ANALYSIS OF SOUND BY RESONANCE.

Description of a Model illustrating the presumed Resonance Mechanism of the Cochlea, with special reference to the Inertia of the Contained Fluids.

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THERE is probably as great a divergence of opinion on the subject of the mechanism of sound perception at the present day, as there has been at any time since Helmholtz announced the resonance theory. It seems, however, to be generally admitted that the theory of tone analysis by resonance if it were in itself tenable, would offer the completest solution of the problems of sound perception that has yet been advanced. There are, however, many difficulties in the way of its general acceptance. If the cochlea contains a series of resonators, they are different in many respects from any resonating instruments with which we are acquainted, and no one has, as yet, offered so complete an explanation of the mechanism of resonance within the cochlea as to enable us to visualise the working of the various parts.

The Basilar Membrane.—If we regard the transverse fibres of the basilar membrane as constituting the resonating elements, Helmholtz's comparison of them to a set of piano strings occurs to one at once as being the form of resonator to which they may be most aptly likened. Nevertheless, the basilar fibres differ in three important particulars from the piano strings—(1) in the minuteness of their scale; (2) in the fact that they are embedded in a mass of cells so as to form a continuous and extended membrane; (3) in that they are immersed in fluid.

(1) *Scale.*—Though the minute scale on which the cochlear resonator is constructed has an important bearing on the delicacy of its response to periodic impulses, and on the duration of its after-vibrations, it is a matter of no moment so far as affecting the capacity of the resonating elements to respond to vibrations of any required frequency. There is much misconception on this point, and the argument is repeated in one text-book after another, that the fibres of the basilar membrane cannot respond, at all events to the lower notes of the audible scale, as they are so short.[1] But the periodicity of each

individual thread is determined by the formula for vibrating strings

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

where n is the number of vibrations per second.
l is the length of the string in centimetres.
t its tension in dynes.
and m the mass of unit length.

Theoretically, for any particular value of one factor such as l, any value whatever may be given to n, by assigning suitable values to the remaining factors t and m. The formula would still hold good were the scale 10, 100, or 1000 times smaller than that of the cochlea. Scale is limited only by the strength, fineness, and flexibility of the material available.

(2) *The fibres are embedded in a mass of cells, so as to form a continuous membrane.*—This, no doubt, impedes the movement of any particular fibre independently of the fibres on either side of it. As a consequence, we have to deal with movements of transverse strips of the basilar membrane, not individual fibres. As the tension is transverse only, the same formula, however, applies. We may take it that the layer of cells on either side of the basilar membrane is extremely flexible, and will offer no appreciable resistance to such small displacements of the basilar membrane as occur in vibrational movements. Their mass is merely one item in the term m of the formula, which we consider under the next heading.

(3) *The basilar membrane is immersed.* — It is this circumstance which creates the real difficulty, in so far as it entirely differentiates the cochlea from any form of resonator with which we are acquainted. It is a factor which has hitherto received scant attention, though in the writer's view, it is the key of the whole problem. It did not escape Helmholtz, though he offers no solution. He says: "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."[2]

The Formula for Vibrating Strings as applied to the Basilar Membrane.

In former papers[3] the writer has put forward his views as to the part played by the fluid in the cochlear galleries, which constitutes the "load" on the transverse sectors of the basilar membrane. This "load" may be expressed in terms of a double column of fluid having the same sectional area as that of the vibrating sector, and equal in height to the sum of the distances of the sector from the oval and round

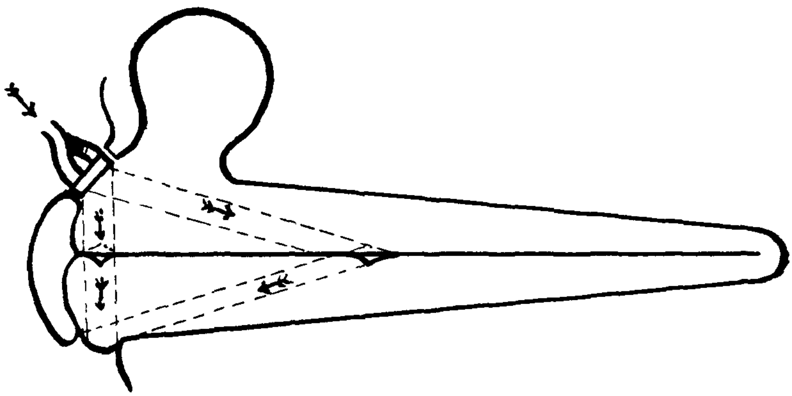


Diagram representing the cochlea unrolled. The two scalæ are shown divided by the basilar membrane. Two sectors of the membrane are represented as vibrating. The fluid enclosed between the dotted lines represents the "load" on each sector.

windows. In speaking of a double column of fluid, it is understood that it is not implied that the fluid moves in the form of a column, but merely that the mass of fluid moved is equivalent to the mass of the double column. It follows that the formula for vibrating strings

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

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

when adapted to the special conditions present in the cochlea.

Where n = number of vibrations per second.
l = the width of the basilar membrane at the level of the sector.
t = the tension.
b = the breadth of the vibrating sector.
d = the sum of the distances of the sectors from the round and oval windows.

Consequently m varies directly as the distance of the sector from the basal end of the cochlear galleries. With regard to *l*, we know that the basilar membrane varies progressively in breadth from about 0·16 mm. at the basal end to about 0·4 mm. at the apical end (Keith).[10] With regard to *t* we know that it increases progressively from apex to base, as shown by the increase in bulk and density of the attachment of the basilar fibres to the outer cochlear wall, *i.e.* the spiral ligament.[4]

