The Journal of Laryngology and Otology

(*Founded in* 1887 *by* MORELL MACKENZIE *and* NORRIS WOLFENDEN)

February 1953

THE SENSE OF HEARING

By GEORGE WILKINSON (Sheffield)

As soon as one begins to approach the problem of hearing, one becomes aware of the difficulty of actually getting near enough to the essentials to be able to form any rational conception of the process as a whole. The physics of sound are surrounded by a formidable barbed wire fence of mathematical formulae, whilst the histology of the inner ear is extremely complicated and even to the present day, contains some fallacies and uncertainties which confuse the picture. The cochlea is deeply embedded in the hardest bony substance of the body (with the possible exception of dental enamel). The structures it contains are extraordinarily delicate and perishable. It requires the highest degree of technical skill to make it visible under the microscope. One finds that medical students regard the anatomy and physiology of the ear as one of the toughest bones they are given to gnaw, nor can they make sense out of the conflicting views set forth in their textbooks; whilst the general reader, or those interested in the subject from the musical standpoint, do not as a rule succeed in penetrating very far into the jungle.

About 80 years ago, there seemed to be some hope for these earnest seekers. Hermann Helmholtz, one of the greatest physicists and physiologists of his day, published his *Sensations of Tone*, putting forward what is usually known as a Resonance Theory of Hearing, the beauty and simplicity of which made an immediate appeal to readers. He started with the assumption that "the analysis of compound into simple pendular vibrations is an astonishing property of the ear. When we turn to external nature for an analogue of such an analysis we find none but the phenomena of sympathetic resonance". He put forward the view that the basilar membrane was a resonating structure. He recognized that two

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requirements must be satisfied by the set of resonators that he was looking for in the cochlea: (1) they must each be connected with the terminals of the auditory nerve, and (2) they must exhibit progressive differentiation of structure corresponding with the differentiation of function implied by their property of each responding to a different note in the musical scale.

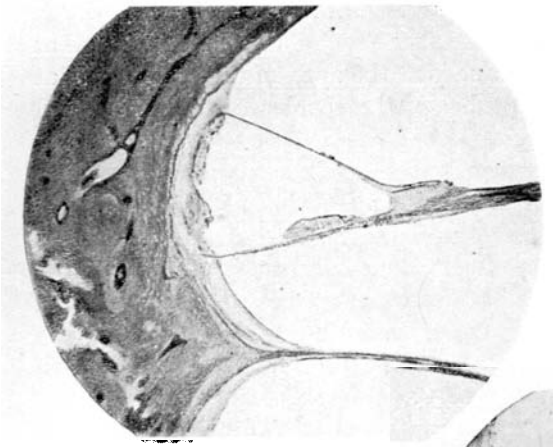
Helmholtz adopted the suggestion of V. Hensen that the resonating elements are the transverse fibres of the basilar membrane. He instances the fact that the basilar membrane breaks up readily transversely, but that its transverse fibres have considerable tenacity, whence he concludes that the membrane is capable of transverse tension, but of no tension in the direction of its length. Each such stretched transverse segment of the basilar membrane would vibrate according to the formula for stretched strings. "If the tension in direction of its length is infinitesimally small in comparison with the tension in direction of the breadth, then the radial fibres of the basilar membrane may be approximately regarded as forming a system of stretched strings; the membranous connection only serving to give a fulcrum to the pressure of the fluid against these strings. In that case the laws of their motion would be the same as if every individual string moved independently of all the others, and obeyed by itself the influence of the periodically alternating pressure of the fluid of the labyrinth contained in the vestibule gallery. Consequently, any exciting tone would set that part of the membrane into sympathetic vibration, for which the proper tone of one of its radial fibres that were stretched and loaded with the various appendages already described corresponds most nearly with the exciting tone; and thence the vibrations will extend with rapidly diminishing strength on to the adjacent parts of the membrane."*

This statement makes it clear that Helmholtz never intended to infer that the individual fibres of the basilar membrane could vibrate independently, though the impossibility of this independent action is often advanced as an objection to the theory. The last sentence of the quotation shows that what Helmholtz pictured was a vibration of transverse *sectors* of the basilar membrane with a maximum intensity of vibration at the mid-point of the sector, and not an independent vibration of individual fibres. The only piece of anatomical evidence which he was in a position to bring forward to show progressive differentiation of the basilar fibres was the measurements of V. Hensen and C. Hasse of the transverse breadth of the membrane at different levels along the cochlear galleries.

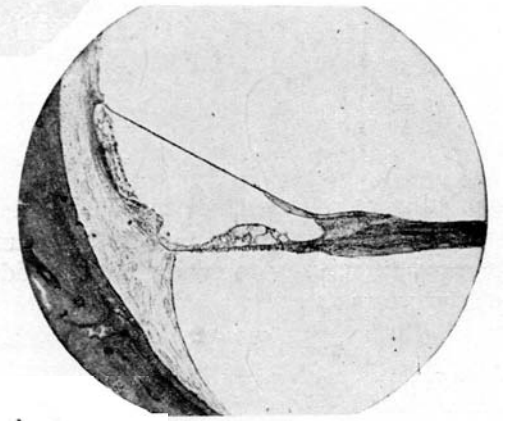
This structure, at its commencement opposite the oval window, is comparatively narrow, and it continually increases in width as it approaches the apex of the cochlea. The figures, as given by Hensen, were 0·041 mm. for the extreme basal end, and 0·495 mm. for the extreme apical portion, that is to say a twelvefold increase. He concludes that the

* "Physiological Causes of Harmony in Music." *Helmholtz's Popular Scientific Lectures*, page 146.

