions show recruitment supports the suggestion that we have such a volume-control system in the cochlea. Many explanations of this phenomenon have recently been put forward. Most of them are based upon the assumption that the excited area of the basilar membrane is small for low intensities, so that the number of recepting organs left in function by the lesion is too small to give a sensation, and the ear is deaf. For high intensities, however, this area is much broader and the number of excited receptors will be practically as large as in normal ears, so that the ear is not deaf any more. However, this explanation can never cope with the phenomenon of hyperrecruitment, which gives a higher loudness sensation for high intensities than in normal ears. This fact shows clearly that we are dealing with a defective automatic volume control. For low intensities the number of intact receptors is too small to detect the faint signal among the noise by place-correlation measurements, and the ear is deaf. For high intensities this detection is simple but the output is too high because of the lack of feedback. Ears suffering from Menière's disease have defective outer and inner hair cells equally divided over the whole length of the organ of Corti. Although the detection of loudness seems to be taken over by the inner hair cells for high intensities we may not explain recruitment by the fact that cochlear lesions sometimes attack the outer hair cells and not the inner ones, for Menière's disease is generally accompanied by recruitment too. Moreover, this would not explain hyperrecruitment. The hearing threshold is not influenced by cutting away two thirds of the cochlear nerve 25)). The remaining fibres probably still cover the whole organ of Corti which may be another proof that detection, or rather correlation measurement, occurs in the peripheral regions. No recruitment can be found in this case, but discrimination is poor and persons with more central lesions also show a poor speech comprehension 26)27)). Too much of the information is lost in this case, although the whole organ of Corti may be functioning quite normally. Cochlear lesions usually give a higher threshold and recruitment, but a rather good speech comprehension 28)). The information, although sometimes from a part of the cochlea, can be handled in the proper way. The function of Rasmussen's bundles, consisting of fibres descending from central regions to the cochlea, is not yet clear. That they have to do with the feedback mechanism is probable. Discrimination, the funnel action, analysis and directivity indication will occur at synapses of the second or higher order and on the cortex, and assimilation of the information is a task for the brains, of which we still know practically nothing.

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V. CONCLUSIONS

In spite of the numerous data which are available in the field of hearing, as we mentioned already in the first chapter, it is impossible at this moment to give a complete theory of human hearing: in fact, the operation of most of the auditory system is still in doubt. The investigations with our model may have yielded good results in some essential items, but some new questions have also added to the long row of existing ones.

It therefore seems to be desirable to give a short review of the work in order to mark the point we have reached. Let us follow the auditory signal on its way from the air to the cortex.

We have seen that the auricle is not much use for human hearing. The external auditory meatus and the middle ear conduct the sound to the receiving organ, the inner ear, which is situated relatively deep in the head. Moreover, the auditory meatus protects the eardrum and the middle ear against damage. Thanks to the small cross-section of this tube we may assume only one mode of vibration of the air for audible signals.

We accepted Zwislocki's model as giving the best picture of the dynamics of the middle ear, although it may be too simple. Owing to the lack of sufficient data we had one degree of freedom, leaving some doubt to the correctness of the components of our network. We may ask ourselves, for example, if the matching between the air and the inner ear is really so bad, because the input impedance of the ear at the eardrum does show some matching to the air in the middle-frequency range.

In any case we may be sure about the following facts:

1. The matching between the air and the ear is enough to avoid appreciable standing waves in the auditory meatus, so that no signals can dominate other ones.
2. The input impedance measured at the eardrum is a stiffness for low frequencies and a stiffness parallel to a mass for high frequencies. In the middle-frequency range this impedance will be determined by damped resonances and anti-resonances.
3. The displacement of the stapes as function of the frequency with a constant pressure on the eardrum gives a rather flat curve up to a certain frequency, above which it falls by 24 dB/oct. The tilting point will probably be situated in the frequency range 2500-5000 c/s.

From our considerations of the dynamics of the inner ear we came to the conclusion that:

4. Only a small layer of liquid at both sides of the cochlear partition plays a role in its motion.
5. The cochlear partition may be considered as being composed of more or less independent elements coupled to each other by the liquid in those thin

layers. The stiffness coupling of neighbouring elements can be neglected.