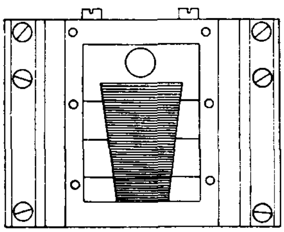
The transverse sectors of the basilar membrane which lie nearest to the *basal* end are shorter, tighter, and less heavily weighted, and will consequently respond to impulses of high frequency. Those at the *apical* end are longer, slacker, and more heavily weighted, and will respond to impulses of low frequency. We have now an explanation of some points that have hitherto appeared obscure. We see why the shorter and tighter fibres are placed at the proximal or basilar end of the spiral and vice versâ. By this arrangement the variations of the three factors in the formula, length, tension, and mass are all in the same sense. We also see why it is essential that the basilar membrane should be a continuous structure, and one reason, at least, why it should be covered by a layer or layers of cells. If the basilar membrane were not continuous and watertight, the fluid surrounding it would eddy in between the vibrating fibres from one side to the other, and there would be no calculable and invariable mass of fluid set in motion. If the mass moved by the movements of the sector were subject to variation, the periodicity of the vibrations would also vary. Any such variations would be incompatible with sound analysis by specific resonance of the sectors of the membrane. The cells covering the membrane, hitherto regarded by many as a hindrance to the vibratory movement of the basilar membrane, are seen to be an essential feature in regulating the vibrations according to the formula, in so far as they render the membrane water-tight, without interfering with its flexibility. We also see why it is that there are two openings into the cochlea from the middle ear. These are the only parts where the organ is not rigidly enclosed. They are both at the basal end of the spiral, at approximately equal distance on either side of the commencement of the basilar membrane. By this arrangement the length of the columns of fluid progressively increases from base to apex, and being of approximately equal length on either side they balance one another.

The explanation offered above of the bearing of the hitherto neglected factor of the inertia of the cochlear fluid on the resonance mechanism, is in the form of a deduction from the more elementary facts of the anatomical structure of the organ. One realises that to make the reasoning convincing one ought to offer some experimental proof, or at least experimental illustration. Direct observation of the cochlear movements is of course out of the question, nor can we attempt any adequate experiment on the minute scale of the cochlea. It has, however, been pointed out, that scale is of no account in the application of the formula for vibrating strings. The model resonator here described appears to the writer to fairly represent the essential conditions under which the basilar membrane works, though on a greatly enlarged scale. To some extent it bears out the applicability of the formula to membranes of varying transverse tension immersed and oriented as is the basilar membrane, and, within limits, it illustrates its presumed resonating action.

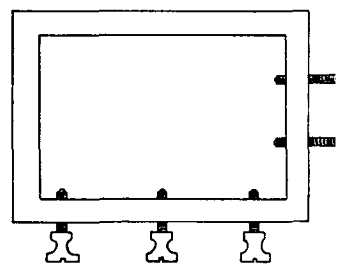
Description of the Model.

The resonator model consists of a brass box $5 \times 5\frac{1}{2} \times 6\frac{1}{2}$ cm. It is divided into an upper and lower chamber, which are separated by a flat brass plate (representing the scalæ of the cochlea and the lamina spiralis). The brass plate has an opening down the middle, wider at the distal than the proximal end, the "basilar fissure," filled up by the "basilar membrane," and also a semicircular opening beyond the "basilar fissure," the "helicotrema." The top of the upper chamber is provided with a glass window, through which the movements of the basilar membrane may be observed. The upper chamber is shallower than the lower (1.75 as against 2.1 cm.). This brings the window nearer to the basilar membrane than would be the case if the chambers were of equal height, so that the movements of the different parts of the membrane may be better observed. The anterior wall of each chamber is provided with an opening, the "foramen rotundum" 2×0.4 cm., and the "foramen ovale," 2×0.9 cm. respectively. These openings are closed by rubber membranes, which are secured in place by sunk washers. A small wooden plunger, the "stapes," is attached to the lower (*i.e.* the larger) membrane. At the back of each chamber are small holes closed by screws, "filling holes," through which fluid can be introduced by means of a syringe with a fine nozzle, to fill the chambers.

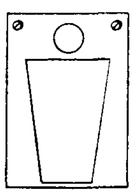
The technical problems to be solved are:—(1) The material suitable for the "basilar fibres"; (2) the method of applying the fibres to the plate; (3) the application of the proper tension to the fibres; (4) the fixation of the fibres so that neither the position of the threads nor their tension will alter; (5) the nature of the embedding material to be used to convert the series of threads into a continuous even membrane; (6) the fixation of the threads with precision at the margins of the "basilar fissure" so as to definitely limit the length of the vibrating segment; (7) the method of demonstrating the move-



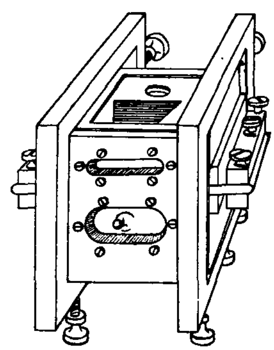
Upper Chamber viewed from above, showing window in centre and screws closing filling holes at back. Interior of chamber seen through window.



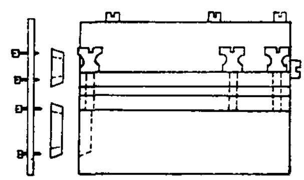
Clamp.



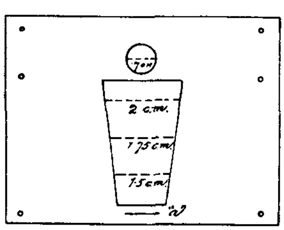
The Covering Plate.



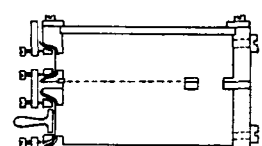
Perspective Drawing of Resonator from the front, showing "round" and "oval" windows and "stapes."



Side View of Resonator.—In front are the sunk washers and the plate and screws fixing them. The screws at the back close the "filling holes." Those at the top hold the plate retaining the glass window in position.



The Plate dividing the Upper and Lower Chambers, showing dimensions of the "basilar fissure" and "helicotrema." The line "a" shows the level of the rubber membranes closing the round and oval windows.



Sectional Diagram of Resonator, showing relative positions of membranes closing windows, "basilar membrane," and the "helicotrema."

Fig. 1.—Cochlea Demonstration Model.

ments of the "basilar membrane"; (8) the means of making the model watertight when complete.

