THE COCHLEAR GEOMETRY AS A FREQUENCY ANALYSER

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EVIDENCE concerning frequency analysis which was drawn together from several sources allowed the suggestion to be made that the design of the cochlea—i.e. its internal geometry—was itself a frequency analyser to a first approximation (Naftalin, 1965). Two sets of biological observations which seem to be of fundamental importance from the physical (acoustic) point of view may be cited as offering support for the hypothesis that the internal geometry of the cochlea performs a frequency analysis. First, the cochlea does not increase in size in proportion to the increasing size of animal from mouse to whale. Instead, the cochlea remains within less than one order of magnitude so that relative to body mass the bats and rodents have the largest and cetaceans the smallest cochlea (Hyrtl, 1845; Spector, 1956). Secondly, in the human subject the cochlea reaches adult size by the sixth month of foetal life (Bast and Anson, 1949): thereafter not only is there no further growth but the geometry does not alter.

These biological facts suggest the probability that fixed size and unchanging geometry are important in cochlear function. A brief consideration of the microanatomy of the inner ear leads to the conclusion that such importance as the geometry may have in the cochlea will not be connected with transduction of acoustic to some other form of energy, but will be related to (peripheral) frequency analysis. An obvious advantage which can be immediately pointed out, of having a fixed geometry is that, if a preliminary frequency analysis were thereby achieved, this would have permanent characteristics and a nervous system once trained within this geometry would not have to relearn its frequency appreciation and interpretation with each new period of growth, i.e. frequency analysis would be the same from birth to old age.

An examination of models and sections of the cochlea from the point of view of seeking structures and arrangements capable of performing acoustic analysis by virtue of geometry led to the conjecture that the shape of the tectorial membrane as a long thin wedge (Shambaugh, 1907; Naftalin, Spencer Harrison and Stephens, 1964) could be important in this connection, and that the continuous increase in cross-section and volume of the scalae, particularly of the scala tympani, from apex to base could also be meaningful.

In order to investigate these problems it was necessary to devise a vibration-sensitive probe and to make models, including one no longer

https://doi.org/10.1017/S0022215100067566 Published online by Cambridge University Press

than the cochlea (33 mm.), in which the distribution of acoustic energy could be determined.

Methods

Apparatus:

To make a vibration-sensitive probe various arrangements were attempted using Rochelle salt piezo-electric bimorphs (obtained mounted with leads, from Government Surplus Stores) until a highly responsive device * was made by an approximate copying of the structure of the Pacinian corpuscle. The layers wrapping the crystal were made from "Silcoset 151" (I.C.I.)—a self curing silicone rubber. This type of capsule can be provided with a tail or lead of filterpaper also treated with "Silcoset" (Fig. 1), or with a thin wooden rod (orange-stick), 8–10 cm. long, plugged into small corks at either end and one cork sealed to the centre of the capsule with "Silcoset", the whole system then waterproofed with the same plastic.

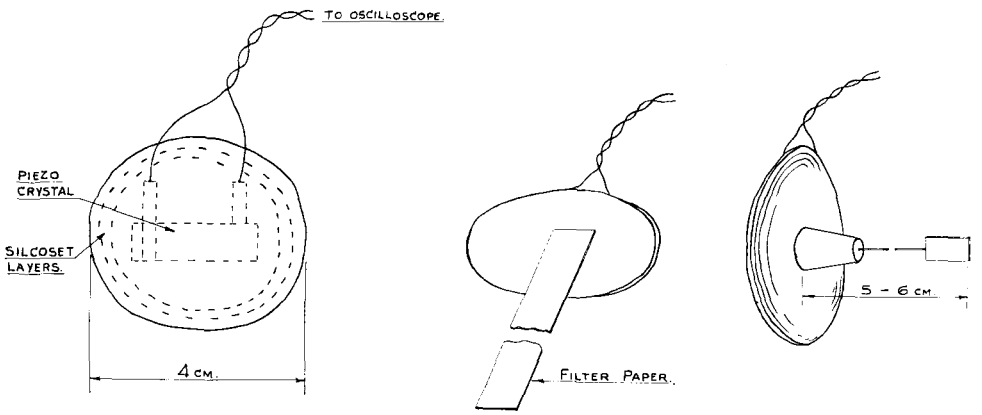


FIG. 1.
Structure of Capsules and Input Leads.

