The Space-Time Pattern of the Cochlear Microphonics (Guinea Pig), as Recorded by Differential Electrodes*

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Pairs of very small electrodes were placed in two or more turns of the cochlea of the guinea pig. The cochlear microphonic from a short segment (about 1 mm) of the cochlear partition can thus be recorded, and without contamination by action potentials. The outputs of the second, third, and fourth turns were compared with that of the first turn with respect to both amplitude and phase as a function of frequency. The space-time pattern thus revealed is a traveling wave which passes up the cochlea to a distance that depends on the frequency. The pattern agrees well with that of mechanical movement (Békésy) except that the cochlear microphonic shows relatively greater amplitude (voltage) in the basal turn. Low frequencies travel farther up the cochlea than do high. The velocity (for a 750 cps tone) is about 100 m/sec in the basal turn and about 2 m/sec in the fourth turn. Phase differences of as much as 5π were observed, by means of Lissajous patterns, between the responses of the first and the third turn. Certain discontinuities in the input-output relationships and in phase relationships were found to be a function of frequency and of position along the cochlear partition. These discontinuities occurred at or near the frequencies that showed a phase difference of 2π from the basal end of the cochlea. The relation of these critical frequencies to position along the cochlea constitutes a new "frequency-map" of the cochlea.

The space-time pattern of the cochlear microphonic proved to be very little affected by removal of portions of the bony wall of the cochlea or delivering acoustic energy through a hole near the apex. It is concluded that, in addition to "direct driving" of the cochlear partition by pressure differences between the two scalae and to "surface waves" arising from such driving, the transmission of transverse waves along the solid structures of the cochlear partition must also be included for a satisfactory interpretation of all of the available data.

1. INTRODUCTION

IN a recent paper[1] a new method of recording cochlear microphonics of the guinea pig was described. This method consists of inserting two fine metal wire electrodes on opposite sides of the cochlear partition, one in the scala vestibuli and the other in the scala tympani. Such pairs are placed in various turns of the cochlea and the electrical responses are recorded with differential amplifiers. It was shown that this "differential method of recording cochlear microphonics" gives information as to the response at the particular region in the cochlea where the electrodes are inserted, with little or no contamination by responses from other parts of the cochlea.

The purpose of the present paper is, first, to describe systematically the properties of the cochlear micro-

phonics as revealed by this new method, and then to analyze the mechanical events which must underlie their space-time pattern. An analysis of the electrical processes themselves is also in progress, but for the present we confine ourselves to the space-time pattern of the microphonics regardless of their origin.

2. METHODS

The experiments were done on guinea pigs under dial anaesthesia (0.05 cc of dial in urethane per 100 grams body weight). The surgical operation of opening the bulla and exposing the cochlea has been described elsewhere.[2] With a dental drill, ground to a very fine tip by rotating it on an oilstone, small holes, approximately 30 microns diameter, were made at various points in the upper part of the cochlea. In our earlier experiments the holes in the basal turn were approximately 120 microns in diameter, because more space is available there than in other parts of the cochlea. Into the smaller holes nichrome-steel wires (approximately 20 microns in diameter), insulated with enamel except at the tip, were introduced. For the larger holes in the basal turn enameled silver wire of 100 microns in diameter, similarly scraped at the tip, was used. The length of the scraped region of the wire was generally 100 microns or slightly less, and just this part of the wire was introduced into the hole. In a later stage of the investigation we used electrodes provided with small spindle-shaped globules of "Radio Service Cement." The globules were formed on the wire by dipping it in a dilute solution of the cement and drying overnight. The wire was cut just beyond one of these globules, which then served to control the depth of the tip of the wire and also to hinder outflow of perilymph
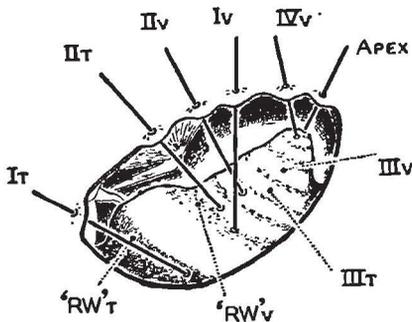

Fig. 1. Cochlea of guinea pig exposed in the bulla, showing typical positions of the various pairs of electrodes. "Iv" designates "Turn I, scala vestibuli," and so on. 'RW'ᴛ designates an electrode in scala tympani as close as possible to the round window.

[1] I. Tasaki and C. Fernández, "Modification of cochlear microphonics and action potentials by KCl solution and by direct currents," J. Neurophysiol. (to be published).

[2] Davis, Gernandt, and Riesco-MacClure, J. Neurophysiol. 13, 73 (1950).

through the hole.[3] The wires were fixed to the edge of the bone of the bulla with dental cement. In the latest experiments the small holes and nichrome-steel electrodes were used in the basal turn also. The small holes caused less injury and, with well-fitting wires, the loss of perilymph became negligible, even with four electrodes in place. The positions of the electrodes selected for the present investigation are shown diagrammatically in Fig. 1. In the apical turn it was not possible to introduce an electrode into scala tympani, due to its extremely small size. We found, however, that a fine wire inserted exactly at the helicotrema can be used as an indifferent electrode for exploring the responses from the apical turn.

The electrodes were connected to cathode-follower preamplifiers, the circuit diagram of which is given in Fig. 2. This cathode-follower stage was introduced to avoid distortion of the recorded potentials by polarization at the tips of the fine nichrome-steel electrodes. With this cathode-follower stage, even with these very small electrodes, we can record the potential of the
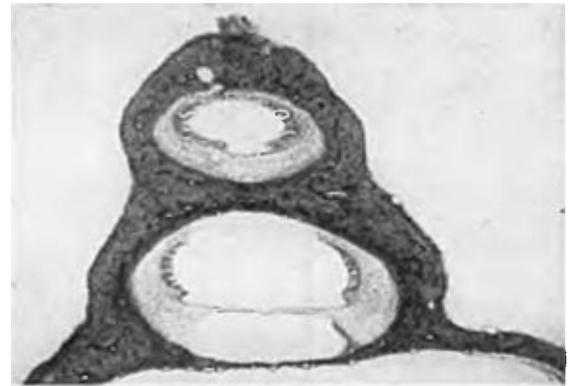
(a)
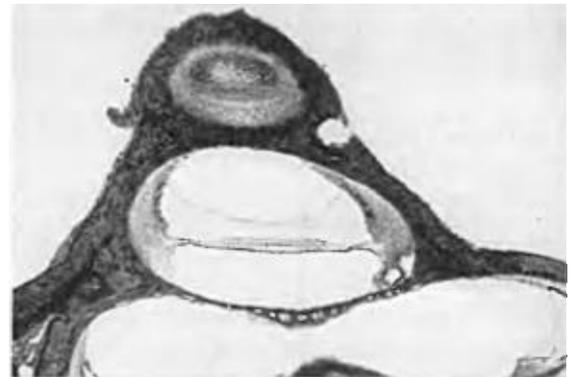
(b)