(1) *Material used for the "basilar fibres."*—It is obvious that a soft animal or vegetable material would conform more closely to the natural "basilar fibres" than any kind of wire, and would give a more delicate response to impulse. Fine elastic threads were first tried, at ½ mm.

intervals, each thread being stretched by an appropriate weight. They failed owing to their imbibing water when immersed, which entirely altered their tension. Well-soaked horse hair was given an extended trial. It was found that horse hair when stretched in water underwent an elongation during the first twenty-four hours, but subsequently retained a fairly constant length. This necessitated the horse hair threads being kept constantly soaked during their application, which was found to be inconvenient. The variation in width of the individual hairs was a disadvantage. Further, it was found impossible to fix the series of threads so as to maintain their exact tension and spacing. Finally one was driven to use wire. The disadvantages of wire are many, but it has the great recommendation of being capable

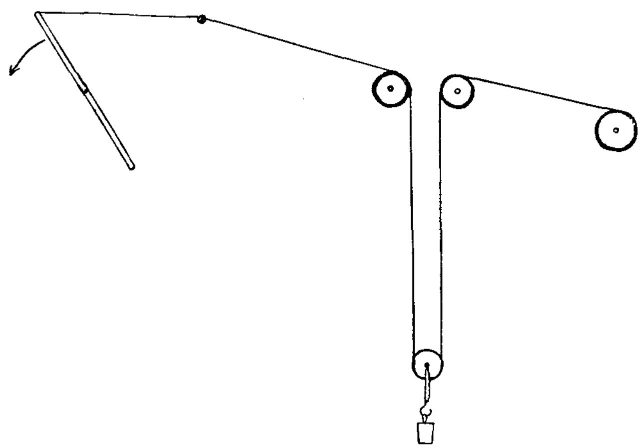


FIG. 2.—Showing the method of winding the wire off the reel through a system of pulleys over travelling guide on to the plate fixed in a lathe.

of being accurately and permanently fixed in position by soldering. Suitable wire must be very fine and pliable, but strong. Fine wire, unless very carefully drawn, has a tendency to curl which makes it impossible to work with. Several kinds of wire have been tried. A soft brass wire 1/14 mm. in diameter gave fair results. At present phosphor-bronze ribbon (as used for suspending galvanometer needles) is being used. The ribbon is 0.23 mm. wide and only 0.012 mm. thick. Its fineness more than compensates for its stiffness and it can be wound very evenly. It is, however, very costly and rather delicate to handle; 25 metres of strip are required for one winding of the plate and a single broken thread ruins the whole.

(2) *Method of application.*—Absolute evenness of spacing of the wires, with close juxtaposition of the threads is aimed at. The plate is placed in a lathe, and the wire lead off the bobbin through a series of pulleys arranged as in the figure (Fig. 2). The lower pulley is

weighted, so that the wire has an even tension during the operation of winding. The ribbon is led to the plate over a small pulley, the axis of which is attached to an arm held by the travelling tool holder of the lathe. One end of the strip is soldered in position on the plate. On the lathe used the smallest pitch of the traveller is 1/84 inch for each turn, almost exactly 0.3 mm. This gives three and 1/3 turns to each millimetre of the plate. The space between each thread will then be 0.07 mm.

(3) and (4) *The production of the tension and fixation of the fibres.*—The opening in the plate (Fig. 3) representing the "basilar fissure" has

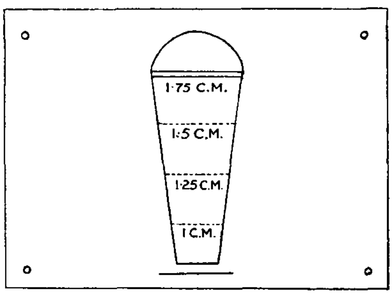


FIG. 3.—Showing dimensions of plate, "basilar fissure," and "helicotrema."

the following dimensions:—length 3.7 cm. At 1 cm. from the level of the membrane filling the round and oval windows, the width is 1 cm.

at 2 cm. it is 1.25 cm. wide.
at 3 cm. it is 1.5 cm. wide.
at 4 cm. it is 1.75 cm. wide.

For reasons to be explained presently, it was found necessary to graduate the tensions arithmetically. This restricts one's choice of predetermined positions for the notes on the scale to two. The positions of the other notes may then be determined by calculation. The plate from which the photographs here reproduced were taken (p. 460), was graduated to give 400 D.V. per second at 1 cm. from the membrane closing the round and oval windows, and 32 D.V. per second at 4 cm. (the distal end of the scale).

Thus at 1 cm. from the proximal end

$$n = 400.$$
$$l = 1 \text{ cm.}$$
$$d = 2 \text{ cm.}$$

for "b" (breadth of the sector along the axis of the basilar membrane) we can select any value we like, so long as it is small, for "t" and "b"

vary proportionately, *i.e.* if we make "*b*" larger, we embrace more threads, and so increase "*t*," which is the sum of the tensions on the individual threads included in the sector.

Call "*b*" then 0.1 mm.

$$n = \frac{1}{2l}\sqrt{\frac{t}{bd}} \quad i.e. \; n^2 = \frac{1}{4l^2}\frac{t}{bd}.$$

$$t = n^2 4l^2 bd = 400^2 \times 4 \times 1 \times 2 \times 0.1 = 128{,}000 \text{ dynes or } 130.5 \text{ grams. weight.}$$

(A small correction has to be applied for the obliquity of the direct distances between the windows and the selected point. This amounts to $\frac{2.2}{2}$.

$$130.5 \times \frac{11}{10} = 143.5 \text{ grams.)}$$

at 4 cm.

$$t = 32^2 \times 4 \times 1.75 \times 1.75 \times 8 \times 0.1$$
$$= 10035.2 \text{ dynes, or } 10.2 \text{ grams. weight.}$$

(the correction for obliquity is very small and may be neglected).

We now require to make a series of weights graduated arithmetically about these fixed points. For the purpose one procures a sheet of lead. From this, a rectangular oblong 10 cm. × 6 cm. is accurately cut off with knife and rule. It is found to weigh exactly 110 grams. One sq. cm. of the lead therefore weighs $\frac{11}{6}$ grams. The weight required to give a tension of 143.5 grams. to a millimetre wide strip of the membrane at a point 1 cm. distant from the windows (400 D.V.) will have an area of $143.5 \times \frac{6}{11} = 78.3$ sq. cm., that at 4 cm. (32 D.V.) $10.2 \times \frac{6}{11} = 5.6$ sq. cm.

In winding the plate, the wire is taken 1 mm. beyond the "basilar fissure" at either end. The whole winding therefore covers 3.9 cm. The 400 D.V. position falls 9 mm. from the proximal end of the winding, and the 32 D.V. at 1 mm. from the distal end.

A base line is cut in the lead sheet 156 cm. long, and marked off in distances of 4 cm. each. There will be thirty-nine such divisions. From these abscissæ, ordinates are erected. The 9th ordinate will be $\frac{78.3}{4} = 19.6$ cm. long, and the 39th ordinate $\frac{5.6}{4} = 1.4$ cm. long.