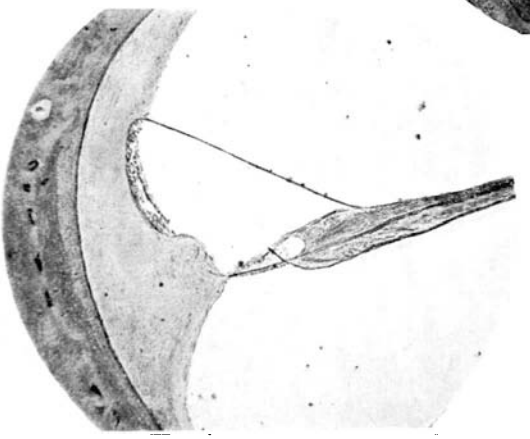
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The Apical Turn
of the Cochlea



The Middle Turn



The Basal Turn

FIG. 1.

Showing the relative bulk and density of the spiral ligament at different levels of the cochlear galleries.

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fibres in tune to resonate to the higher notes of the audible scale must be looked for at the narrow end close to the oval and round windows, whilst those tuned to the deeper notes must be at the broad apical end. Note that the broad end of the basilar membrane is at the apex of the cochlea, i.e. at the narrow end of spirally wound tubes of the cochlea containing it, and vice-versa.

Later anatomists have not confirmed Hensen's measurements. Keith* estimates the increase in width of the basilar membrane as less than threefold (0·17 mm. to 0·4 mm.). Fraser agrees pretty closely with Keith. His figures are 0·16 mm. wide at the vestibular end, and 0·52 mm. near the helicotrema, a 1 to $3\frac{1}{4}$ variation. This represents about an octave and a half, whilst the ratio of 1 to 12 which Helmholtz accepted would give a range of about $3\frac{1}{2}$ octaves. With regard to the other factors—t and m—in the formula for the vibration of stretched strings

$$n = \frac{1}{2l}\sqrt{\frac{t}{m}}$$

l = length of string.
t = tension on the string.
m = mass of unit length of string.
n = number of vibrations per second.

Helmholtz infers that there must be differentiation of the basilar membrane in these respects also, but that anatomical investigation had not advanced sufficiently to enable him to adduce any evidence. It was not until 30 years later that any fresh anatomical facts bearing on the resonance theory were discovered. In 1900 a notable advance was made by Albert A. Gray†, who gave the first adequate description of the spiral ligament. This structure attaches the basilar membrane to the outer wall of the cochlear galleries. It is made up of fine fibres radiating fan-wise from the point of insertion of the basilar membrane and is quite a striking feature in a section of the cochlea and can readily be seen with the naked eye. It is, in fact, one of the most obvious component parts of the whole structure. Its form and disposition at once give the impression that it is exercising tension on the basilar membrane. Indeed, so far as the writer is aware, no other explanation of its significance in the cochlea has ever been offered. Most writers have overlooked it altogether, and this strange oversight has continued up to recent times, but the most striking feature of the spiral ligament is its progressive differentiation. In the apical turn it shows only a few sparse, radiating, delicate fibrils which are attached to the outer bony wall of the cochlear galleries. Here its thickness does not exceed $\frac{1}{10}$ mm. At the extreme basal end it is a dense and bulky structure, made up of closely packed radiating fibres (Fig. 1). How it came about that a structure which shows so prominently in sections of the cochlea, as does the spiral ligament, should have escaped the very able anatomists and histologists of

* Wrightson and Keith.
† *Journal of Anatomy and Physiology*. Volume 34, page 324.

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Helmholtz's day is something of a mystery, but we must remember that the technique of making sections of decalcified tissues had not then been elaborated, and that they were dependent almost entirely on teased specimens. Albert Gray was a superb technician.

Helmholtz would eagerly have welcomed any evidence which would have helped to elucidate the problem of the tension of the basilar membrane. He says: "For this purpose we require to estimate the stability of the several parts, and the degree of tension and flexibility, with more precision than can be deduced from such observations as have been made on *isolated parts, as they casually group themselves under the microscope.*" Had Helmholtz been able to point to a progressive differentiation in tension as well as in length, both differentiations being in the same sense, there is little doubt that he would have established the resonance hypothesis thenceforward on so firm a basis of probability, that it would have been difficult for its position to have been shaken by subsequent criticism.

What actually happened was that contemporary imagination was captured by the boldness and simplicity of the theory, but a severe reaction set in when it was realized that the slender basis of anatomical fact on which the theory rested was utterly inadequate to meet the numerous difficulties and objections brought forward by the more critical school of experimental physiologists of the next generation. This reaction was all the stronger by reason of its first rather indiscreet enthusiastic acceptance. When Gray's work on the spiral ligament was published, the tide of opinion had set strongly against the resonance view and the significance of new facts brought forward by Gray was largely overlooked. This neglect has continued almost to the present day, especially amongst continental writers, who seldom mention the spiral ligament.

In the formula for vibrating strings, in addition to length and tension, there is a third factor—mass of unit length. Helmholtz was not oblivious of the bearing of this element of the problem, though he did not see it in any clear light. He did, however, make one very important reflection. He states: "That such short strings should be capable of corresponding with such deep tones must be explained by their being loaded in the basilar membrane with all kinds of solid formations; *the fluid in both galleries of the cochlea must also be considered as weighting the membrane*, because it cannot move without a kind of wave motion in the fluid." This shows that he realized that the fibres of the basilar membrane were relatively heavily loaded as compared with other stringed instruments, and that consequently the term m in the formula being large, the pitch, as represented by n (number of vibrations per second) might be so far reduced as to account for low tones even in such short strings; but he did not recognize any variation in the amount of the loading of the strings at different levels in the cochlea, and so he missed the bearing of this factor on the progressive differentiation of their periodicities.