Several modifications of the lead to the capsule were used depending on the experimental arrangement, e.g. for investigating energy distribution in long narrow tubing a length of brazing rod was "Silcoset"-sealed to the corks. This was found more convenient to handle, though giving the same results, than a similar wooden one: the signal in each case was received through the expanded face of the cork at the bottom.

* This device is the subject of British Patent Applications, Nos. 9913/64 and 22884/64 held by the National Research Development Corporation.

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Another arrangement (Fig. 2) consisted of a cork (2 cm. diam. by 2 cm. long) with a slit cut in the tapered end to accept a shortened wooden tongue-depressor; to the narrowed end of the wooden strip was applied a 1 cm. long 2 mm. wide strip of 3 M.M. Whatman filter paper. The whole arrangement was sealed with substantial coating of "Silcoset". The paper tip, about 0·5 mm. thick and 2 mm. wide protruded beyond the end of the wooden holder by about 3·5 mm. This probe was used for investigating the distribution of acoustic signals in the model approximating the dimensions of the cochlea.

When connected to the input of an oscilloscope the crystals proved to have different sensitivities and the more sensitive were selected for work with signals of near-threshold energies. This was determined by

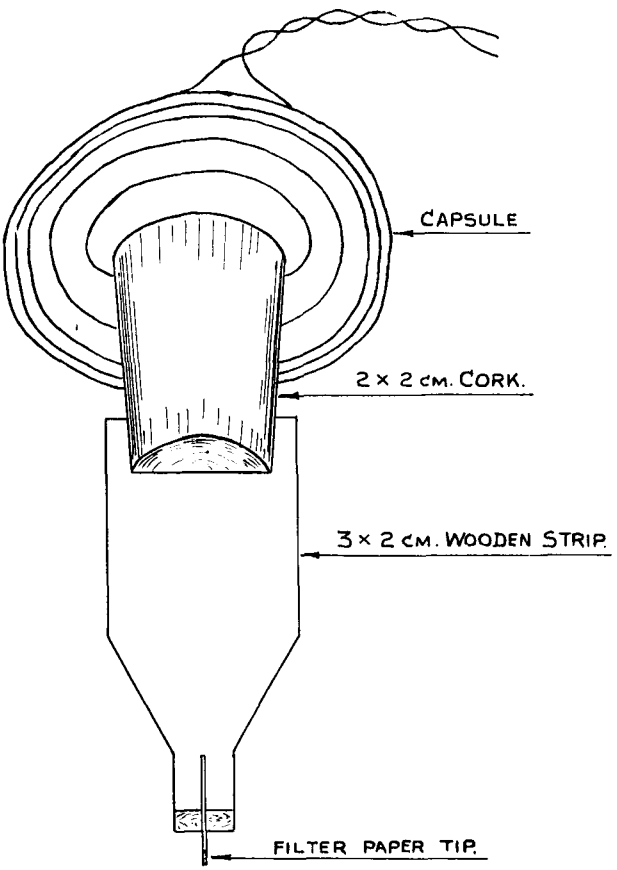


Fig. 2.
Construction of Probe for examining Acoustic Energy Distribution in Small Cavities.

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striking a tuning fork and holding it until the sound was just dying away and then applying the base of the fork to the end of the tail to the capsule. A signal of up to 0·5 volt could still be registered by this device under these conditions. The question of direct mechanical displacement of the crystal within the capsule does not arise since the same response is obtainable with a long flexible tail or string held so as to curve under gravity and the end of the tail applied to the tuning fork.

When working with such crystal devices it is important to remember that each preparation has its own resonant frequencies and these must not be misinterpreted. This point is important also with the cochlear models to be described, since each model has overall natural resonances which could give rise to false observations if the natural resonances are not plotted during the first investigation.

Other instruments used included an audio-frequency signal generator (Advance Type SG 66) and matching electrical to mechanical transducer. A cork was bored half-way to fit snugly on to the mechanical output of the transducer; the inside and outside of the cork were liberally treated with "Silcoset". The face of this cork could then be applied directly or through a "columella", similarly made from orange-stick, cork and "Silcoset", to the "oval window" of the cochlear models.

A set of tuning forks was also used to check on the one hand that the visual signal on the oscilloscope was not a false observation due to electromagnetic induction and on the other that the probe-oscilloscope system was functioning properly.