The top of these ordinates are joined by a straight cut, which is continued to the two ends of the area marked out by the ordinates. If the sheet is now cut up along the base line, the ordinates and the upper limiting line, we shall have a series of 39 weights graduated arithmetically, each differing by

$$\frac{143.5 - 10.2}{30} = 4.44 \text{ grams.}$$

the weight of each being equal to the tension in grams. required on the corresponding 1 mm. wide strip of the "basilar membrane."

The wires are now soldered along the upper edge of the plate, and clamped down. A thin strip of silver is soldered along the length of the wires at the back of the plate, parallel to and about 1 cm. from the clamp. The wires are cut across between the clamp and the silver strip. Holes are drilled in the silver foil at intervals of 1 mm. The plate is fixed upright in a vice, and the threads allowed to hang down.

Several attempts were made to graduate the tensions so as to obtain equal spacing of the octaves. This necessitated dividing the silver strip into sections 1, 2, or 4 mm. wide, and hanging the

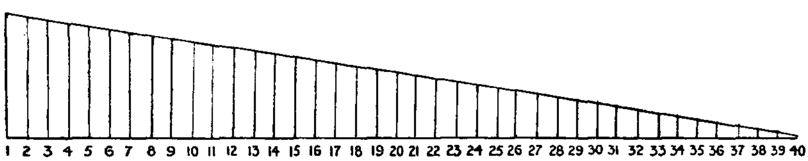


FIG. 4.—Lead sheet marked out for series of weights. Scale: $\frac{1}{10}$ one sq. cm. of lead weighs $\frac{11}{6}$ grammes.

weights from the strips of fibres so divided up. However, it was found almost impossible to carry out the delicate operation of dividing the silver strip without detaching one or more wires, which ruined the whole winding. Further, it is very difficult to get the wires back into perfect alignment after dividing the strips. Consequently, it has been found better to leave the strip undivided, and to hang the weights along it at regular intervals of 2 mm.

In this way only an arithmetical graduation of tensions is possible, but this is of no practical importance, as it has proved impossible up to the present to tune the strings with any high degree of accuracy. The theoretical positions of the different notes can be calculated.*

The weights are suspended from the strip at varying levels so that they may hang clear of one another, and each exerts its appropriate tension (see Fig. 5).

* The position of a note of frequency n is given by the formula

$$n = \frac{1}{2(\cdot 75 + \cdot 25x)} \sqrt{\frac{\{143\cdot 5 - 44(x-1)\}\, 981}{2x \times \cdot 1}}$$

where x = the mean distance of the segment giving the note from the membranes closing the windows.

(5) *Embedding the threads.*—The threads are embedded by pasting on to either side of them a piece of thin cigarette paper soaked in formalised gelatin. The lower paper is cut to the exact shape of the opening. The upper overlaps the opening in every direction. The gelatin used is a 5 per cent. solution, to which is added 1/3 of its bulk of 10 per cent. formalin solution after melting and before applying. Care

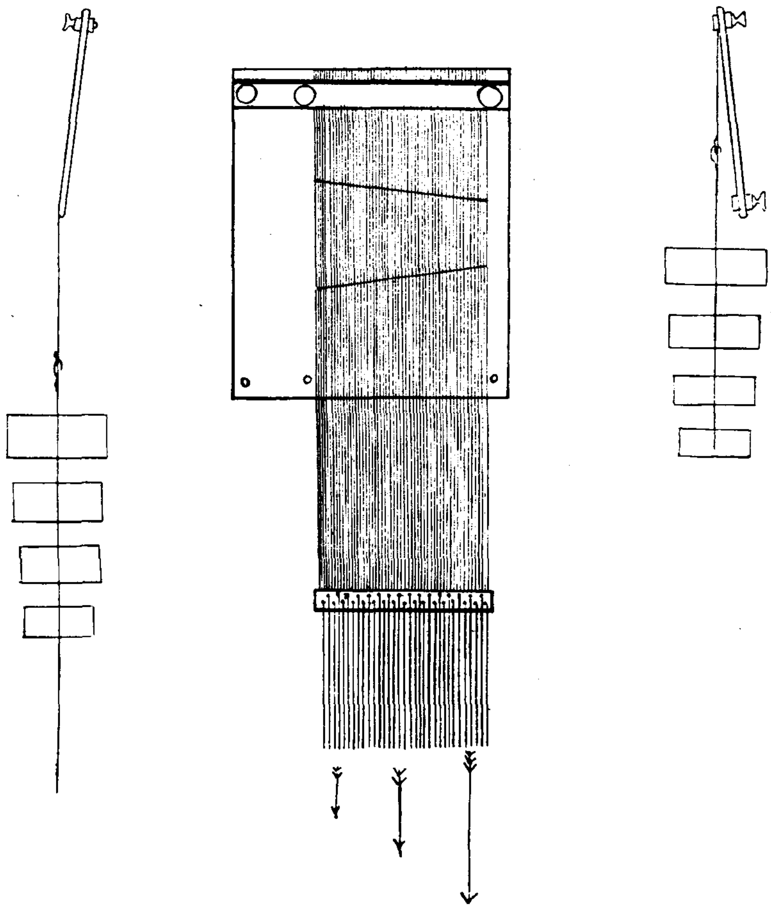


FIG. 5.

is required to prevent air bubbles being left between the two films. When dry, the upper surface of the film is painted over with undiluted formalin to harden the surface, the liquid being immediately dried off with filter paper. The formalin gelatin, when soaked, makes a very flexible film which is fairly durable. Moulds grow upon it, and to guard against this a 0.5 per cent. formalin solution is used in place of pure water for filling the resonator.

(6) *Fixation of the ends of the vibrating segments.*—This is effected by means of an upper plate having an aperture to correspond with that of the lower plate, on to which it is screwed at the distal end. The outside edges of the upper plate fit into a groove in the lower surface of the upper box which presses it down in position when the parts of the model are clamped together. A straight edged folded slip of cigarette paper, soaked in formalised gelatin, is laid accurately along the outer edge of the opening in the plate, on either side under the covering plate, to make pressure on the threads and to limit the length of the vibrating segments.