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George Wilkinson

In Wilkinson and Gray's *Mechanism of the Cochlea* I put forward the contention that the basilar fibres are also differentiated for mass. Reverting to the analogy of the piano strings, we may note that the bass strings are wrapped with copper wire. The core of these strings is of elastic steel wire similar to the other strings. The copper wire is wrapped round the steel wire simply to add mass to the combined string without unduly increasing its stiffness, they are "loaded". The wrapping must be close so that there is no possibility of independent movement between the string and its load, and it must be even, so as not to alter the form of the vibration of the string. Similarly, the basilar fibres of the cochlea are closely and evenly loaded by a mass of cochlear fluid which moves as they move. I illustrated this by a rather crude diagram (Fig. 2).

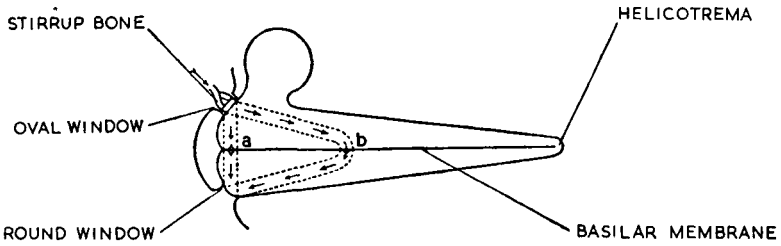


FIG. 2.

Diagram showing direction of displacement of fluid indicated by arrows within the cochlea, with each impulse transmitted from the stirrup bone, (a) for High Pitched Tone, (b) for Medium Pitched Tone.

Suppose a small transverse sector of the basilar membrane to move from its central position towards the scala tympani. Its movements will displace a certain amount of fluid, and this displacement will travel along the scala until the membrane closing the round window is bulged to a similar extent. Otherwise there would be some compression of fluid between these two points, which may be ruled out, as water is practically incompressible; or the walls of the galleries must be bulged out, which is precluded by their being rigidly encased in bone. It follows that a quantity of the fluid equal to that displaced by the movement of the sector will be displaced across each transverse section of the scala from the level of the vibrating segment to that of the round window. The mass of the fluid moved will be equal to that of a column the base of which is equal to the area of the vibrating sector and the length of it to the distance from the sector to the round window. A similar mass of fluid will be displaced in the scala vestibuli, but in the opposite direction. Of course, the fluid in the galleries does not move in the *form* of a narrow band or column, but the mass moved is defined as being that of two such columns. The mass of fluid is quite definite and invariable for each sector. It does not depend upon the

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amplitude of the movement. This only affects the amplitude of the displacement, not the mass.

The mass of the sector of the membrane itself, with its adherent organs and cells will be inconsiderable as compared with the fluid which constitutes the load. Its specific gravity will not differ greatly from that of the fluid in which it is immersed. The whole mass may, therefore, be reckoned in terms of that of the columns of water. The fluid itself has a specific gravity not greatly differing from that of water. In centimetre-gramme units, the mass will be equal to the volume of the double column.

As m is the mass of *unit* length, it will not vary with variations in the transverse breadth of the basilar membrane, i.e. length of basilar fibres. For sectors of the same width it will vary only with the distance of the sector from the round and oval windows. In other words, m progressively increases from the base to the apex of the cochlea. This will cause a differentiation in the periodicity of vibration of the sectors in the same sense as the variations in length and tension. The load is greatest on the sectors that are longest and least tense.

Thus, in the formula for vibrating strings, we may substitute db for m. But what is d? It need not actually be the distance along the coiled basilar membrane, but the shortest distance between the vibrating sector and the windows which follows the inside of the spirally curved galleries and is very difficult to determine accurately. This introduces an element of uncertainty in the formula and, of course, there are many other considerations such as fluid friction, whorls or eddies in the fluid which cannot very well be computed, but the important conclusion is that the factor m varies directly with the distance of the vibrating sector from the windows. Probably there are many different ways in which this matter of the fluid load can be treated mathematically, but this is the only one which falls within the writer's limited mathematical competence.

The factor b in the formula is the width of the sector and t in the formula the total tension on the sector of width b. With regard to b, it will be obvious that we can give any value we choose (provided it is small) without affecting the result, as t and b vary proportionately, that is to say, t being the sum of the tensions on the individual fibres comprised in the sector, if a larger width is taken more fibres are included, and if a smaller width, fewer. The sum of the tensions equals the average tension multiplied by the number of fibres. The average tension is approximately the tension on the middle fibre of the group.

We are now in a position to give a definite form to our conception of the cochlea as a resonator. We follow Helmholtz in regarding the transverse fibres of the basilar membrane as the resonating elements. They alone of the structures found in the cochlea exhibit a degree of differentiation consistent with a range of periodicities extending over 10 to $10\frac{1}{2}$ octaves. They

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are differentiated for length, tension and mass, this differentiation being progressive and in the same sense in each case. The fibres which are shortest are also tightest and least heavily loaded, and those that are longest are least tense and heaviest loaded by long fluid columns. The anatomical evidences of this threefold differentiation, viz. the varying length of the basilar fibres, the varying distances at which they are placed from the windows, and the varying bulk of the spiral ligament which attaches them to the outer wall of the cochlea, may all be classed among the more salient features of the structure of the organ.