FIG. 3. (a) Two holes, seen in cross section, entering the third turn of cochlea. These small holes are characteristic of the later experiments of the series. Note that the smaller hole, at "7 o'clock," passing through the spiral ligament to the scala tympani, is about twice the diameter of the blood vessels in the edges of the stria vascularis (pigmented) just above. (b) Two holes, one in the bony wall the other in the spiral ligament of Turn II. These larger holes are characteristic of the earlier experiments of this series. The organ of Corti is cut tangentially in Turn II. The blood vessels in the stria vascularis of Turn III are very well shown.
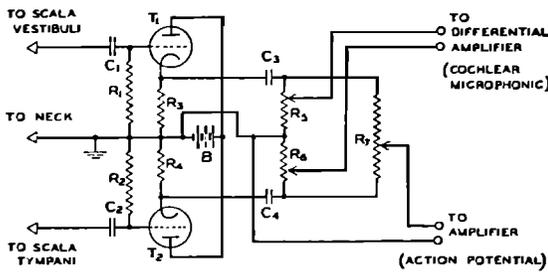

FIG. 2. Cathode-follower preamplifier stage and the balancing network used to eliminate either action potential or cochlear microphonic. Components and values are: R_1, R_2 = resistors (5 to 10 megohm); R_3, R_4 = resistors (9000 ohms); R_5, R_6 = linear potentiometers (100,000 ohms); R_7 = linear potentiometer (500,000 ohms); C_1, C_2 = capacitors (0.02 μf); C_3, C_4 = capacitors (0.2 to 2.0 μf); T_1, T_2 = RCA 1620 in triode connection; B = dry battery (225 v).

fluid, without appreciable change in size or phase, over the entire range of frequencies and voltages that we encounter. The advantage of using this particular network is that we can thereby record action potentials and cochlear microphonics simultaneously, as explained below.

In developing the technique of drilling a hole of the desired size in the right place on the cochlea, the method of postmortem dissection of the cochlea under a microscope was frequently used to check the position of the hole. When more accurate information was needed, the specimen was fixed with Heidenhein-Susa solution, decalcified, imbedded in celloidin, stained with hematoxylin and eosin, and subjected to thorough microscopic examination.

When the surgical operation was satisfactory, the opening of the hole in scala vestibuli or tympani was

[3] Davis, Fernández, and McAuliffe, Proc. Nat. Acad. Sci. 36, 580 (1950).

actually 25 to 35 microns in diameter [see Fig. 3(a)]. When the drill was sharp enough, the size of the hole was determined by the accuracy of the centering of the drill. The opening of the hole near the surface of the bony wall of the cochlea was generally 40 to 80 microns; it varied according to the thickness of the bone. (The conical shape fitted the spindle-shaped globule of "Radio Service Cement" near the tip of the electrode-wire.) When the drill was not accurately centered the spiral ligament became detached from the bone and bits of bone chipped off around the hole; but even from those poor preparations we often obtained fairly large microphonic responses with almost normal time and space patterns.

In some of the preparations in which we wanted to drill a hole into scala tympani of the third turn, we later found that the hole had not entered the scala tympani but the scala media of the same turn. As the response of the third turn in those preparations did not differ from that of other normal preparations, we did
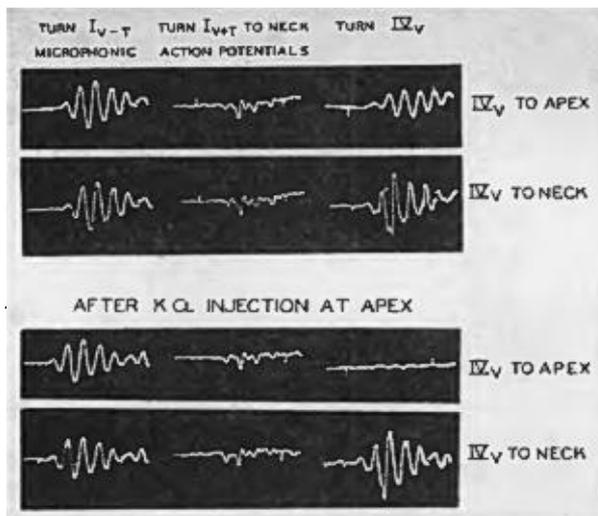
FIG. 4. Responses to a 500-cps tone-pip recorded from Turn I (left and center columns) and from Turn IV (right). Differential electrodes (Fig. 1), balanced to eliminate action potentials (Fig. 2), were used for the left column. Differential electrodes, balanced in parallel and referred to the neck, show action potentials in the center column. The markers before and after (or on) the tone-pips were introduced electrically and serve as reference points for time measurements.

not discover the error in operation until the histological examination was made. In some other preparations, the hole did not penetrate the spiral ligament of the third turn and the tip of the electrode apparently stayed in the layer of ligament. In those cases, too, the responses from the third turn were good and the phase pattern was normal.

In all of our histological preparations the basilar membrane and Reissner's membrane were intact. It is our impression, from other experiments, that a surgical injury of these structures leads to deterioration of the response of the whole cochlea.

For sound stimuli we employed pure tones and also brief "tone-pips" such as we have described elsewhere.[2,4] The transducer was an Atlas PM-25 loudspeaker. It was coupled to the animal's ear by a piece of garden hose and an otological speculum. The latter was sewed securely in place to insure a closed acoustic system. The surgical wound was usually closed lightly but not sewed, and it could easily be opened to remove excess fluid if any accumulated in the bulla.

3. PRINCIPLE AND METHOD OF ELECTRONIC CANCELLATION

It is well known that the cochlear potential, as recorded with one electrode introduced into the basal turn or the apex of the cochlea and the other on the neck of the animal, consists of at least two components.[2,3] One is the cochlear microphonic, which reproduces very closely the time course of sound waves applied to the ear. The other is the action potential,

⁴ Davis, Silverman, and McAuliffe, J. Acoust. Soc. Am. 23, 40 (1950).

which represents the nerve impulses in the fibers of the auditory nerve ("NI") and probably of the brain stem as well ("NII"). The action potential "spike" has a nearly constant shape and may cause serious distortion of the smooth course of the cochlear microphonic. We shall report elsewhere the details of our studies of the NI action potential, but it seems very clear that NI depends upon the activity of the nerve fibers between the spiral lamina and the internal auditory meatus. The distribution of potential caused by this activity is such that the potential does not vary much from point to point within the basal turn of the cochlea. The cochlear microphonic, on the contrary, changes its magnitude and sign when the exploring electrode is shifted from the scala tympani to the scala vestibuli.