(7) *The "indicator."*—It is extremely difficult to detect the vibration of the threads with the eye, or even with a lens. We are thus driven to use an indicator powder on the surface of the membrane to show up the points of maximum vibration. This is a coarse method. No doubt the finer vibrations of the threads are unrecorded. It is, unfortunately, just these finer vibrations that we wish, but are unable to follow. Various powders have been tried. Heavy powders weight the membrane too much. Those that are too light or too fine diffuse themselves in the liquid and obscure the view. Very fine powders appear to be more affected by the currents in the liquid than by the vibrations of the membrane, and are unsuitable (*cp.* Rayleigh, *Sound*, vol. i., p. 368). A coloured powder shows up better than a white one. Blue enamel powdered so as to pass a sieve 60 to the inch, but to be stopped by one 80 to the inch, is used. This shows up well, and the grains are about the right size, and the specific gravity is neither too high nor too low.

8. *Method of sealing up the box to render it watertight.*—Under this heading we have to consider (*a*) the fixing of the glass window, (*b*) the fixing together of the upper and lower chambers and string plate, and (*c*) securing the membranes closing the round and oval windows.

(*a*) *The window* is set round the edges with a mixture of litharge and glycerine, and held by a small fixing plate screwed into the top of the upper chamber.

(*b*) *Fixing the chambers and plate together.*—In order to make a watertight joining, the surfaces which bear on the plate must be fairly wide. This is why the walls of the chambers are made so thick (0.5 cm.), and also why they are provided with flanges at the sides to increase the bearing surface where the wires come through, where leakage is most liable to take place. Various forms of wax have been tried for cementing material. A form of modelling wax, known as "play wax" at the toy shops, answers very well. It is just about the right consistence and clean to work with. The wax is spread thinly and evenly on all the bearing surfaces. The upper and lower chambers are fixed in position on the plate, and the front plate is held in position till the clamps are applied round the whole, and fixed by gradual tightening of the screws. The excess of wax is pressed out of the cracks as the screws are tightened, and a watertight junction is made all round.

(*c*) *The membrane closing the round and oval windows.*—This gave a good deal of trouble in the earlier experiments. In the present model the membranes are secured by sunk brass washers fitting into deep grooves round the windows. In order to fix the washers there is a plate with holes in it to correspond with the oval and round windows, surrounded by screws. This plate is clamped on to the model when it is finally put together, and by tightening the series of screws the washers are pressed home. The wooden plunger or stapes is glued on to the lower membrane. This membrane is fixed with its lower edge close to the edge of the oval window, so that it moves as though hinged at its lower margin, and the greatest movement is at the upper edge.

The whole interior of the model is now filled through the filling holes with fluid by means of a fine syringe. Boiled water is used, to which formalin is added to 0.5 per cent. One reason for boiling the water is to expel dissolved air, otherwise small bubbles will form within the cavity which are very difficult to detach and get rid of. Larger bubbles can be avoided by careful filling.

As the model is filled with the windows downwards, the membranes closing them are bulged outwards somewhat, by the pressure of the fluid. When tested immediately after filling, the various notes in the scale are found to be raised one or two millimetres higher than they are later, when evaporation of some of the fluid through the rubber membranes has caused the latter to return to their proper place or even to be drawn inwards. The reason for the variation is, of course, that the length of the columns of fluid is increased when the membranes are bulged, and decreased when they are in-drawn. After standing twelve to twenty-four hours a bubble will usually be found within the model. Air is sucked in when the pressure is reduced by evaporation beyond a certain point, probably around the membranes. This only necessitates removing a screw from one of the filling holes and introducing a few more drops of fluid.

Working of the Model.

The transverse sectors of the "basilar membrane" in the model are thrown into more or less well defined and localised sympathetic vibration by touching the "stapes" lightly with a vibrating tuning fork. A fork of 32 D.V. provokes response only at the extreme end of the membrane (4 cm. from the level of the oval and round windows).

The 64 D.V. fork gives a fairly well localised response limited to the middle of the segment of the membrane lying between the 3 and 4 cm. lines. As will be seen by comparison of Figs. 6 and 7 the indicator powder is cleared off this area, whilst that on the part of the membrane higher up is but little disturbed. The surface of the membrane is not so even as one could wish in this region, particularly at "*d*," where there is a "hillock" which interferes with the sliding of the grains of the indicator.

The response to the 200 D.V. fork (Figs. 8 and 9) is not so satisfactory. The calculated position for 200 D.V. is almost exactly at the 2 cm. line, the middle line of the scale. The point of maximum response is actually considerably lower, at about 2·5 cm. and the whole reaction is more diffuse than it should be. The graduation of the tension in this part of the membrane is evidently imperfect. There is also a partial vibration approximately at the 100 D.V. position (3 cm. line).

The 400 D.V. reaction appears very close to the calculated position at the 1 cm. line, just a shade below (Figs. 10 and 11). It is quite well localised, but there is a well-marked partial vibration at the 200 D.V. position, and another less marked at the 100 D.V. position.

The results shown in the photographs (Figs. 6-11) are coarse results obtained by distributing the indicator powder thickly over the membrane and applying the forks sufficiently forcibly to produce a considerable displacement of the powder. Much more delicate and better localised responses are obtained by powdering the membrane sparsely and applying the forks with only just sufficient force to elicit a visible response, but the result can only be followed by observing the movements with the eye, and could not be demonstrated in a photograph. Nevertheless, the writer contends that even these coarse reactions show clearly that the "basilar membrane" possesses progressive differentiation in the periodicity of its vibrations.

A response to 512 D.V. is obtained in the region above the 1 cm. line. The resonance, therefore, extends over 4 octaves.

Sources of error.—The model in its present form, imperfect though it is, is the outcome of many trials and failures with different models and materials from which the writer has learned a good deal as to the sources of inaccuracy. The essentials for definite localisation are *sensitiveness* and *accuracy of graduation of tensions.*

Sensitiveness.—To obtain this essential, the materials used for the basilar threads must be extremely fine. If coarse, their "initial stiffness" is too great, and much force must be applied to make them

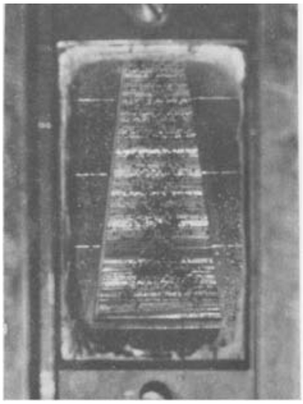


FIG. 6.—Before.