They are not purely histological features, they are all appreciable to the naked eye.

It has been pointed out by several observers that the spiral ligament shows one striking anomaly only seen in such microscope sections as pass through the plane which contains the axis of the cochlea and the extreme basal end in the region of the windows. At its extreme basal end, instead of increasing in bulk and density, it shows a definite decrease. Anomalies like this are always worth careful consideration and often open up further insight into the phenomena. When one comes to consider this apparent anomaly, it is readily explained. In the formula for vibrating basilar sectors

$$n = \frac{1}{2\iota}\sqrt{\frac{t}{db}}$$

the distribution of pitches is shown to be inversely proportional to the square root of the distance of the vibrating sector from the oval window. This factor increases very rapidly as the distance diminishes and its effect becomes predominant. It is *more* than sufficient to account for the whole pitch graduation without any concurrent increase of tension or diminution of length of the fibres. The result of this would be undue congestion of pitches in this region, which would have a very distressing effect on the hearer. To avoid this congestion of pitches in the upper register and to maintain an even pitch gradient it is necessary that there should be a *relaxation* of tension in this region. Such a relaxation manifests itself by diminution of the spiral ligament which preserves the even graduation of pitches. It is rather a striking confirmation of the view of progressive loading of the basilar membrane by fluid columns, put forward above, and tends to show that the conception is no mere figment of the writer's imagination.

Thus, Helmholtz provides us with a complete mental picture in place of mathematical disquisitions. It seemed to many very beautiful, but "too good to be true". The idea of the basilar membrane being "played upon" by waves of sound as a pianist plays upon the keys of his instrument, is very attractive, but the arguments in support of the theory appear to many people to be insufficient. This gave rise, as an alternative, to the so-called "telephone theory" of hearing put forward by Rutherford, of Edinburgh,

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on the analogy of the telephone receiver. He regarded the function of the cochlea as merely to record variations of pressure of sound waves which were transmitted to the brain centres where the analysis into separate tones was made. This was apparently a safe, but inglorious retreat.

Nobody knew, or does know, what happens inside the brain and so it was exceedingly difficult to refute this assumption; but the telephone theory never had any verisimilitude, for a greatly extended membrane, like the basilar, seems singularly ill adapted for this purpose. The cochlea is an extremely delicate and complicated mechanism; a much simpler contrivance would seem to be adequate for so simple a function. The nerve supply is so very rich. How could a simple telephonic recorder require 25,000 nerve fibres to link it up with the brain? The recording of sound waves is now an everyday process. It is done by the recording gramophone and also by the sound film. The eye can make nothing of these records. They have to be reconverted into sound waves and passed through our ear before they become intelligible. It looks as though we shall have to go back to Helmholtz as no real progress has been made on any other line. It is a significant fact that musicians, when they try to give any physiological explanation of the phenomena of consonance and dissonance, or the interference of tones differing but little in frequency, etc., are obliged to assume the truth of Helmholtz's theory, based on his pronouncement that resonance is the only known means of resolving musical sounds into simple pendular vibrations.

In order to define the problem, let us consider the nature of sounds so as to see what we are really called upon to explain. We divide sounds into musical tones and noises. What are musical tones? Most people know that they are made up of waves in which the same form repeats itself over a definite period. This is not a definition, but an interesting scientific fact. Some of the great masters of music were probably unaware of it, especially those who lived before the time of Mersenne (1639), who first put forward the undulatory theory of sound, and we may doubt whether this conception entered into the minds of great musicians such as Bach and Haydn in the manipulation of tones in their compositions. The only satisfactory definition is that musical sounds are sounds that have a recognizable pitch. What then is pitch? Again the only satisfactory definition is that it is *position* in a series. Thus at the outset, we are compelled to look for, in the internal ear, an extended area on which these positions may be duly recorded without confusion. The basilar membrane has a total length of some 4 cm. Its width is only 0·17 mm. at the basal end and 0·4 mm. at the apex. It thus seems to provide a fair field for the display of responses ranging over some 10 or 10½ octaves. Our sense of relative pitch is much more reliable than our sense of absolute pitch. Our aesthetic sense measures position much more readily and accurately than our measuring scales. For instance, we know at a glance if the curved lines in a pattern are not true,

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or if the proportions of a building are not satisfactory, but it would probably take very long and careful measurements with calipers and scales to verify the fact.

Helmholtz gives an interesting example of the analysis of tones by stringed instruments. "If we suppose the dampers of a pianoforte to be raised, and allow any musical tone to impinge powerfully on its sounding-board, we bring a set of strings into sympathetic vibrations, namely, *all* those strings, and only those, which correspond with the simple tones con tained in the given musical tone. Here, then, we have, by purely mechanical process, a resolution of air waves precisely similar to that performed by the ear. The air wave, quite simple in itself, brings a certain number of strings into sympathetic vibration, and the sympathetic vibration of those strings depends on the same law as the sensation of harmonic upper partials in the ear." The musical tones employed may be those of a sung vowel sound, ā, ă, ē, i, or ō. The piano strings will then return the sound of the vowels each recognizable as being the particular vowel sounded and no other. The piano will continue to sound the same vowel for a considerable period. Vowel sounds when sung to the same note are distinguishable from one another on account of the partials present, the preponderating partials being different for each vowel. The different strings of the piano pick up and resonate these partials, giving out a compound tone which is recognizable as the vowel sound. The vowel sound cannot be reproduced by a single resonator tuned to the fundamental on which the vowel is sung. In order to get the proper mixture of simple tones which when recombined, are recognizable as a vowel, the simultaneous resonant vibration of a number of resonators (that is to say, of strings, in the case of a piano), is required. As a matter of fact, a suite of piano strings does not form a very delicate or efficient resonating system. The important point, however, is that even so imperfect a resonating system does possess the power of analysing compound tones. The experiment may be repeated by anyone who has access to a piano (especially a grand piano) and it is interesting and instructive.