Models

As the approach to the problem of acoustic energy distribution in the cochlea was biased to begin with in the direction of assuming that the shape of the tectorial membrane was the most important factor, wedges of agar-gel, 6–8 per cent were made and laid in water in an open metal tray. These agar wedges were about 35 cm. long by 6–9 cm. wide, being 4–5 cm. thick at the "apical" end tapering to 0·25 cm. at the "basal" end. The acoustic energy input to the water in the tray was via a metal rod connected to the end of the transducer. Separation along the gel of maximal signals for widely separated frequencies was obtained with this system sufficient to warrant further model making but it was now realized that the geometry of the container was also important. Thus, after the preliminary experiments, the investigation began with the construction of a "Perspex" tank with a uniform cross-section. This tank, Model 1, had dimensions and rubber windows, made from toy balloons, as in Fig. 3 a. and b.

Experience with Model 1 (M.1) enabled a series of modifications to be made progressively so that the models gradually approached the internal geometry of the cochlea. First, a horizontal tapering gap was intro-

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duced, M.2: in the next model this gap was retained but the rectangular design was abandoned, the sides being angled so that a "scala tympani" was formed in which the cross-section gradually narrowed towards the apex of the model (M.3).

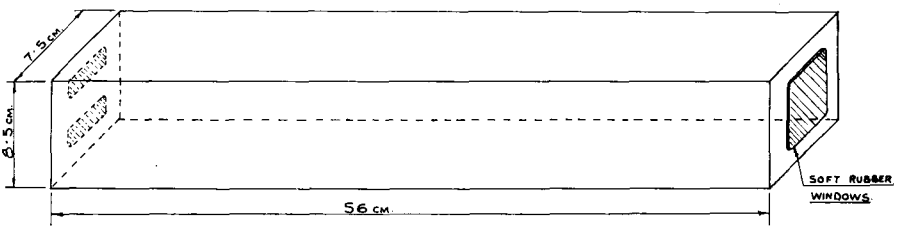


FIG. 3a.
Dimensions of Rectangular Tank made from $\frac{1}{4}$ in. Perspex.

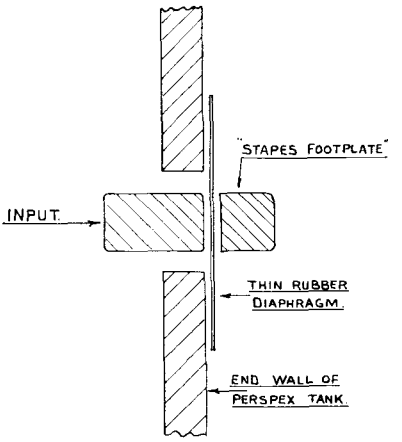


FIG. 3b.
Construction of "Stapes" Input. Rubber-Perspex Joints made with "Bostik" clear adhesive No. 1.

Experience with these models enabled a larger model, M.4, to be designed. The starting point in the construction was the "basilar membrane gap" which was cut, in Perspex, so that it was ten times as wide at the apex as at the base. To accommodate the tip of a vibration probe the narrow (base) end of the basilar gap was made 3 mm. wide; the apical end of the basilar gap was therefore made 30 mm. wide. Limitations of materials and space forbade the model being made to scale as regards length since 210 cm. would have been required. Fortunately, this proved unnecessary, and a length of 53 cm. was found to be adequate (Fig. 4a).

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The new feature in this model (M.4) was the graded "scala tympani". Estimates were made from a number of photomicrographs of longitudinal sections through the cochlea and from cochlear dimensions given in Stevens and Davis (1938) and Littler (1965) that the depth of the "scala tympani" should decrease from base to apex by a factor of three (Fig. 4b) This requirement governed, partially, the cross-section but a kind of

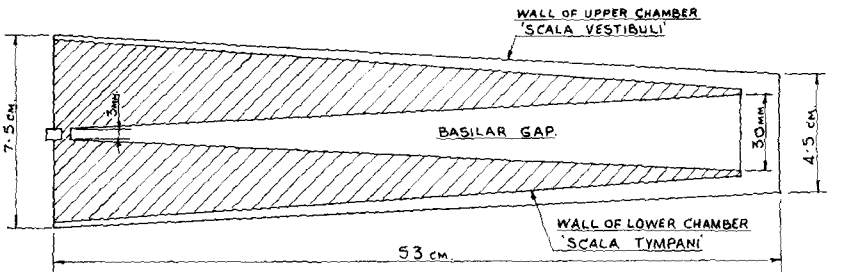


FIG. 4a.
Sectional Plan of M.4. (Not to scale).