Let "Iv-Neck" denote the potential generated in response to a pure tone and recorded between one electrode in scala vestibuli of Turn I and another on the neck; and let "It-Neck" denote the corresponding potential recorded with one electrode in scala tympani of the same turn. Then we have the relation

$$Iv\text{-Neck} = E_{Iv} \sin\omega t + AP, \quad \text{and} \quad It\text{-Neck} = E_{It} \sin\omega t + AP,$$

where E_{Iv} and E_{It} are the amplitudes of the microphonic potentials recorded from Iv and It, respectively, and ω is 2π times the frequency of the sound. Since, as mentioned above, $E_{It} = -\alpha E_{Iv}$ (α being a positive factor) it is possible to separate the microphonic and the action potentials with the cathode-follower stage shown in Fig. 2 by adjusting the potentiometers R_5 and R_6 in such a manner that the two cathode-followers give exactly the same voltage amplification. The outputs are led to a differential amplifier. Then

$$Iv - It = (1+\alpha)E_{Iv} \sin\omega t.$$

That is to say, the potential difference between two small electrodes in the basal turn consists of pure microphonic potentials, and the action potential which was common to both recordings relative to the neck is eliminated. (In this discussion and in our experiments we disregard the relatively small "summating potential" described by Davis, Fernández, and McAuliffe.[3] As we shall show elsewhere, this potential makes a contribution to the potential difference $Iv - It$, and sometimes makes it deviate from a pure sinusoidal form.)

The cochlear microphonic is eliminated by adjusting the potentiometer R_7. Denoting the resistances above and below the center tap of the potentiometer R_7 by r and s, respectively, the potential difference between this center tap and the ground is given by

$$\{(E_{Iv} \sin\omega t + AP) - (E_{It} \sin\omega t + AP)\}\frac{s}{r+s} + E_{It} \sin\omega t + AP$$

$$= AP + \left\{-\alpha + (1+\alpha)\frac{s/r}{1+s/r}\right\}E_{Iv} \sin\omega t.$$

Therefore, when

$$s/r = \alpha,$$

the second term in the last expression drops out, and the pure action potential record can be obtained. Under the conditions of our experiment, the factor α was generally between 0.7 and 1.1. As this value varies slightly from preparation to preparation and also with the frequency in one and the same preparation, we had to adjust the potentiometer R_7 in every experiment to eliminate the sinusoidal component of the potential as completely as possible.

Figure 4 illustrates the separation of the cochlear microphonic from the action potentials. The stimulus is a 500-cps tone-pip which elicits three or four volleys

of action potentials. A satisfactory isolation of the microphonic from Turn IV was obtained by using a reference electrode that entered the cochlea exactly at the apex (upper right). The response beneath it, obtained with the neck as reference point, contains an obvious mixture of cochlear microphonic and action potential. The microphonic that is recorded in this way is not generated at the apex, however. First, the latency of the microphonic (relative to the arbitrary marker) is only very slightly longer than in Turn I but very much shorter than in the upper record (IV-Apex). (The differential response from Turn IV-Apex lags considerably behind the response from Turn I because of the time required for the traveling wave to reach Turn IV.) Second, the response from IV-Apex can be eliminated by local injection of an isotonic solution of potassium chloride without appreciably affecting the response recorded between Turn IV and neck. In the experiment of Fig. 4 a hole about 50 microns in diameter was drilled into scala vestibuli near the helicotrema. After the first two sets of responses had been recorded a drop of isotonic KCl solution was introduced by means of a small pipette. In a short time the response from IV_v-Apex disappeared (as described in detail elsewhere[1]) while the conventional IV_v-Neck response remained almost unaltered.

This experiment is clear proof that a large part of the microphonic in the IV_v-Neck response is generated in the basal part of the cochlea even when the stimulus is a rather low frequency pip or tone. A closer study of the latency (see below) of the remaining response (lower right in Fig. 3) indicates that in this case most of it was generated in the apical half of Turn I and the basal half of Turn II. Symbolically we can write

$$(IV_v\text{-Neck}) = (\text{microphonic from Turn IV}) + (\text{microphonic from basal turn}) + (\text{action potential}).$$

The last two terms in this expression are common to the responses from both IV_v-Neck and Apex-Neck and they therefore disappear from the IV_v-Apex combination.

The strong microphonic response from the lower part of the cochlea that appears in IV-Neck is rather surprising. It appears also when one electrode is placed in III or II and the other is on the neck.

The most popular theory of the origin of the cochlear microphonic is that an electric current is generated by the cells in the organ of Corti in response to sounds. In a series of unpublished experiments, we have obtained very strong evidence in support of this theory. The current generated by these cells should produce a field of potential in the fluid medium inside the cochlea.

It has been pointed out in a previous paper,[1] however, that the structure of the cochlea is such that the current produced by a group of cells in one restricted region of the cochlea does not spread along the cochlear partition more than 1 to 2 mm. The electrical impedance across the cochlear partition was found to be 100 to 200 ohms-cm in the basal turn at an ac frequency of 500 cps and about 15 percent less at ac frequency of 6000 cps. The longitudinal resistances of the two scalae are determined by the cross-section areas of these scalas and by the specific resistance of the perilymph, which is of the order of 70 ohms-cm. The areas of the two scalas of the guinea pig cochlea were measured recently

by Fernández.[5] At the point in the basal turn where the area of the scala vestibuli is about 0.5 mm², it is expected, from a simple one-dimensional picture of current spread along a partition (well known in nerve physiology), that the current spreading along the cochlear partition should decay at a rate of about ⅓ per mm. In the upper turns of the cochlea the two scalas are smaller and the partition is wider, and the decay of the spreading current should therefore be more rapid in the upper turns than in the basal turn. The fact (see Sec. 6) that we could (by the differential method) record cochlear microphonics having a phase difference of 90 degrees at two points in the third turn separated by about 1 mm is strong support for our argument. It is therefore not legitimate to attribute the "ghost microphonic" picked by the electrode on the neck in the experiment of Fig. 4 to the direct spread of current along the cochlear partition from the basal turn to the region of the lead-off electrodes.