6. Von Békésy's paradox is due to the fact that the cochlea contains an excess of liquid outside the thin layers.
7. The development of the cochlea gave room for more receptors in the hearing organ so that we could reach a higher degree of analysis, and a better discrimination, by correlation measurements between those receptors.
8. The construction of the cochlea, consisting of a membrane to which the receptors are coupled, all being surrounded by liquid, follows from the fact that it developed from the saccule.
9. Another construction would not have done, however, because:
   a. A construction with liquid coupling, but with a homogeneous membrane, would have given characteristic frequencies.
   b. A construction without liquid coupling would also have given characteristic frequencies, even with a non-homogeneous membrane (think of a trumpet).
10. One of the consequences of this construction is the place-frequency relationship on the cochlear partition. The displacement of the partition by a pure tone has a maximum, behind which it decreases rapidly and vanishes. This maximum and the vanishing point shift towards the stapes if the tone is raised. It seems plausible that this type of mechanical analysis is used. However, the existance of two types of absolute hearing, and the speech of the parrot, point to the fact that this place-frequency relationship is of secondary importance. We can do without it and the eventual purpose of the development of the cochlea may not have been the creation of this type of analysis. Moreover, if this analysis were absolutely necessary to give our ear the properties which it has, the cochlea, which was developed during a later stage of evolution than the middle ear, would have properties which are not used because of the poor quality of the middle ear.
11. Since an acoustical trauma caused by a pure tone gives the largest hearing loss about half an octave higher, the pitch of a pure tone is probably not determined at the place of maximum activity.
12. The mechanical system of the inner ear has a high degree of damping in order to have short reaction times. This means that the place analysis is poor, but a magnification of this analysis is probably found in the nerves.
13. The maximum amplitude of pure tones on the cochlear partition as a function of frequency is rather constant for a constant displacement of the stapes. That means that these amplitudes are fairly independent of frequency if the pressure on the eardrum is constant below the cut-off frequency of the middle ear.
14. The main reason for the increase of the slope of the threshold in the high-frequency range is to compensate for the middle-ear cut-off. The reason for the slope of the threshold curve in the low-frequency region must be sought in the properties of the nerves. The mechanical system has a flat frequency characteristic here.

15. The difference in bandwidth of the ears of different mammals is mainly caused by a difference in the mechanical properties of the middle ear and inner ear. Their differences in sensitivity and discrimination may be a question of different densities of receptors along the basilar membrane.
16. The fact that the part of the organ of Corti where tones $>$ 5000 c/s are detected is not so easily destroyed by heavy noises may be due to the middle-ear cut-off.
17. Pitch recognition takes place by measuring time intervals between remarkable moments in the signal found at different points along the basilar membrane. We dare not say that pitch recognition takes place by measuring periodicity, for the mathematical periodicity found in the signal at a certain point of the basilar membrane does not always correspond with the heard pitch. The assumption of place and time correlation measurements in groups of hair cells helps to explain some phenomena. Moreover, these correlation measurements would enable us to detect signals in noise more easily and give our ear a larger resolving power. It seems probable that the phase at different places of the travelling wave along the cochlea plays a role in pitch hearing. If the cochlea were absent, some complex signals would have been heard with a different pitch.
18. The timbre may be related to the shape of the cochlear spectrum. The recognition of a sound is the recognition of timbre. It is possible that timbre recognition is done by place detection alone, although we believe that it is also possible to do it by other means (think of the parrot).
19. Near the basal side of the cochlear partition all the components of a sound are still present, and nearly in the proper phase (except for the phase change in the middle ear). Transients will form the pulses N_1 and N_2 there, which are useful time-markers for the arrival of the signal in the ear. These time-markers, among others, give the information needed to locate the sound source in space.
20. The subjective intensity of a sound, its loudness, is probably regulated by an automatic volume control, due mainly to the action of the middle-ear muscles, and perhaps partly to an inhibiting mechanism among the hair cells, and feedback by the bundles of Rasmussen.
21. Residuetones and beats of mistuned octaves are not caused by products of distortion.

We may ask ourselves now which are the most urgent problems to be solved in the future. It is clear that in the first place new investigations in the physiological field are needed. Simultaneous recording of pulse volleys in a single fibre or in a bundle of fibres, at different places in and along the auditory nerve for a certain time, may reveal something about the above-mentioned correlation measurements. This should be done with complex sounds too, for example speech sounds and residue tones. It would be interesting to know whether synchronism between the signal and the nerve pulses really stops above 4000 c/s, and what is happening then with the pulse rate in a bundle of fibres. It is important to measure the selectivity magnification along the auditory nerve and the frequency-place relation in the cortex especially in animals with no cochlea or a very short one. But also the middle-ear action should be restudied, especially for frequencies higher than 2000 c/s, if possible. The probability functions of the pure-tone threshold need to be restudied accurately for low, middle, and high frequencies, together with the difference between the monaural and binaural threshold, with tones heard through headphones. And there are still unsolved problems in the phenomenological field, such as the *q* effect and its eventual relation with linear or polar types of hearing. And, of course, our investigations with the models were rather shallow, and we have to go further into the matter. In any case, new techniques are enabling us to penetrate deeper and deeper into the matter, in order to get a better insight into the mechanism of that important and marvellous sense organ, our ear.