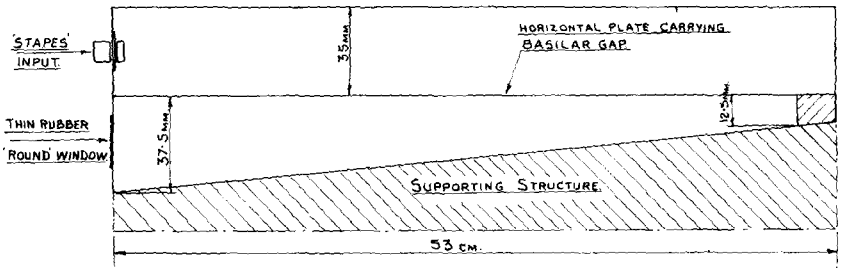


FIG. 4b.
Elevation of M.4. (Not to scale).

cone was achieved by the sides being set at an acute angle to the base, approaching one another at the apex. Thus, in this model, a lower chamber was formed which was widest and deepest at the basal end and narrowest and shallowest at the apical end while the horizontal taper (basilar membrane gap) lay in the reverse direction—narrow at the base and wide at the apex. As with earlier models the basal end was provided with rubber windows; on the upper window was fixed a "stapes footplate" as in Fig. 3b.

To determine that the pattern of acoustic energy being observed was not due to the flat sides and rectangular cross-section of these Perspex models, further models were made using glass tubing of 2·5 cm. diam. and 75 cm. long; over one end of the tube was stretched a large

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size finger stall equipped with a "stapes footplate" and held in position with sticky tape. Larger diameter tubing—drain piping—was also used. Metal cones with circular cross-section were also set up, but the most successful demonstration in this part of the work was obtained with a cone-shaped polythene brush holder, M.5, the dimensions of which are given in Fig. 5.

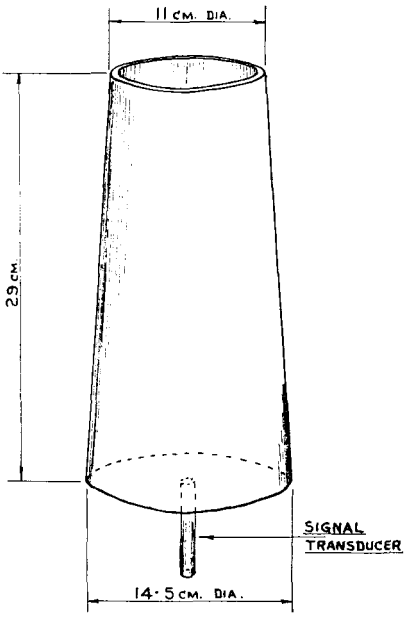


FIG. 5.
Dimensions of Polythene Cone which showed "selection" of Maxima–275 c.p.s. at the narrow top-end to 900 c.p.s. near the bottom.

A further model, M.6, was now constructed having dimensions closely similar to M.4 but with the new features of a semi-circular tapering "scala tympani", made from glass wool rovings and 6 per cent Perspex cement, and of a "vestibule". The latter feature was introduced since in the mammalian labyrinth the longitudinal axis of the stapes is at a right angle to the opening into the cochlea. There is, therefore, in the natural labyrinth, a chamber in which reflection, of an acoustic signal from the stapes, can occur before the signal enters the fluid systems of the cochlea; M.6, Fig. 6 attempted to imitate this arrangement.

Finally, a model, M.7, was constructed in solid Perspex (built up by fusing layers together) into which a cone was drilled 33 mm. long (i.e. the length of the human basilar membrane) with a base opening of 1 cm. diam. An 8 mm. wide gutter with parallel sides was made from

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the top of the Perspex block down to the roof of the drilled out cone, and this roof then entered by a slit 3·5 mm. wide running the length of the roof. Towards the apex the actual opening through the roof narrowed to the dimensions of the cone. A basilar membrane gap was made from thin stiff card soaked in Perspex cement and dried and a horizontal taper cut so that the gap was ten times as wide at the apex as at the base. The card was shaped to fit along the centre of the drilled out cone and extended beyond the base to form the floor of the vestibule (2·5 cm.^{2}) into one side wall of which, i.e. at right angle to the cochlea, was put a small rubber window with stapes and footplate made of Perspex.

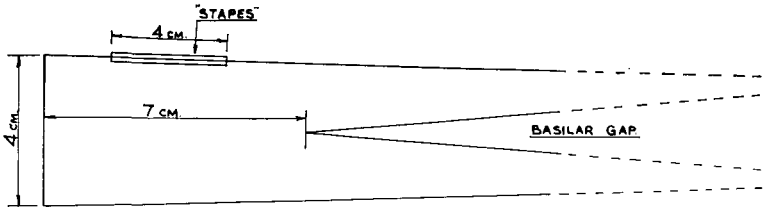


FIG. 6.
Construction of Vestibule in M.6. Plan View of Top of Model.