We may note that recorded wave forms are no guide to the contained partials. Two entirely different seeming curves may give a precisely similar combination of sound. The shape of the curve depends largely upon the phase relationship of simple pendular vibrations of which the compound curve is made up. These phase combinations are readily and rapidly altered without our perceiving any difference in the character of the sound. Reflection of a compound sound wave from a wall would alter its shape, though no difference is perceptible in the sound by the ear.

Fourier's Theorem and Ohm's Law

The mathematical treatment of resolution of compound sounds to simple harmonic vibrations was worked out by Fourier (1822). His Theorem states that "any given regular periodic form of vibration can

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always be produced by the addition of simple vibrations, having pitch numbers which are once, twice, three, four times, etc., as great as the pitch numbers of the given motion", and this was applied to the ear by Ohm nearly 100 years ago. His law states that "every motion of the air, which corresponds to a composite mass of musical tones, is capable of being analysed into a series of simple pendular vibrations, and to each such single simple vibration corresponds a simple tone, sensible to the ear, and having a pitch determined by the periodic time of the corresponding motions of the air". The vibrations of each sector of the basilar membrane are harmonic or pendular. It follows that the resonant responses of the membrane to each component tone (so called partials) will be recorded separately by the vibrating sectors—that is, the tones will be analysed.

Our ears are constantly being assailed by sounds of all kinds. The ear distinguishes these sounds and we are able to judge their source. For instance, when listening to an orchestra, the characteristic sounds emitted by each instrument are readily recognized and the particular instrument producing them, identified. This is entirely due to the relative strength of the partial tones accompanying the fundamental. By partials is meant tones of 2, 3, 4, 5, ... n, times the frequency of the fundamental. At the same time, we are very conscious of any noises such as scraping of feet, coughing, rustling of dresses and conversation, and we recognize the sources of these sounds.

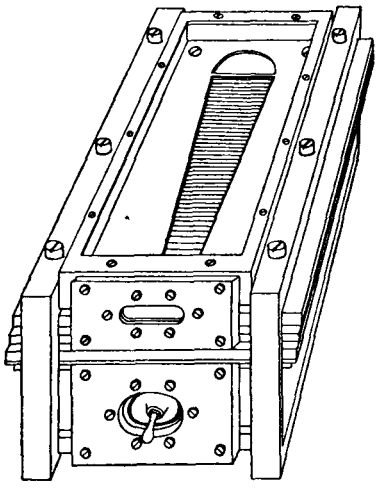
Most of the sounds we encounter contain an element of musical tones in various proportions. This musical quality is present in ordinary conversational speech and gives a pleasant (or unpleasant) character to the voice. We say of some people that their voices are musical, but we are not attracted by those voices which have constantly an underlying emotional element. Noise in itself is not disagreeable, unless too shrill or harsh. It keeps our minds alert and in touch with the world around us. When we do not hear it we miss it. There is nothing more appalling than a quarter of an hour in a sound-proof chamber where there is absolute silence. The life of those who are absolutely deaf is most depressing and deplorable. We make use of sound more for the purpose of giving and receiving information than for emotional expression. This information is not entirely conveyed by resonance analysis of tones it contains, but by its general pattern—that is a succession of sounds of differing character such as a click which is a tone of medium pitch followed immediately by a tone of high pitch of short duration, or a hiss which is a tone of medium pitch followed by a high pitch of long duration. And so our language is built up.

Models

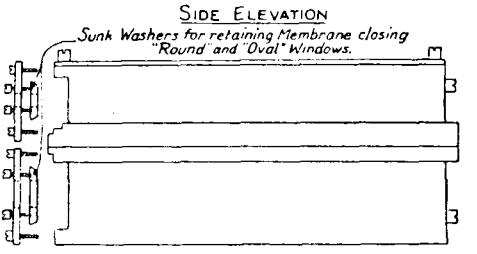
Working models representing a length of the basilar membrane were made by me from 1920 onwards. I was, indeed, engaged in making various models for several years and I produced 10 or 12 of them which showed a

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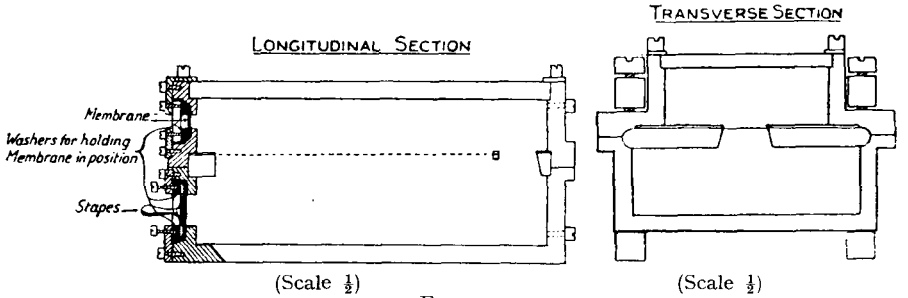
gradual increase in efficiency. The general features of the models are shown in Fig. 3 and will be fairly obvious on inspection of the figure. The models consisted of a brass case of two compartments divided by a plate of brass, in the middle of which is a large opening corresponding to a portion of the basilar fissure and having a semi-circular opening at the broad end to



Model viewed from in front and above (Scale $\frac{1}{2}$).