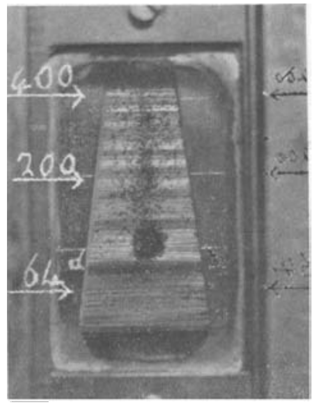


FIG. 7.—After.

Applying a tuning-fork giving 64 D.V. per sec. to the "stapes." The point of maximum vibration agrees fairly closely with the calculated position, as shown by the arrow.

FIG. 8.—Before.

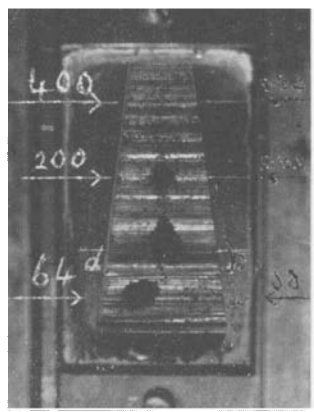


FIG. 9.—After.

Applying a tuning-fork giving 200 D.V. per sec. to the "stapes." The point of maximum vibration comes out about 0·4 cm. below the calculated position, as shown by the arrow.

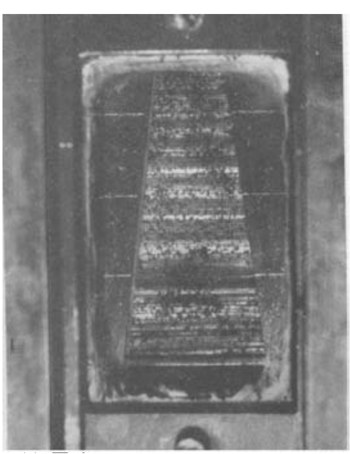


FIG. 10.—Before.

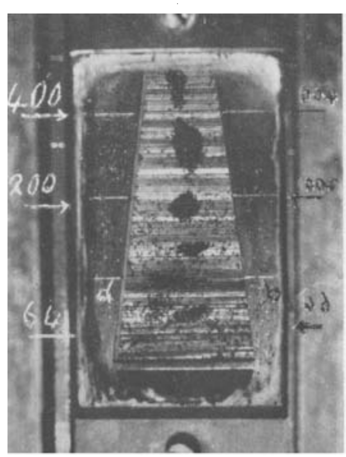


FIG. 11.—After.

Applying a tuning-fork giving 400 D.V. per sec. to "stapes." The point of maximum vibration agrees closely with the calculated position, as shown by arrow. Lower down the scale there are indications of partial vibrations of "basilar fibres" at various points.

SHOWING DISTRIBUTION OF THE INDICATOR POWDER.

move at all. It is an essential condition for eliciting the true note of any form of resonator, that the stimulus applied should be only just sufficient to evoke response. With excessive stimulus all resonators show forced vibration for notes on either side of the fundamental. Further, the formula for vibrating strings is only applicable to vibrations of a very small amplitude as compared to the length of the string. For vibrations of greater amplitude, the periodicity is altered, and

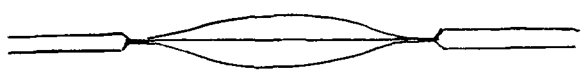


FIG. 12.

resonant response is less accurate. To maintain the sensitiveness of the membrane it is also essential that the embedding film should be thin and flexible.

The formula for vibrating strings is subject to modification by two factors, which we may term the *stiffness* and the *resiliency* of the strings. Wire that possesses stiffness when clamped at two points vibrates in the form shown in Fig. 12, what one may call a double ogival curve, whereas the true theoretical form of vibrating string is what one may call a lenticular curve (Fig. 13).

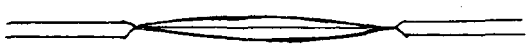


FIG. 13.

It is obvious that in the first form the effective length of the string is shortened, and the tone will be raised. The factor is a large one where the string is short.

If a wire be clamped at one end and bent out of the straight, the force tending to bring it back to its original direction is *resiliency*. In the formula for vibrating strings resiliency reinforces tension.

The formula may be written more accurately

$$n = \frac{1}{2(l - k_1)}\sqrt{\frac{t + k_2}{m}}$$

where k_1 is a constant depending on the stiffness, and k_2 a constant depending on the resiliency of the string.

The bearing of these factors is well seen in a former model strung with brass wire 0.07 mm. gauge. The responses obtained were all about $\frac{1}{2}$ to $\frac{2}{3}$ octave too low, *i.e.* the pitch of the strings themselves was too high by a corresponding amount.

Accuracy of graduation of tension.—The greatest difficulties in the construction of the model fall under this heading. In the first place, absolute evenness of spacing of the threads is necessary, as the total tension in each segment of the membrane is the sum of the tensions of the individual threads included in that segment. If one mm. segment contains 2 and the next 4 threads, the tension of the one will be approximately only half that of the other. Even spacing is very difficult to attain in the lower part of the scale where the tensions are low, and insufficient to take all the "set" out of the wires.

In the process of soldering, some heating of the wires takes place, and after fixing they cool and contract, thus raising the tensions.

After putting the waxed parts of the model together, and during the tightening of the clamps an alteration of tension of some of the wires always occurs from the drag of the wax on them. This is shown by the fact that whenever it is necessary to take the model to pieces, rewax and refix it together, the tuning of the wires is always altered in some part of the scale.

Partial vibrations and overtones.—It is rather surprising to find partial vibrations so readily set up in the strings that are so short. All the notes in the upper part of the scale show well-marked partials at the level of the octave below, and those at the top of the scale show a whole series of partials, unless the exciting fork is applied with only just sufficient force to evoke the minimal perceptible movement of the primary tone. Similarly, the overtones present in the lower forks produce corresponding reactions on the membrane, unless the forks are struck very gently, and applied lightly.

The "helicotrema."—In the earlier experiments the hole at the bottom end of the plate, representing the helicotrema, was made very small (2 mm.). The result was unsatisfactory, as it was difficult to elicit any localised response, merely a diffuse tumultuous movement resulting on stimulating the membrane. At Professor Leathes' suggestion, I enlarged the helicotrema to 7 mm. and immediately began to obtain indication of localisation. In the present model the helicotrema is represented by a semicircular opening of the same diameter as the end of the basilar membrane (1·75 cm.). There is a small vibrating pointer in the helicotrema, which can be seen to be thrown into vibration when the lower forks (32 D.V. and 64 D.V.) are applied to the stapes. Vibrations are not perceptible with the higher forks though they are probably present. It is evident that the helicotrema is an essential structure in the organ of sound perception, acting as an escape for the "unexhausted energy" of the sound wave, and thus allowing the differential effect due to resonant action to develop without being obscured by diffuse forced vibrations.