Gels

Each model had made for it a wedge-shaped gel made from agar-agar (6–8 per cent). The dimensions of the gel were such that the length was smaller than the horizontal (basilar) gap by a "helicotrema", the width was uniform and as wide as the narrow end of the model would accommodate without the gel actually touching the vertical sides; and the thickness, for the larger models, given by a smooth gradient produced by a thickness of 1·5 mm. at the base to 15 to 20 mm. at the apex. These gels were made by allowing the agar to set in Perspex gutters which were raised at the open (thin) end to produce the appropriate slope.

The models were filled with tap water. Observations were most conveniently made at frequencies between 200 and 1,200 c.p.s.

Results

Model 1:

A repeating pattern of maximal and minimal signals was demonstrable for different frequencies, each frequency having its own spatial distribution. If one frequency was put in from the signal generator and a different frequency superimposed with a tuning fork placed on the end

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wall beside the stapes, the pattern of Fourier synthesis was observed on the oscilloscope when the probe was close to the input, but when the probe was moved away towards the further end, the separate signals could be registered by passing through their respective maxima.

The repeating pattern was found to be 3-dimensional since the position of maxima was partly dependent on the depth to which the probe was placed.

Model 2:

The results obtained by introducing the horizontal gap were not greatly different from Model 1 except for some selective emphasis for maxima when the probe-face was between the lips of the horizontal Perspex plates. The emphasis showed greater maxima for the low tones towards the model's "apex".

Model 3:

The gradient in the width of the water column introduced by the non-parallel sides of the model, added to the horizontal tapered gap, considerably increased the selective emphasis of maxima. The emphases could be abolished by inserting strips of Perspex to reproduce the rectangular shape; the simple repeating pattern was then once again in evidence. Both with M.1 and with the rectangular inserts in M.3 the attempt was made to change the spatial distribution of the maxima and minima by the use of a "false" end—a well-fitting sheet of Perspex which could be moved along the tank thus changing the longitudinal dimension and affecting end to end reflection of the signal. The position of the false end was found to make no difference to the repeating pattern until a relatively near approach was made to the input.

Model 4:

In this model a further gradient was introduced into the geometry, as previously described. Even without a gel in place across the basilar gap M.4 showed a selection of frequencies, from 230 c.p.s. at the apical end to 800+ near the base. The selection consisted in the occurrence of unequivocal maxima: for the lower frequencies the repeating pattern could be observed with the signals being of reduced amplitude toward the base. With a good smooth gel in place across the basilar gap the results shown in Table I were obtained. These results were obtained by placing the probe face gently on the gel surface. For some frequencies a spread of perhaps a cm. or more would be found for a maximal signal, but for others the maximum would be restricted to within 1 or 2 mm.

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Similarly repeating patterns were found in the uniform containers with circular cross-section. However, an additional observation was made using the polythene brush-holder, which yielded a frequency analysis from 275 c.p.s. at the top to 900 c.p.s. at the bottom, without the use of a rubber window and stapes, but with the signal transducer output placed directly against the bottom of the jar, as in Fig. 5.

The results with M.6 were closely similar to those obtained with M.4; it was possible, however, to observe a "dead" spot in the centre of the vestibule for practically all frequencies. This "dead" spot was evidenced also in the vestibule of M.7, the 33 mm. long cochlea. Because of the difficulties imposed by the small size the demonstration of frequency separation could not be made in M.7 beyond the finding of maxima for 300, 550 and 700+ at appropriate positions along the gel.

In further experiments the gel was cut across its width to produce four different sections. When placed appropriately across the basilar gap no significant difference in signal distribution was found.

Discussion

The repeating pattern of maxima and minima observed in the containers of uniform geometry would seem to be most easily understood as 3-dimensional interference patterns formed by reflections from the walls and from the air-water interphase. The creation of standing or stationary waves by reflection from the ends cannot explain the findings since the wavelength in water of a 300 c.p.s. acoustic signal is approximately 550 cm. and a train of waves to create superposition is not possible in these conditions. Furthermore, the experiments with the moving ends in M.1 and M.3 prevent the formulation of the concept of standing wave production from purely end reflection.