(Scale $\frac{1}{2}$)



(Scale $\frac{1}{2}$) (Scale $\frac{1}{2}$)

FIG. 3.

represent the helicotrema, making communication between the upper and lower compartments. The upper compartment is provided with a glass window through which the behaviour of the basilar membrane may be observed. Beyond the narrow end of the basilar opening there are openings into both of the compartments representing the round and oval windows. Both windows are closed by loose rubber membranes. The membrane of the lower, or oval window, is firmly fixed to a wooden plunger or piston to represent the footplate of the stapes. Both membranes are secured in position by brass washers. The basilar fibres are represented by very thin

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phosphor-bronze ribbon which is wound on to the plate under a tension which is least at the upper or broad end, and gradually increases towards the basal or narrow end. These windings are secured in position by soldering it on to the plate. The portion of winding that crosses the basilar fissure on the under side is cut away. The "basilar fibres" are coated on either side by fine cigarette paper impregnated with formolized gelatine. Two screw holes at the end of the case, beyond the helicotrema, are left for the purpose of filling the model with water. Stout iron clamps bind the upper and lower cases and the plate firmly together, and a certain amount of plasticine has to be applied in various parts to prevent leakage of fluid (Figs. 9, 10).

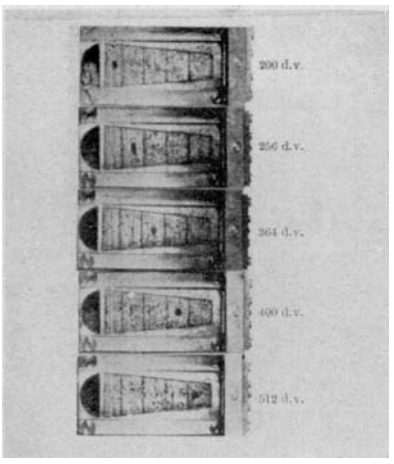


FIG. 9.—Model 10.

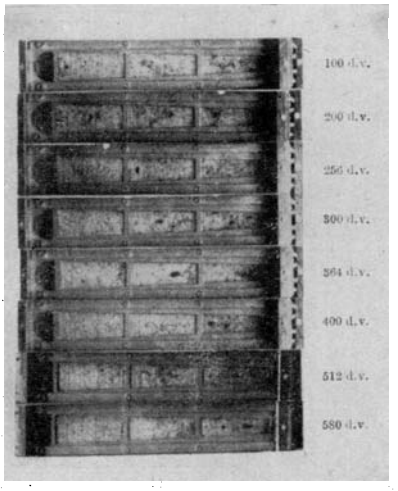


FIG. 10.—Model 11.

The black spots in the above photographs represent the indicator powder of coloured glass collected in heaps. The position of these heaps varies according to the pitch of the tuning forks used to produce them. It will be noticed that in each set of reactions, they occupy positions at regular intervals from the helicotrema, varying with the pitch of the tuning forks. The use of this indicator powder is not a very satisfactory device, but is the best available for obtaining a permanent photographic record. It will be noticed that above about 800 d.v. the reactions become diffuse and rather indefinite, the reason being that these higher pitched tuning forks have a much smaller amplitude of vibration to convey a much greater amount of energy, and so produce "forcing" effects. The position of the heaped powder is due to currents and eddies in the fluid filling the model, as explained in the text. We should be cautious in concluding that similar eddies and currents are, or could be, set up in the cochlea itself. The galleries are of such small dimensions, and the force of the sound waves impinging on the cochlea are so minute, as compared to the vibrations of a tuning fork, it is very doubtful that such eddies could be set up in it.

It is obvious that it would be useless to produce vibrations of the membrane in the models without some means of making these vibrations visible and recording them photographically. I took a hint from Chladni's plates, the vibrations of which were rendered visible by thinly sprinkling sand on them. Instead of sand, I used a powder of coloured glass, carefully sieved to exclude too coarse and too fine particles. I expected to find the

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powder would be thrown off the vibrating segments on to those at rest, but the reverse is what actually occurred. Chladni himself found he got a reversed effect when he used a very light powder, such as lycopodium, as an indicator. Faraday supplied the explanation of this anomaly; a very light powder was transported by currents in the air set up by the vibration of the plates. Immersed in water, the glass powder used by me acted as a light powder, and its movements were controlled by currents in the water set up by the vibrating sectors. In my earlier experiments, I used the powder too thickly spread, and consequently, obtained rather confused photographs. Later on I spread the powder more sparsely. My first experiments with the models showed me that I could get no well-defined indications of vibration without an ample sized helicotrema. The opening shown in the picture of the model is fairly to scale with the actual helicotrema and the basilar membrane.

Of course, the model is an extremely coarse representation of the minute and delicate basilar membrane and misrepresents the conditions under which it vibrates in several important particulars, so we have to recognize the limitations in the application of observations on the model to what happens in the cochlea. The first great difference is that of size. The model may be taken to represent a portion of the basilar membrane differentiated to respond to about 2 octaves out of the $10\frac{1}{2}$ octaves dealt with by the basilar membrane. Its linear dimensions are at least 40 times those of the cochlea. Its scale with regard to area is, therefore, some 1,600 times and with regard to cubic capacity is some 64,000 times that of the cochlea. The other obvious discrepancies are in the materials used in the model as compared with the delicate materials of which the cochlea is made up, and that the fibres of the basilar membrane in the model are made of wires and, therefore, possess stiffness, and they are fixed to the plate by soldering. This process requires considerable heating and cooling, during which process the tensions will undergo rapid changes. The model is a rectangular box, not a spirally coiled tube like the cochlea. It is thus subject to reflected waves which will affect the position of responses. Also, the method of identifying the position of resonant responses by means of an indicator powder is very rough, but I was unable to devise anything better. Nevertheless, I think that the model does illustrate roughly what Helmholtz was thinking of in his resonance theory and shows the possibility of such "pitch-position" vibrations as he had in mind.