"*Bone conduction.*"—Well-localised responses are elicited by applying the butt of the large tuning-forks to the front end of the model without touching the stapes, but to elicit this effect the vibrational energy of the fork must be ample. It cannot be elicited by the smaller forks.

In view of all these sources of inaccuracy, one cannot claim that the model is in any way an instrument of precision. Possibly it can be still further improved to eliminate some of the defects. It can only aspire to copy in some sort of remote, inaccurate, and coarse fashion, the marvellously delicate resonating mechanism of the cochlea.

Deduction from the Model, as to Sound Analysis in the Cochlea.

The question now arises, what light does the model resonator throw upon the mechanism of sound analysis in the cochlea?

It may be fairly claimed for the model that it demonstrates that the transverse sectors of the "basilar membrane" are "loaded" by the fluid in the chambers, and that the load varies directly as the distance of each particular sector from the round and oval windows. The same relationship between "load" and relative position will hold for the sectors of the basilar membrane in the cochlea.

Now we know that the basilar fibres vary in length, and that the increase in length is progressive from the basal to the apical end of the basilar membrane.

Further, we have good grounds for assuming that there is a progressive increase in tension on the basilar fibres from apex to base. This assumption is based on the fact first pointed out by Albert Gray,[4] in 1900, that the spiral ligament which attaches the basilar fibres to the outer wall of the cochlea increases progressively in bulk and density from the apex to the base of the cochlea. It is difficult to imagine any explanation of this striking fact other than that the spiral ligament is actually the organ for regulating the tension of the basilar membrane, the tension it exerts on each basilar fibre being proportionate to the bulk and density of the ligament at the point where it is attached.

We therefore have a threefold differentiation of the basilar fibres, for length, tension, and mass. In all three cases the variation is in the same sense. The fibres that are shortest are also tightest and lightest, those that are longest are loosest and most heavily loaded. Now every tense string has a definite periodicity of vibration, depending on its tension, mass, and length.* If these factors vary progressively, the periodicity of the strings will extend over a longer or shorter scale. If a periodic impulse whose frequency falls within the limits of the scale acts on them, the string of the same periodicity will

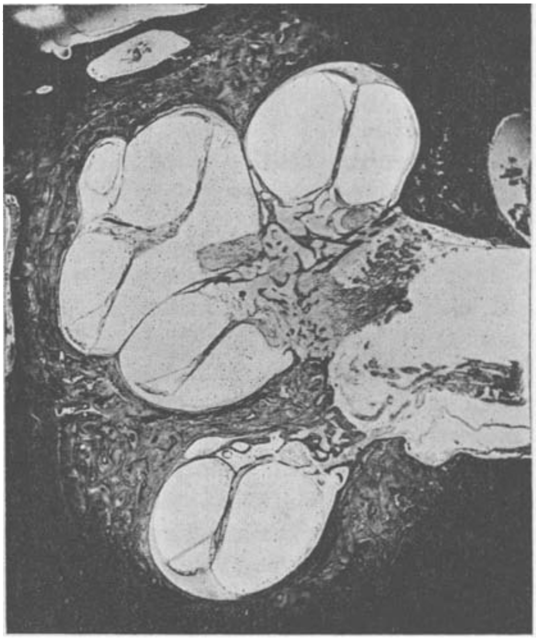


FIG. 14.—Section through the axis of the cochlea, magnified 15 diameters. The progressive increase in bulk and density of the spiral ligament from the apical to the basal turns of the cochlea are clearly shown.

vibrate sympathetically. We cannot prove that the degree of differentiation of the basilar fibres is sufficient to give the 10 to 10½ octaves of the audible scale, but we can calculate approximately the upper and lower limit of tension necessary to give the required differentiation.

* It has been wrongly assumed that the basilar fibres must be "elastic" if they are to vibrate, but the formula for vibrating strings takes no account of elasticity. Many writers on the subject use "elasticity" in the sense of "extensibility." A fibre which extends in length under the increase of tension to which it is subject during the vibrations conforms to the formula less closely than one which does not stretch.

Limits of Tension of the Basilar Membrane.—The calculations for the upper and lower limits of tension of the transverse sectors of the basilar membrane have been given in the writer's former article.[5] The maximum tensions for the extreme basal fibres were found to be somewhere about 18·6 grams. weight (approximately $\frac{2}{3}$ ounces) for a strip 1 mm. wide and the minimum for the extreme apical fibres, 4·6 mgrms. (approximately $\frac{1}{14}$ gram. weight). The result of experiments on the breaking strain of various animal fibres is also given. By reducing the sectional area of the fibres tested to that of a strip of basilar membrane, the following results were obtained—

For silk-worm gut	159 grams.
Human hair	60 ,, 84 ,, 52 ,,
Mouse-tail tendon	69 ,,

from which the conclusion was deduced that the basilar membrane could readily withstand the maximum tension calculated according to the formula, supposing the material of which it is composed to have a tensile strength at all comparable to that of silk-worm gut, human hair, or mouse-tail tendon.

The range of tensions as calculated above, is not merely a possible one with regard to the strength of materials, but has a certain *a priori* probability. The lower limit is low, but not infinitesimal, and the upper limit is fairly high, but well within the limits of safety for any ordinary accidental increase of strain, such for instance, as from explosive noises.

Theories of Hearing.—No theory of hearing can be taken seriously which fails to give a reasonable explanation of, at all events, the more elementary and obvious features of the structure of the cochlea; for, after all, our conceptions of the working of the cochlea have to be deduced from what we know of its structure. The structural factors with which we have been dealing, 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 attachments 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 histological features; they are all appreciable by the naked eye. The inference to be drawn, viz., that there is a threefold differentiation of the basilar fibres for length, tension, and mass, and that this differentiation is progressive, and in the same sense, each factor appears to the writer to be entirely logical, and indeed inevitable. So well marked a differentiation of structure must connote a corresponding differentiation of function. If this be not for the purpose of sympathetic resonance, the writer fails to see any alternative explanation.