Our explanation of this "ghost microphonic" is to ascribe it to the variation in the ratio of the cross-section area of the scala vestibuli to that of the scala tympani.[5] This ratio shows a minimum in the basal turn at a point about 3.5 mm from the round window. At this point, scala vestibuli is about 0.4 mm² and scala tympani is about 1.2 mm² giving a ratio of approximately 0.3. The ratio reaches its maximum in the third turn, where scala vestibuli is about 2.6 times as large as scala tympani. Between these two points in the cochlea, the cochlear partition is, so to speak, "tilted" in the cochlear duct, with the upper surface of the partition facing toward the third turn. Without going into analytical treatment of the problem, it should be clear that a source and a sink of electric current located in this tilted region of the cochlear partition (with the moment of the doublet perpendicular to the plane of the partition) can produce a difference of potential between the two ends of the cochlea even where there is no direct spread of current from the active region. The ratio of the cross-section areas of scala vestibuli to scala tympani changes continuously as a function of distance along the length of the cochlear partition. The "ghost" microphonic is therefore produced by an integration of this tilting effect over the whole cochlea. According to the result of direct measurements,[1] the potential of the neck is very close to the average of the potentials of the two scalae in the basal turn. The electrode on the neck is therefore effective in picking up this somewhat disturbing "ghost."

4. OUTLINE OF EXPERIMENTAL PROCEDURES

We have measured the following relationships of the cochlear microphonic to the parameters of the stimulus and to the positions of the differential recording electrodes: (a) the input-output characteristic, i.e., the voltage of the microphonic as a function of the input sound-pressure level, (b) the voltage as a function of frequency, (c) the relative sound pressure required to produce a given relative output voltage, (d) the time required for a given traveling wave to go from one position to another along the cochlea, (e) the phase relations between the microphonic outputs at different positions as a function of frequency; and we have calculated (f) the velocity of the traveling waves. In several of these functions we have found a critical frequency at which there is a more or less clearly marked "break" or discontinuity. The critical frequencies are closely related to the positions of the exploring electrodes.

In general we have measured differences between the responses from two positions on the cochlea. Turn I,

[5] C. Fernández, "Dimensions of the cochlea (guinea pig)," J. Acoust. Soc. Am. (in preparation).
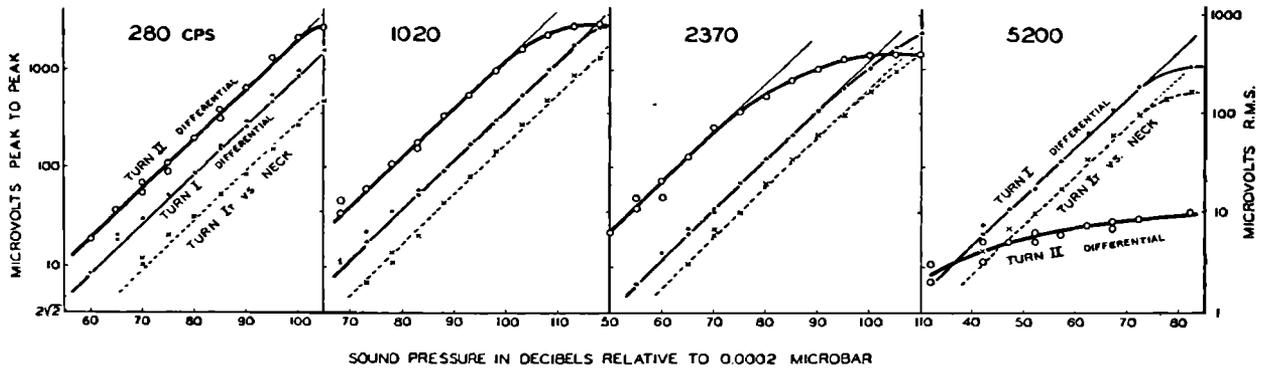
FIG. 5. Voltages (peak-to-peak) of cochlear microphonic from Turn I and Turn II as a function of sound-pressure level. Heavy line=Turn II (differential electrodes): lighter line=Turn I (differential): broken line=Turn I (scala tympani) referred to neck. This last is practically the equivalent of the classical round-window-to-neck combination. Measurements were from oscillograms.

or more exactly the position on Turn I 3.5 mm from the basal end of the basilar membrane, has been the usual reference point. In measuring the output from one of the apical turns as a function of frequency we adjusted the sound-pressure level in such a way as to maintain a constant output from Turn I. The measurement thus tells us the *relative* output, with the basal turn as the reference point. The great advantage of this procedure is that the cochlea provides its own internal control and we avoid difficulties and uncertainties arising from measurements of sound-pressure level and from the transmission characteristics of the middle ear.

5. INPUT-OUTPUT RELATIONSHIP OF THE COCHLEAR MICROPHONIC

Many previous investigators[6,7] have measured the electrical output of the cochlea as a function of the sound-pressure level of the stimulus. As a rule the electrical potential was measured between the round window and a reference electrode on the neck. The output has therefore contained action potentials, and also cochlear microphonic from the middle and perhaps also the apical turns (see Sec. 3). We have shown that our differential method measures the cochlear micro-
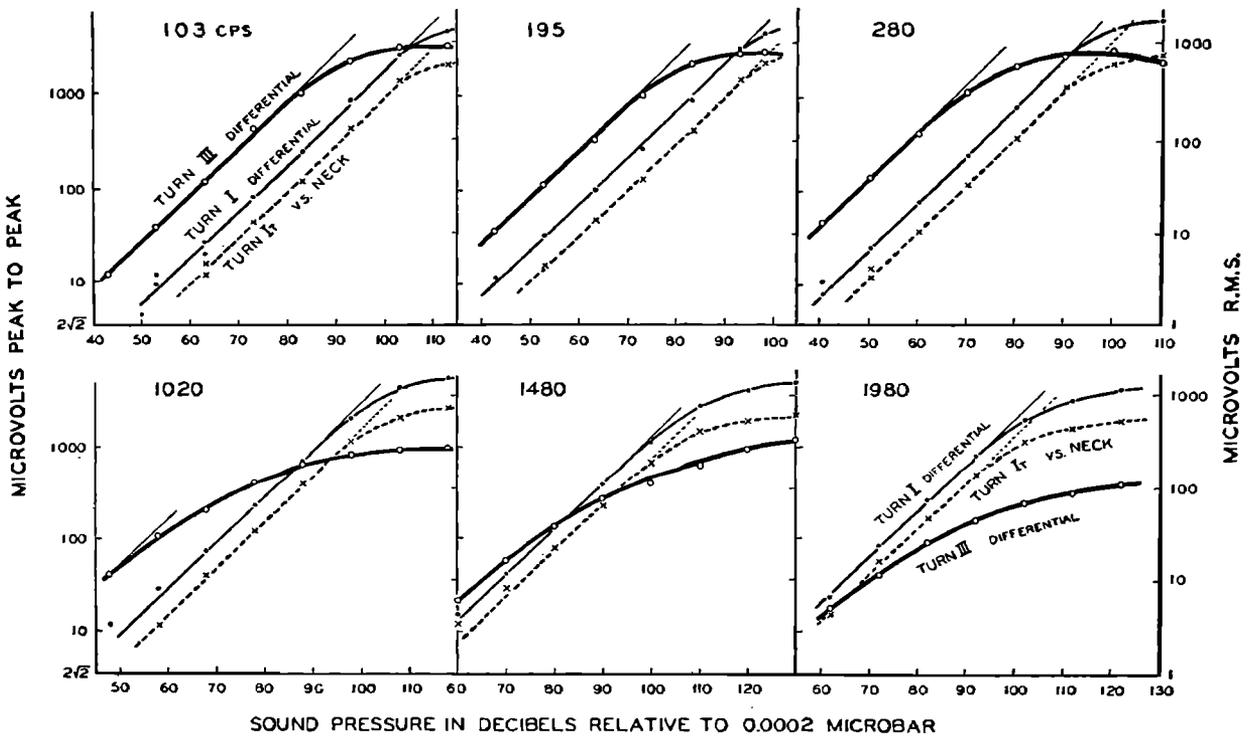