In eliciting the responses in the model by applying vibrating tuning forks of different pitches to the stapes, a certain control of "touch" is necessary, as indeed it is in eliciting the resonance responses in all musical instruments, so as to eliminate as far as possible "forcing". Only just as much impulse should be communicated to the stapes as is required to give a visible movement to the indicator powder, and the powder itself should be sparsely distributed over the membrane.

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The part played by the helicotrema on the resonant action of the basilar membrane is also seen in "beats" and "combination tones". It has been put forward as an objection to the resonance theory of hearing, that, if sound waves in the cochlea were completely analysed into their constituent simple tones, there would be no combination tones at all. This would only be true on the supposition that the basilar membrane absorbed the *whole* energy contained in the sound waves transmitted to it, but in actual fact, the helicotrema provides a path of escape for such waves as are not completely absorbed by the basilar membrane, and allows them to reach the round window. In a graphically recorded wave picture the differential and summational tones are represented by decided peaks rising above the level of the other vibrations. The summational tone, having a frequency equal to the *sum* of the constituent tones, is the highest in pitch, and so would be the first one to be partially absorbed by the membrane in the passage of the wave over its surface. The impulses giving rise to the beat tones are relatively large, that is, as big as the sum of the two wave impulses from which they are made up, because they have a frequency equal to the difference in frequencies of their constituent tones. They give periodic variations in intensity to the sound record, and so are capable of setting up localized responses on the basilar membrane which are perceived as tones of corresponding frequency, when they become too rapid to be perceived as separate "beats". It would seem that any peaks in the sound record, if occurring at regular intervals are capable of giving rise to a tone. Probably the existence of a free path through the helicotrema throws light on this phenomenon. The energy of the waves is not entirely absorbed by resonant action of the basilar fibres and these peaks still remain and are able to impress themselves on the basilar membrane. The absence of well marked pitch reaction in the model when insufficient escape is provided by only a too small "helicotrema", supports this supposition.

Electrical Reactions in the Cochlea

A very large and important field of research was opened up by Wever and Bray (1930). These American observers announced the results of a very startling experiment. They exposed a region of the auditory nerve by removing the cerebrum of a cat and inserted an electrode into the auditory nerve, another electrode being applied to the external bony wall of the cochlea. A current was set up whenever sound waves entered the cat's ear and these being passed through amplifiers to a "loud-speaker", reproduced very faithfully those sounds and even simple melodies. Their first conclusion, naturally, was that the sound passed unanalysed into its component tones to the hearing centres in the brain. This experiment was repeated and confirmed by a number of competent observers, particularly Adrian and Rawdon-Smith in this country, but the current of action was so widespread over the surface of the temporal bone and the brain stem,

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that it appeared that the origin of the current was in the cochlea itself and not in the auditory nerve. The inner ear behaved as an electric condenser of high power relative to its size, whose charge was in very unstable equilibrium which might readily be disturbed by slight mechanical movements in the basilar membrane. Thus, the phenomena were of highest importance to the general question of the nature of nerve impulses, but did not seem to affect the problem of the analysis of sound in the cochlea. Similar electrical changes of potential in various tissues have been familiar to physiologists for a very long time. Indeed, Helmholtz was one of the first to investigate them. They have been traced in many forms of tissue reaction, in all nervous tissues, brain tissues, muscle and even secretory glands and rapidly proliferating cells, and indeed, it seems as though they were a universal concomitant of the vital activities of animal and vegetable tissues. Amongst others, two hypotheses have been put forward to account for them. (1) Ionizable colloids; (2) Polarized membranes, or surfaces of separation between two media. Colloids are molecules of great size and complexity. Ionizable colloids possess molecules which readily break up into a large ion, sluggish in its movements, and a small, mobile, high velocity, ion. Such ionizable colloids in a medium bounded by a surface, or a very thin membrane become "polarized". The small mobile ion readily passes through the surface into the medium beyond, but the large sluggish ion cannot penetrate the surface. The large ion has a positive charge and a small ion a negative charge. Thus, they attract one another and form up on either side of the surface in a double line. Bayliss compared them to sheep with their lambs in a fenced field; the volatile lambs are able to pass the fence, but the sheep are not; but their mutual attraction keeps them lined up opposite one another at the fence unless something happens to disturb them, when the lambs fly off again. So we may imagine that the sense cells in the cochlea possess polarized surfaces whose balance is easily upset by mechanical vibration. The negative ions entering the naked axis cylinders of the auditory nerve within the hair cells are able to set up a nerve current which travels through the auditory nerve to the brain. It is possible that this is the normal way in which nerve currents are set up. Of course, this is all speculative, and being very fundamental, will probably provide subject for experiment and discussion for many years to come; but it will be seen that this ionic stimulation would act as an amplifier to the mechanical stimulus, very similar to the amplification of small currents by the Fleming thermionic valve. We are rather apt to be complacent about the "triumphs of modern science", but we sometimes find that nature has been using these same devices for millions of years before we hit upon them.