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Samenvatting

Het in dit proefschrift beschreven onderzoek had tot doel door combinatie van reeds bekende gegevens uit de anatomie, de physiologie, de dynamica van het oor en de gehoorphenomenologie te komen tot de bouw van een elektrisch model van het gehoororgaan, om daarmede een beter begrip van de werking van ons oor te verkrijgen.

In het eerste hoofdstuk wordt de evolutie van het oor beschreven waarbij speciaal opvalt dat het middenoor eerder is ontstaan dan de cochlea.

Het tweede hoofdstuk behandelt de cochlea. Na een anatomische inleiding wordt de bewegingsvergelijking opgesteld, welke behulpzaam is bij een beschrijving van de physische verschijnselen die in de cochlea plaatsvinden. Zo blijkt het mechanisch gedrag van het cochleair tussenschot bepaald te worden door de mechanische eigenschappen van dit schot en een dunne laag vloeistof aan weerskanten daarvan. De cochlea bevat kennelijk een overmaat vloeistof hetgeen Von Békésy's paradox doet verklaren. De merkwaardige constructie van de cochlea blijkt de enig bruikbare, andere meer voor de hand liggende constructies zouden niet voldoen. De afgeleide bewegingsvergelijking wordt vergeleken met die welke door Zwislocki, Peterson en Bogert, Fletcher en Ranke zijn gegeven. Vervolgens wordt de beschrijving gegeven van het elektrisch model van de cochlea dat wij construeerden met behulp van gegevens, voornamelijk geput uit het werk van Von Békésy. Dit model bestaat uit honderd discrete aan elkaar geschakelde elementen, die ieder een spanning afgeven welke aequivalent is met de uitwijking van het cochleair tussenschot op een met zo'n element corresponderende plaats. Het verschil in topfrequentie tussen naburige elementen bedraagt derhalve een halve toon. De eigenschappen van het model voor sinusvormige signalen alsmede de ingangsimpedantie zijn gegeven.

Het derde hoofdstuk handelt over het middenoor. Nadat weer een anatomische inleiding is gegeven wordt beschreven hoe is gekomen tot de constructie van een elektrisch model, hetwelk in principe gelijk is aan dat van Zwislocki. Er zijn echter nog te weinig mechanische gegevens bekend om tot een bevredigend geheel te komen. Wel vertoont dit model zekere overeenkomsten in zijn eigenschappen met die van het middenoor, doch anderzijds rijst sterke twijfel aan zijn algemene juistheid. Het bleek echter zinloos naar een verbetering te zoeken, aangezien het gedrag van het middenoor voor frequenties boven 2000 Hz nog niet bekend is. Een vergelijking met modellen van andere onderzoekers is gegeven. Aan een discussie over het middenoor is tevens de bespreking van kunstoren gekoppeld. Het belangrijkste dat het onderzoek aan het middenoor heeft opgeleverd is zijn overdrachtskarakteristiek, waarmee bedoeld wordt de uitwijking van het ovale venster bij constante druk op het trommelvlies als functie van de frequentie. Deze karakteristiek verloopt horizontaal tot een frequentie in het middengebied om daarna steil te vallen.

De combinatie middenoor-inwendige oor wordt in het vierde hoofdstuk bestudeerd. Het verloop van de toondrempelcurve kan in zekere mate verklaard worden. De grootste gevoeligheid van het oor in het horizontale gedeelte van de kromme in het middenfrequente gebied wordt bepaald door een ruis, echter niet door die ruis die het gehele mechanische systeem geeft. De helling van de kromme in het lage tonen gebied wordt veroorzaakt door eigenschappen van de gehoorzenuw, die in het hoge tonen gebied hoofdzakelijk door de filterwerking van het middenoor.

Vervolgens wordt de apparatuur beschreven waarmee het cochleair spectrum is gefotografeerd. Opnamen worden getoond van de omhullende van de uitwijking van het cochleair tussenschot bij samengestelde signalen, alsmede die uitwijkingen zelf zoals ze op bepaalde plaatsen langs het tussenschot te zien zijn. Gewerkt werd met zuivere tonen die door andere zuivere tonen of ruis gemaskeerd worden, de sommatie van twee zuivere tonen, wel en niet gefilterde blokvormige signalen, in amplitude gemoduleerde signalen (residu) en spraaksignalen.