FIG. 6. Similar to Fig. 5 except that the heavy line represents the output from Turn III (differential).

[6] E. G. Wever, *Theory of Hearing* (John Wiley and Sons, Inc., New York, 1949).
[7] S. S. Stevens and H. Davis, *Hearing* (John Wiley and Sons, Inc., New York, 1938).
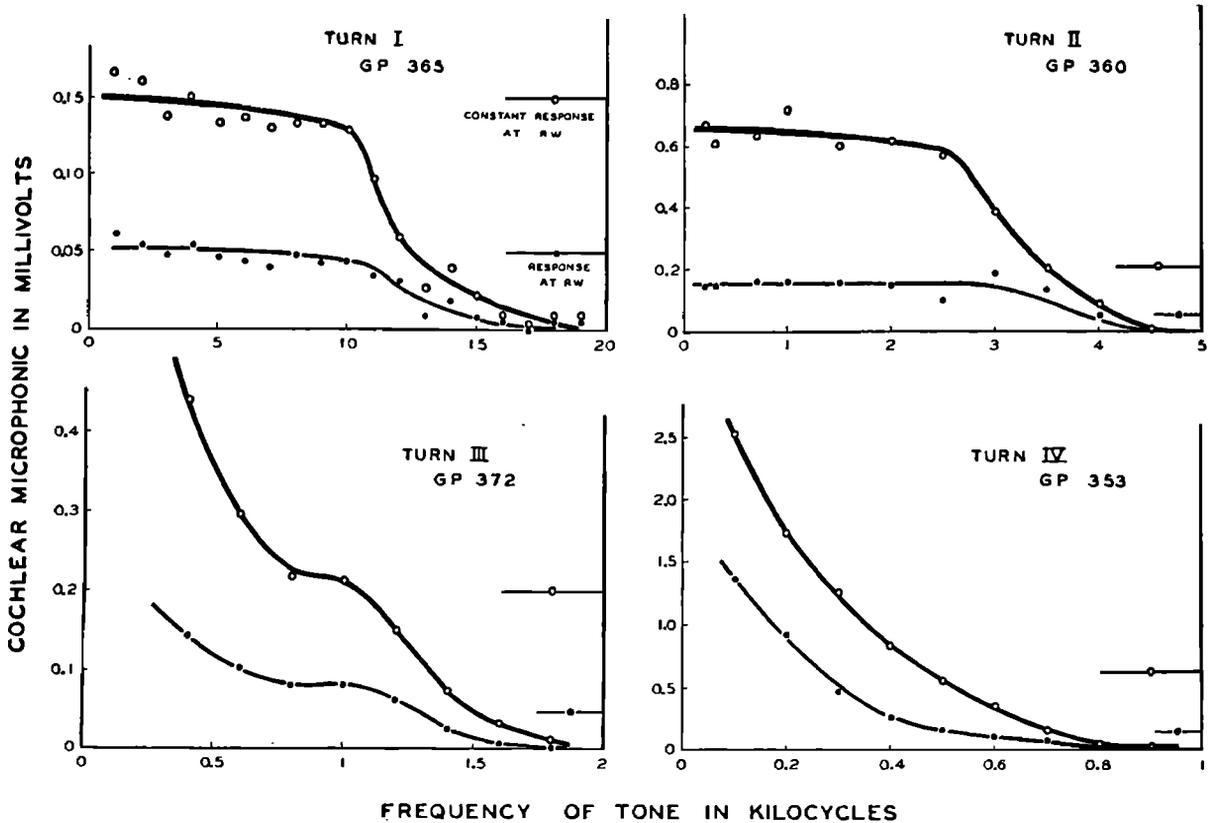
FIG. 7. Voltage of cochlear microphonic (peak-to-peak) as a function of frequency. The sound-pressure level was adjusted at each frequency to keep the output from Turn I (or 'RW' for the Turn I experiment, No. 365) constant at the level shown by the corresponding horizontal line at the right of each graph. Note that the scales are all linear but differ in extent from graph to graph.

phonic (without action potentials) of only a very short segment (1 or 2 mm) of the basilar membrane.[1]

A typical set of data for Turns I and II, obtained with pure tones of various frequencies, is shown in Fig. 5. The voltages of cochlear microphonics are plotted on a logarithmic scale. Responses below about 10μv (peak-to-peak) were not measured because of the uncertainty introduced by the background noise, but there is no reason to doubt that the linear relationship shown in the figures continues as the strength of the stimulus is decreased. The voltage of the cochlear microphonic is in general a linear function of the sound-pressure level (a straight line with slope of 1.0 in the double-logarithmic coordinates of Fig. 5 and 6) up to a limit that varies with the frequency of the tone and also with the position of the electrodes. Above this limit the curves flatten off. At high frequencies the output then passes through a maximum, while at lower frequencies the wave form becomes so distorted by harmonics that measurements of peak voltage at high intensity become meaningless.

These observations are in good agreement with the classical measurements made from the round window. The two sets of data from Turn I parallel one another, although the voltages from the differential electrodes in Turn I are systematically a little higher than those

measured between scala tympani and the neck. The results shown in Figs. 5 (Turn II) and 6 (Turn III) are typical of five similar experiments. None of our input-output curves for differential electrodes have shown straight-line segments with slopes that differ significantly from unity.