Probably the chief difficulty we have in visualizing the action of the internal ear is due to the discrepancy between the size of the sound waves and the minute basilar fibres which respond to them.

The displacement communicated from the basilar membrane to Corti's

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organ must be extremely minute. A transverse displacement of a vibrating string in any musical instrument does not exceed $\frac{1}{50}$th of the length of the string. That means that the maximum displacement of the basilar fibres would not exceed ·01 mm. at the extreme apical end and ·003 mm. at the extreme basal end. These are maximum displacements, but the range of magnitude between maximum and minimum displacement (that is just sufficient to give rise to a nerve current) is very wide; indeed, thousands of times less than the maximum. Thus, it appears that we are dealing with displacements of microscopic or even ultra-microscopic dimensions. There certainly seems to be a need for some amplifying mechanism to arouse the sense of hearing.

With regard to the loudness of sounds we hear, there is a good deal of uncertainty as to what this depends upon. Certainly the disturbance of the basilar membrane corresponding to even the most definite sensation of pitch, spreads over a considerable width. Gray explained this by what he called the Principle of Maximum Stimulation: "Let any blunt-pointed instrument be pressed into the tip of the finger quite gently, and sensation of pressure at a point is produced in our consciousness. Let the pressure be increased. Still in our consciousness it remains pressure at one point. Let it be increased still to considerable intensity, and still we are only conscious of pressure at one point. But if we look at the finger now, when the point is pressing firmly into the pulp of the finger, we will observe that the skin over a comparatively large area around the point is undergoing very considerable pressure; so much so indeed that the skin is rendered bloodless for an area of about half a square inch. It is quite clear, therefore, that we are in this case stimulating a great many nerve-endings, and yet so far as our consciousness tells us we are only stimulating one. The point at which we feel the nerve-ending to be stimulated is the point at which the maximum degree of stimulation is taking place. It is only at this point that we are conscious of any stimulation of the nerve-fibres, though we know by looking at the finger that a large number of nerve-fibres are actually being stimulated. Hence it is clear that we estimate the locality of our sensation of touch, not by the fact of a certain nerve-fibre being stimulated and evoking a corresponding sensation in the brain, but by an integration of the stimuli applied to a large number of nerve-fibres, such an integration eliminating, so far as our consciousness is concerned, all those stimuli except one." The intensity of sound corresponding to the loudness of the sound heard probably depends very largely upon the area affected, that is to say, the number of nerve-fibres stimulated. Indeed, if we accept Adrian's "all or nothing" hypothesis, loudness depends entirely upon the number of nerve-fibres stimulated and not on different intensities of stimulation of any particular fibre; but this is not definitely settled at present.

The fundamental problem of hearing is how a *numerical relationship*,

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1-2; 1-3; 1-4; . . . . 1-n can be converted into *distances* along the scale. This points to an *even* graduation of pitch positions along the basilar membrane and implies the necessity of some "tuning" device. As the length of the basilar fibres is fixed by the dimensions of the basilar groove, and the "load" is fixed by the distance of each segment from the windows, the only factor remaining is tension, which we regard as a function of the spiral ligament. All stringed instruments are "tuned" by alterations of tension of the strings. The tissue cells of the spiral ligament have had many thousands of years education and we may presume that they know their business. This does not imply a "consciousness" in these tissues. We should rather look for some nervous mechanism automatically correlating tension with pitch graduation. The even arrangement of pitch positions must be either in the basilar membrane itself or in its representation in the cortex of the brain in the auditory centre. The auditory nerve is composed of many more nerve-fibres than are required for transmission of pitch position to the brain. There is also a rich supply of ganglion cells in the spiral ganglion connected with the nerve which give off many branches. We may, therefore, assume that in addition to the fibres directly connecting pitch position with auditory centres, there is a plentiful cross communication in the nerve, and it may be supposed that these connect the pitch positions of the fundamental tone with those of the tones most frequently found in association with it. As these are the harmonic partials, this would establish a sense of close connection between the chief partials and especially in the case of the octave, which is so strong in our musical sense as to amount to "identity". We naturally regard the octave as a termination of one set of intervals and the starting point of another identical set of intervals. Recognition of the chief intervals—the octaves, fifths, fourths, etc., is a very early development of our aesthetic sense. Pythagoras does not say that when the length of a string is halved we get an interval which we will call an octave, when it is halved again the longer segment gives an interval which we will call a fourth above, but that we get the octave and fourth above, so it is obvious that he must have regarded the sense of these intervals as inherent, or at least, firmly established, and that he already knew perfectly well what these intervals sounded like. The sense of harmony had probably already a long period of education by means of the lyre and harp. Our musical scales are not identical with the Greek, but probably derive from them. They are harmonic scales based on a "fundamental" note and its overtones. There are many other scales in existence other than the harmonic, but the harmonic mode is the richest, most copious and capable of an infinite variety of combinations. In other words, it is the sanest, and we may hope that it will retain its primacy at least as long as the world remains sane, but our aesthetic senses are peculiarly adaptable and ready to accept new modes, that is to say, subject to fashion. There will always be many to whom novelty appeals—the experimentalist and romanticist.

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The Sense of Hearing

It seems probable that our most important evidence of the nature of the hearing process will always be derived from deducing function from form. Up to the present time, direct experiment does not seem to have advanced matters very much, but we must beware of teleology, that is the search for evidence of design in nature. This can never be a scientific approach to natural phenomena. Still it may be doubted whether the idea of design can ever be far away from the minds of those who contemplate this truly astonishing and admirable work of nature—the hearing organ.

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