No attempt will be made here to offer a mathematical analysis. The derivation of a formula to express the wave form in a non-uniform tube is not easy: to try to formulate an expression for the changing relations produced by the three different gradients of the water boundaries would be correspondingly more difficult. The complexity is increased by the fact that the gradient of one of the water boundaries runs in the reverse direction to the other two, and is further increased by the geometry of the gel.

From the biophysical point of view, however, it is worth noting the relation between the gel and the water medium. When the gel was allowed to dry the results became progressively poorer. Thus the water-structure of the gel was seen to be important in the transference of the acoustic signal with minimal loss from the liquid water to the lattice of the soft solid.

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The Cochlear Geometry as a Frequency Analyser

In an earlier discussion (Naftalin, 1965) reference was made to work by Némethy and Scheraga (1962) in which the importance was adduced of hydrogen bonding in water structured in the presence of protein, the water structure being, nevertheless, in equilibrium with the surrounding layers of liquid water. The physicochemical nature of the tectorial membrane (Naftalin, Spencer Harrison and Stephens, 1964) make it a most suitable material for such linking between the liquid water state and the lattice structure of the solid phase, making the transfer of acoustic energy possible without the loss involved in crossing an interphase.

The long thin wedge shape given to the agar gel was thought to be the best approximation to the shape of the natural tectorial membrane (Shambaugh, 1907; Naftalin *et al.*, 1964) and though this wedge-shape is unlikely to be absolutely correct the experiment does demonstrate the great importance of the geometry of a material in the condensed state, in the distribution of acoustic energy within it.

An observation made with these gels may have some clinical importance in the interpretation of diplacusis. The gels are slippery and difficult to hold in position so that a form of "diplacusis" was readily noted for sharply defined frequencies when the gel was moved a cm., from its original position. The sharply defined maxima moved with the gel.

Although most of the experiments used the rubber and Perspex "stapes" as input, the signal could be put in at the apical end with, as in the natural cochlea, the same internal distribution of signals that ocurred with "oval window" input. No "basilar membrane" was used in any of the models and the energy input varied from that equivalent to a strongly sounding tuning fork down to signals near threshold.

It seems reasonable to conclude from these experiments that the internal geometry of the cochlea by its very design constitutes the first peripheral frequency analyser. The absolute size of the cochlea does not appear to be very important so long as the internal proportions of the scalae and other structures are not changed. In nature the relatively constant small size of the cochlea throughout the mammalia is probably an expression of economy of material and is not smaller in the bats and rodents than in larger animals because of the physical limitations imposed by the size and number of the nervous elements required for the large range of frequency appreciation.

In the light of the results and conclusions described in this paper it is worth suggesting that the problem of electrophonic hearing should be reviewed.

Responses from frequencies intermediate to those listed were also obtained but were not always as clear cut due to obvious resonance interference from the model or to harmonics. A number of frequencies showed broader maxima and therefore some degree of local overlap with signals of frequency above and below.

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TABLE I.

POSITION OF MAXIMAL SIGNALS IN MODEL 4 WITH A FULL LENGTH AGARGEL LYING FROM ABOUT 3 MM. AWAY FROM THE "STAPES" WALL TO THE APEX LEAVING A CM. GAP AT THE APICAL END AS A "HELICOTREMA".

Frequency c.p.s.	Cm. from "stapes"	Comments
240	50	Lesser signals at 19 and 10 cm. Harmonics nearer stapes.
256	48·5	
330	43	Sharply defined placing. Lesser signal at 40.
470	30	
512	26·5	
565	20	
675	15	Not well defined; additional signals with maximum
705	13	Fairly sharp placing of signal.
780	5·5	Sharply defined placing.
880	2·5	

Summary

Biological data were interpreted to mean that the internal geometry of the cochlea performed a first frequency analysis, and models were accordingly constructed by a step-by-step series of 'modifications to imitate the essential characteristics of this geometry. Experimental results showed that a frequency distribution did in fact occur, and that this sharpened to a linear analysis when a thin wedge-shaped gel, in imitation of the tectorial membrane, was added to the model.

Acknowledgments

I am indebted to Mr. A. Stephens, M.B.E., and Mr. F. Long for help in the construction of the models and to Mr. A. Stephens for discussion of the observations. I also wish to thank Mr. G. A. Church, Principal of the Technical College, Lincoln, and Mr. F. B. Lockwood of the Electrical Department of the Technical College for loan of equipment and I am most grateful to Mr. J. B. Priestley of the Mechanical Engineering Dept., for executing the drawings.

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