We define the "limit of linearity" as the point of divergence by 1 db between the straight line fitted to the low intensity points and a smooth curve drawn through the high-intensity points. This limit is reached at lower and lower levels of output as the frequency is increased. The progression is clearest at Turns II and III (heavy lines in Figs. 5 and 6). At Turn III the limit is reached at lower frequencies (for comparable strengths of stimulation) than at Turn II. For example the Turn III curve at 280 cps corresponds approximately to the Turn II curve at 2370 cps, and a very flat curve like that for 5200 cps at Turn II is found at Turn III for frequencies near 2300 cps (not shown in the figure).

In general the input-output function becomes flattened and nonlinear under conditions which are a function of both frequency and of position along the cochlea. At a given position the restricted electrical output for the higher frequencies is obviously not due to the inability of that section of the cochlea to produce
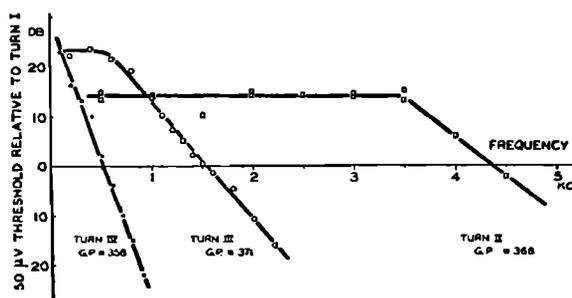
FIG. 8. Differences in sound-pressure levels required to produce a cochlear microphonic of 50 microvolts (peak-to-peak) at Turn I and at Turn IV, or III or II. Note that the scale of sound-pressure level is logarithmic (decibels) but that the frequency scale is linear.

electricity. The output is large enough at slightly lower frequencies. We believe that *the restricted output at the higher frequencies is due to a failure of the mechanical amplitude of movement at a particular point to increase linearly with sound-pressure level beyond a certain limit. The higher the frequency the lower is the intensity of this limit of linearity.*

6. THE AMPLITUDE OF THE COCHLEAR MICROPHONIC AS A FUNCTION OF FREQUENCY AND POSITION

Figure 7 shows the results from four typical experiments in which the cochliar microphonic, recorded by differential electrodes, was measured as a function of *frequency*. The intensity of the stimulus was adjusted as necessary, as the frequency was changed, to keep the output constant at Turn I. (In order to study the relationships at "Turn I" another pair of differential electrodes was placed in Turn I still closer to the round window. This second pair ('RW' in Fig. 1) served as monitor for the conventional Turn I electrodes.) Two different levels of output for the monitor electrodes were used in each experiment; they are indicated by the short horizontal lines at the right of each graph in Fig. 7. These levels lay on the linear part of the input-output curves for Turn I (cf. Figs. 5 and 6) at all frequencies employed.

The output from the monitor electrodes changed somewhat as the frequency changed unless the voltage to the loudspeaker was adjusted. In general the adjustments were not large. We calibrated the sound-generating system, using a 1-cc coupler and a 640-AA microphone, and found that many of the necessary adjustments corresponded to demonstrable resonances and antiresonances in our sound system. Because of the uncertainties of coupler calibrations at high frequencies, the resonances in the ear canal and the unknown transmission characteristics of the middle ear, we have not attempted to express our data in terms of input sound-pressure level, but we can say that over the range of frequencies that includes the abrupt changes in output at Turns II and III the input sound-pressure level actually remained approximately constant.

The response at "Turn I," 3.5 mm from the basal end of the basilar membrane, remains nearly constant relative to the response at "*RW*," 2.0 mm closer to the round window, as the frequency is raised from 1000 to 11,000 cps. Above 11,000 cps, however, the ratio falls off exponentially. The rate of fall is about 3 db per kilocycle. The frequency at which the "break" occurs is regularly a little lower when measured for a higher monitor voltage (cf. Fig. 7). (It is worth noting that the difference in response from the two pairs of electrodes ('RW' and 'Turn I') within 2.0 mm of each other becomes as much as 20 db or more at frequencies above 15,000 cps. This is further evidence that our differential electrodes are highly selective and pick up the output from only 1 or 2 mm of the cochlear partition.)

The output at Turn II, when the output from the conventional Turn I electrodes is held constant, also falls off sharply above a particular frequency. The average frequency of the "break" was 3400 cps in six experiments. The measurements are more erratic at Turn II than at Turn I, however, because the sinusoidal shape of the oscillogram of the cochlear microphonic is almost always distorted in the frequency range from 2700 to 4000 cps. The distortion is worse at high output levels and the form varies as the frequency is changed. We attribute this distortion to an action potential (and/or a "summating potential"[3]) that is generated in the cochlear duct near the electrodes. We shall discuss this additional component in another communication. Its presence, however, makes the identification of the "break" and the estimation of the slope of the exponential fall less certain than at Turn I. Our best estimate of the slope is 12 db per kilocycle.

At Turn III the relation of output to frequency shows another complication. The final exponential fall with increasing frequency is still clear and a "break" can usually be identified at about 1250 cps. The ratio of the output at Turn III to the output at Turn I is not substantially constant, however, as in Turns I and II. Instead there is another exponential fall with increasing frequency, as shown in Fig. 7. The rate of fall is less rapid than the terminal fall, the most characteristic slopes being about 10 db and 20 db per

TABLE I. Terminal fall of microphonic with increasing frequency (see Figs. 8 and 9).

Turn	Rate of Fall db/kc	Method	Number
I	3	Amplitude	3
	3	Threshold	2
II	12	Amplitude	6
	18	Threshold	3
III	21	Amplitude	8
	26	Threshold	8
IV	30	Amplitude	4
	50	Threshold	4

kilocycle, respectively. The slopes varied considerably from one preparation to another and sometimes no clear "break" or "angle" appeared, as if the slope of the upper segment of the curve sometimes became as great or greater than the rate for the lower segment.

Some of this variability of slope may have been due to the slight surgical injury involved in the introduction of the electrodes. Deliberate and more severe injury was found (in three experiments) to (a) shift the "break" to a *lower* frequency and (b) to increase the rate of the terminal fall of the curve.

At Turn IV no plateaus and no clear breaks in the output curves could be found. The curves shown in Fig. 7 are characteristic of four such experiments. The ratio of the output to that of Turn I falls along a single curve that is best described as "nearly exponential." The rate of fall is about 30 to 35 db per kilocycle.

Another method for determining the relationship between the amplitude of the microphonic, the frequency and position is to measure the difference in sound-pressure level necessary to produce the same voltage at Turn I and at some more apical position. The method is legitimate because the output is directly proportional to the sound-pressure level (see Figs. 5 and 6), but obviously the measurements must be confined to the ranges of frequencies and intensities over which this simple linear relation holds at Turn I. A change in the relation between the necessary sound-pressure levels at the two positions indicates that the input-output relation has ceased to be simple and linear at one (or both) of the positions. Examples of very clear breaks and exponential falls are shown in Fig. 8. The scale of ordinates is logarithmic (decibels) and an exponential fall therefore appears as a straight line sloping downward toward the higher frequencies.