Only one assumption has to be admitted in order to deduce that the basilar fibres are differentiated for periodicities covering the whole audible scale, viz., that these tensions vary between limits of approximately 20 grams. and 4 mgrms. per millimetre strip.

If, however, this be not admitted, it must be granted that the degree of differentiation which the basilar membrane undoubtedly exhibits, must entirely do away with the possibility of its acting, as a whole, in recording pressure variations transmitted by the stapes. This puts out of count the theories, for example, of Rutherford, Lipps, and Wrightson. Nor is the basilar membrane adapted for the formation of "pressure patterns" as conceived by Ewald and Waller. Ewald's artificial cochlea misrepresents the basilar membrane in every particular.[6] It is not differentiated as to width, or tension and its "windows" are placed in an entirely different relation to the basilar membrane than obtains in the cochlea. The "travelling bulge" theories of Meyer and ter Kuile may serve as an elaborate analysis of a single harmonic impulse within the cochlea, but they leave out of account the inertia of the cochlear fluids, and when applied to a series of such impulses they mean sympathetic resonance pure and simple. As Lehmann well puts it, "only that part of the basilar membrane which has the period of oscillation of the oval window will regularly make room for the fluid displaced by the latter. Parts nearer will be bulged out first, but they will clash with the period of the stirrup at once, and so the fluid displaced will be pushed onwards till it gets to the part in tune with the motions of the stirrup. Then the oval window, that part of the basilar membrane, the round window and the columns of fluid between these windows and the basilar membrane will pendulate synchronously and any vibrations of other parts will be damped out."[7]

Luciani[8] adopts the view that the tectorial membrane is the organ for sympathetic vibrations. This view has been advocated by Shambaugh, Hardesty,[9] and others. It offers no explanation of the threefold differentiation of the basilar membrane, and is entirely confuted by the histological work of Keith,[10] ter Kuile,[11] Wittmaack,[12] and others, from which it is clear that the tectorial membrane in the undamaged cochlea is attached to the apex of Corti's organ. Its movements must follow those of the basilar membrane, which its extremely loose texture and delicate stalk of attachment to the denticulate lamina enable it to do without hampering the latter.

If the threefold differentiation of the basilar membrane be admitted, it can no longer be maintained that "there are no structures in the cochlea capable of performing the function of resonators." If the basilar membrane has any functional significance at all, it must be for purposes of resonance. The real difficulty is one inherent in every system of resonators, viz., that no form of resonator is absolutely true in the sense of reacting exclusively to a note of one periodicity. There is always a response, though of less intensity, to tones lying on either side of the principal tone.

Consequently, in the cochlea, resonating elements on either side of the "maximum" must be set in motion at the same time. How is it that we hear a single note of decided pitch? It is plain that at this point we reach the limit of what can be accomplished by the *mechanical* part of the analytical apparatus. The result is handed on to transmitting apparatus through the auditory nerve terminals, and this has to apply the corrective factor. The position of the "maximum point" within the resonating scale determines our perceptions of pitch, whilst the total number of sense elements excited is interpreted as something else, either loudness or volume of sound. For the nature of this corrective action which determines pitch according to the position of the "maximum" on the resonating series we are not entirely without guidance. Albert Gray shows that a similar process of central analysis is applied in the location of pressure sensations by the sense of touch.[4] We have to suppose a "blocking" of the smaller by the greater stimuli, in one or other of the lower centres through which the cochlear nerve fibres pass before reaching the cortex. Such an assumption is an entirely different matter to that which is made by those who hold that the brain analyses sounds according to the frequencies of the stimuli communicated to the nerve terminals in the cochlea. This involves the instantaneous recognition by the presumed central analytical mechanism of the most minute intervals of time, *i.e.* not merely of the vibrational frequencies of the notes from 20 to 30,000 per second, but even of differences in vibrational periods of those notes which are much more minute quantities. Now the measurement of time intervals is in the essence mechanical. Time intervals have always to be converted into measurements of length before they can be estimated. The measurements of length may be those of distances travelled by a uniformly moving body, or of distances travelled by a body with uniform circular motion, or of a body performing harmonic vibrations (which is the linear component of uniform circular motion). This latter method is the most convenient in practice, consequently all our instruments for measuring time depend on harmonic vibrations, *e.g.* the sun's motion as measured on a dial, the pendulum of a clock, the balance wheel of a watch, the tuning-fork in timing physiological experiments; and, for those who accept the resonance hypothesis, the harmonic vibrations of the basilar fibres of the cochlea for measuring the minute periods of sound waves. No one, so far as the writer is aware, has attempted to explain the nature of a central nervous mechanism capable of measuring these periodicities. The advocates of "central analysis" have been content with saying, in effect, that if it cannot be explained at least it cannot be disproved. The only suggestion that has been made, is that there may be central nerve tracts, each "tuned" to the transmission of stimuli of a particular frequency.[13] But how could such tracts be developed? Only through association with some mechanical apparatus capable of applying stimuli of that particular frequency, and no other. In the transverse fibres of the basilar membrane, we have such a mechanical apparatus based on harmonic vibrations. The hypothesis of "central analysis" of sound leads no further.

The contentions put forward by the writer may be briefly summarised as follows :—

(1) The fibres of the basilar membrane are differentiated progressively for length, tension, and mass.

(2) Their vibrational frequencies, therefore, range continuously over a considerable scale.

(3) This differentiation can only be explained by crediting the basilar membrane with the function of analysing sound by sympathetic resonance.

(4) A membrane so differentiated cannot be made to function in any other manner than by sympathetic resonance.

(5) Analysis, as effected by the basilar membrane, is imperfect. Corrections within the central nervous system have to be applied to the results. For these corrections we have analogies in sense of touch and sight.

(6) The measurement of small intervals of time, *e.g.* periodicities of sound waves, can only be made by mechanical means. "Central analysis" of sound is inconceivable.

My warmest acknowledgments are due to Professor J. B. Leathes, F.R.S., head of the Physiological Department at the Sheffield University for affording me laboratory accommodation and every facility for carrying out my experiments, for the kind and stimulating interest he has taken in my work, and for the valuable suggestions he has made from time to time. He has also done me the great favour of placing the assistance of his laboratory engineer, Mr C. E. Stewart, at my disposal. Mr Stewart has made the parts of the model from my scale drawings with great accuracy and skill.

I am indebted to Professor J. R. Milner, F.R.S., for reading my manuscript and criticising it from the physical standpoint.

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