Combinatie van alle gegevens uit bovenstaande verkregen leidt tot een discussie waaruit blijkt dat nog geen gesloten gehoortheorie kan worden gegeven, doch dat de juistheid van bepaalde reeds bestaande theorieën valt te betwijfelen. Een gehoortheorie mag niet berusten op vermeende eigenschappen van de cochlea, waarvan geen gebruik kan worden gemaakt gezien de eigenschappen van het middenoor. Wel wordt een mogelijke verklaring gegeven van bepaalde gehoorphenomenen, zoals het waarnemen van toonhoogte, timbre, luidheid en de oorzaak van bepaalde soorten zenuwdoofheid. Bepaalde correlatiemetingen in plaats en tijd tussen de receptoren en tussen de zenuwvezels moeten aanwezig zijn, doch een plaatsdetectiemechanisme, zoals in de zogenaamde plaatstheorieën wordt beschreven, is geen noodzakelijkheid.

In het vijfde hoofdstuk tenslotte zijn die uitkomsten van het onderzoek waaromtrent enige zekerheid bestaat nog eens puntsgewijs bijeengebracht.

STELLINGEN

I

De vermindering van de richtingsgevoeligheid van cardioïde electrostatische microfoons in het gebied van lage tonen moet worden toegeschreven aan de extra fasedraaiing van het geluid die bij lage frequenties in het inwendige van de microfoon optreedt tengevolge van de luchtbeweging in de nauwe spleet tussen de vaste electrode en het membraan.

C. Wansdronk, Proc. 3rd Intern. Congr. Acoustics 638, 1961.

II

De volgens de normalisatievoorschriften gemeten frequentiekarakteristieken van hoortoestellen geven slechts de eigenschappen van deze toestellen onder zeer speciale omstandigheden weer. De invloed van de bevestigingsplaats van deze toestellen op die karakteristieken en het verschil tussen het oor van de patient en het bij de metingen gebruikte kunstoor is echter zo groot, dat met deze gegevens weinig valt te zeggen over de frequentiekarakteristiek die de slechthorende in de praktijk krijgt aangeboden.

C. Wansdronk, J. acoust. Soc. Amer. **31,** 1609-1612, 1959.

III

Bij het zoeken naar de voor een slechthorende gewenste frequentiekarakteristiek van een hoortoestel kan men het beste uitgaan van het spiegelbeeld van de drempelkromme bij een geleidingsgeval en van het spiegelbeeld van de kromme van aangename luidheid bij een perceptiegeval.

IV

Alvorens geluidsoverdragers die een extreem hoog vermogen kunnen afgeven te gaan toepassen op dove kinderen dient men eerst te weten in hoeverre er kans bestaat op beschadiging van het oor of andere organen in het hoofd.

V

De eenheid ,,phon" dient niet meer te worden gebruikt.

VI

De verkaring die Grønlund en Moore geven van de asymmetrie in de hoekverdeling van door ionenbombardement verstoven materiaal bij schuine inval van de ionen is waarschijnlijk niet juist.

F. Grønlund and J. W. Moore, J. chem. Phys. **32,** 1540-1545, 1960.

VII

Het zichtbaar maken van dislocaties door ionenbombardement wordt waarschijnlijk in hoge mate bepaald door de invalsrichting van de ionen.

VIII

De ruis van lineaire vierpolen waarbij een signaal aan de ingang een daarvan lineair afhankelijk signaal aan de uitgang geeft, kan worden geleverd door een ruisspanningsbron en een daarmee gecorreleerde ruisstroombron aan de ingang van dezelfde ruisvrij gedachte vierpool. Dit door Becking, Groendijk en Knol voor electrische vierpolen gegeven theorema kan ook met vrucht worden toegepast op niet electrische zoals electro-akoestische vierpolen.

A. G. Th. Becking, H. Groendijk en K. S. Knol, Philips Res. Rep. **10,** 349-357, 1955.

IX

De officiele invoering van de titel Drs. kan, althans theoretisch, tot gevolg hebben dat men na een promotie de titels Dr.Drs. gaat voeren, hetgeen een tegenspraak inhoudt.

X

Het regeringsbeleid in Nederland dient minder onder invloed te staan van slechts een beperkt belang vertegenwoordigende lichamen.