The slopes found by these two methods are summarized in Table I. The threshold method regularly yielded steeper terminal slopes. The frequencies of the "breaks" (cf. Fig. 13) shown by this method agree with those shown by the first method, however, within the range of variation shown by each method alone. No clear "breaks" were found by either method at Turn IV, only the falling exponential segment.

7. FREQUENCY ANALYSIS IN THE COCHLEA

It is obvious from Figs. 6 and 7 that the cochlea acts as a frequency analyzer in the sense that the higher the frequency of a tone, the nearer to the round window does it encounter a region of inefficient nonlinear response. The behavior of the cochlea as a frequency analyzer is illustrated directly by oscillograms in Figs. 9 and 10. In Fig. 9 the amplifications in the three channels were adjusted to make the waves approximately equal in height at 200 cps and the response in the basal turn was held constant (to the nearest 1.0 db step) as the frequency was increased. The response at Turn II went through a very slight maximum (relative to the basal turn) at 2000 cps and then fell off rapidly.
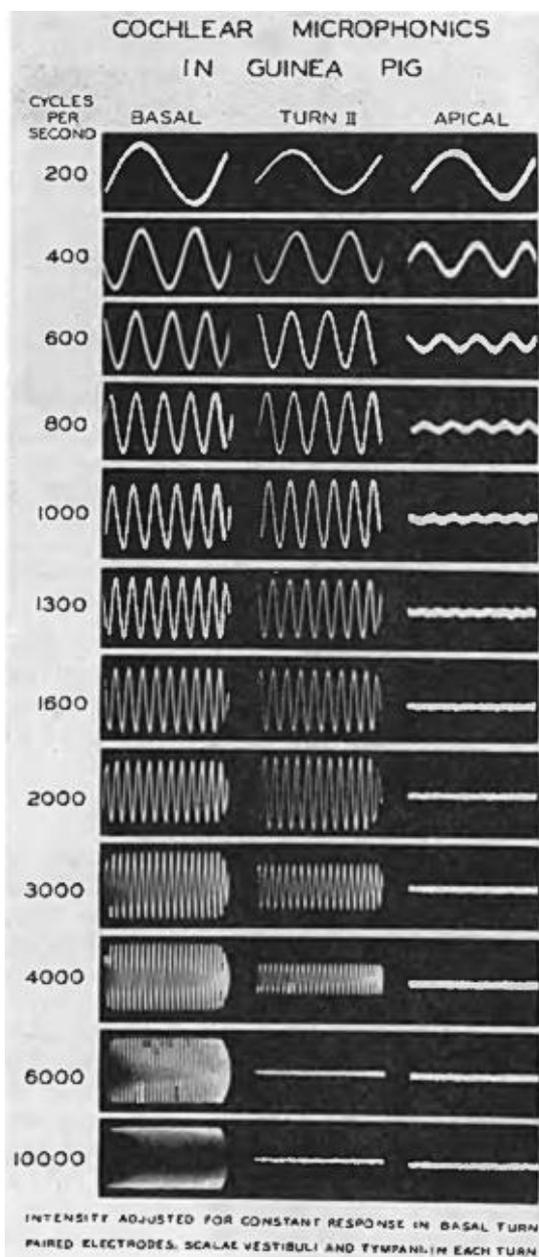

Fig. 9. Simultaneous oscillograms from Turns I, II, and IV. The amplifications of the three channels were initially adjusted to give approximately equal responses in all three turns at low frequencies. As the frequency was changed the sound-pressure level was adjusted to maintain a constant response (200 μv, peak-to-peak) from the basal turn (left column).

The response in Turn IV (apical) fell when the frequency was increased from 200 to 400 cps. At 1600 cps the response at the apical turn was no longer visible, but the responses from the basal Turn (I) and from Turn II were still equal. At 10,000 cps the original voltage could still be obtained from the basal turn, but no response could be seen from Turn II.

Figure 10 shows that complex tones are separated in the same way. The separation of 8000 from 250 cps
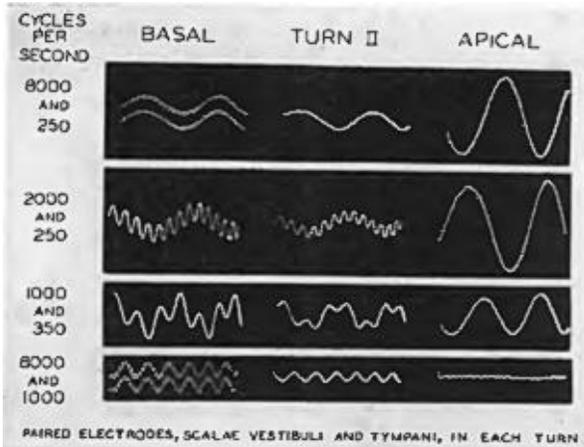
FIG. 10. Same as Fig. 9 except that the amplifications are the same in all three channels. The intensities of the two tones, at the frequencies indicated at the left, were adjusted to give equal responses (160 μv, peak-to-peak) in the basal turn. The corresponding response from Turn IV was exceptionally large in this experiment (680 μv).

takes place between Turns I and II. So does the separation of 8000 from 1000 cps; but 250 cps reach the apical turn while 1000 cps do not. Tones of 2000 and 250 and also 1000 and 350 cps are separated between Turns II and IV.

8. PHASE SHIFT IN THE COCHLEA

Direct observations of the basilar membrane and the study of appropriate models by Békésy,[8] and mathematical formulations of the action of the cochlea by Reboul,[9] Ranke,[10] Zwislocki,[11] Peterson and Bogert,[12] and Fletcher[13] have led to the well-established concept of a traveling wave as the space-time pattern of activity in the cochlea. (In this context we use the term "traveling wave" to describe the space-time pattern of the movements of the cochlear partition without any implications as to the mechanism by which that pattern is generated.) We have measured the phase shift of the cochlear microphonic (relative to a reference position in Turn I) at different positions by means of Lissajous figures on the oscilloscope, obtained from the interaction of the responses from two pairs of electrodes. This is a very convenient and accurate method for measuring the phase shifts associated with the traveling wave.

Typical series of Lissajous patterns obtained from Turns I and III are shown in Figs. 11 and 12. Figure 11 shows oscillograms taken at frequency intervals

[8] G. v. Békésy, Akust. Zeits. 7, 173 (1942); J. Acoust. Soc. Am. 21, 233 (1949).
[9] J. A. Reboul, J. phys. et radium 9, Ser. 7 (1938).
[10] O. F. Ranke, Akust. Z. 7, (1942); J. Acoust. Soc. Am. 22, 772 (1950).
[11] J. Zwislocki, Acta Oto-Laryng. Suppl. 72 (1948); J. Acoust. Soc. Am. 22, 778 (1950).
[12] L. C. Peterson and B. P. Bogert, J. Acoust. Soc. Amer. 22, 369 (1950).
[13] H. Fletcher, J. Acoust. Soc. Am. 23, 637 (1951).

corresponding to $\pi/4$. Figure 12 shows only the figures at integral multiples of $\pi/2$. In this experiment the series could be extended to a phase difference of 4.5π. The greatest phase difference we have been able to measure with certainty is 5π.

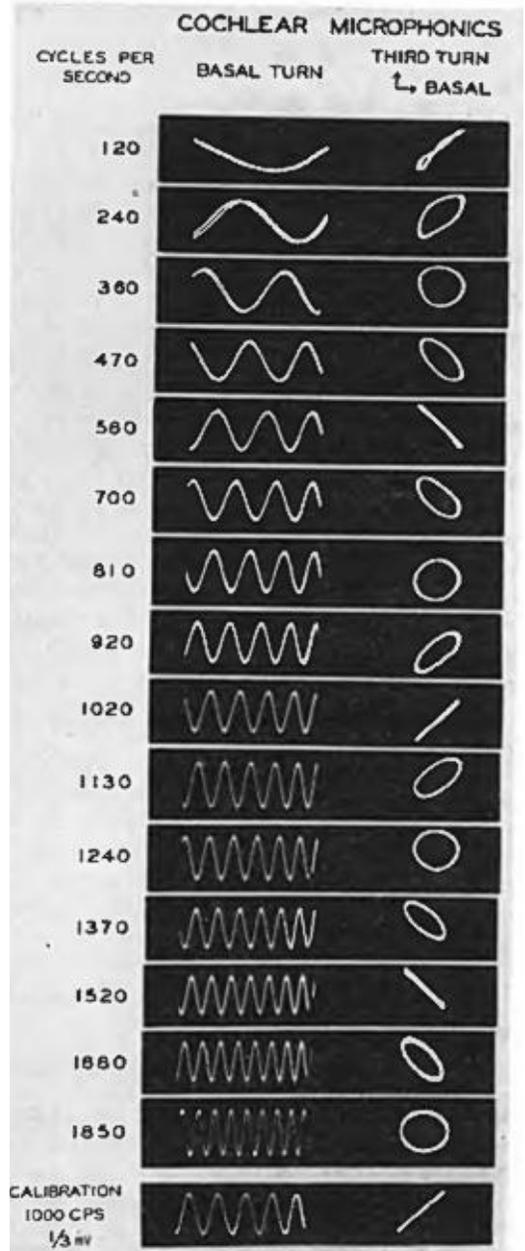The phase differences of π and its integral multiples

FIG. 11. Lissajous figures obtained by connecting the output from differential electrodes in Turn III to the vertical plates and from Turn I to the horizontal plates of the oscilloscope. The frequency was adjusted to give straight lines (integral multiples of π), "circles" (multiples of $\pi/2$) and the intermediate ellipses (multiples of $\pi/4$). The sound-pressure level and amplification (Turn III) were adjusted as necessary to maintain constant outputs from both channels. Some distortion of wave form at the lower frequencies is obvious.
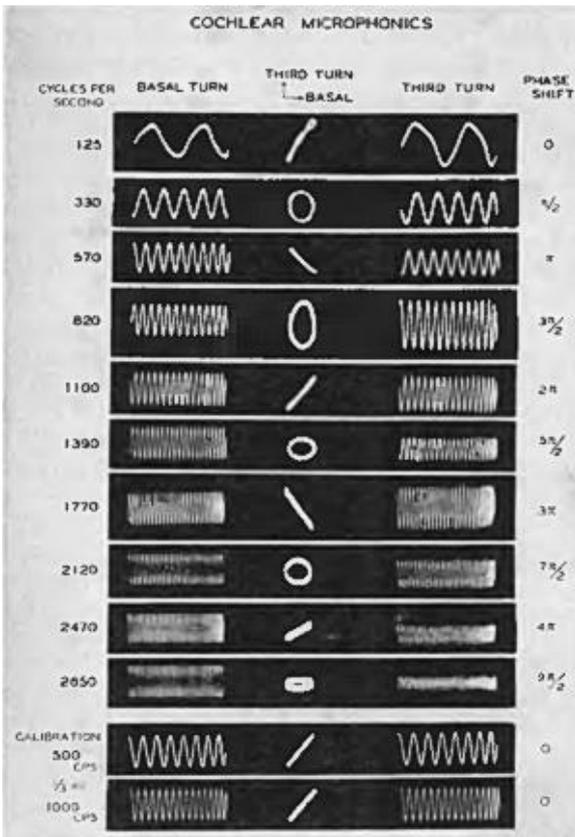
FIG. 12. Same as Fig. 11 except that the outputs from both Turn I and Turn III are shown separately as well as in a Lissajou pattern. The outputs were held approximately equal by adjusting the amplification for Turn III to the nearest 10-db step.

TABLE II.[a]

Refer-ence	Electrodes					Frequencies			
	mm		Exploring	mm		π	n	2π	n
	F	B		F	B	cps		cps	
RW	1.5	1.7	I	3.5	3.2	9,300	2	11,500	2
I	3.5	3.2	II	10.5	8.7	2,030	4	3,220	5
I	3.5	3.2	III N	14.0	12.5	595	7	1,020	14
I	3.5	3.2	III D	14.7	13.0	495	7	850	12
I	3.5	3.2	IV	17.5	16.4	227	3	473	3
			Helico-trema	18.5	18.5				

[a] Positions of the reference and exploring electrodes are given in the columns at the left. The distances in millimeters from the basal end of the membrane are reckoned according to the anatomical data of Fernández[a] (F) and of Békésy[14] (B), respectively. The frequencies for which the phase differences are π and 2π, respectively, are given at the right. n – number of experiments performed.

the guinea pig cochlea.[14] (The inclusion of Turn I with reference at RIV in the same graph with data from other turns relative to Turn I is justified because, as shown below, the whole basal turn vibrates very nearly in phase at low frequencies.)

The π- and the 2π-frequencies vary slightly with changes in intensity. At Turn III an increase of 10 db lowered the 2π-frequency by 50 cps and a 20-db increase lowered it by 100 cps. This is in good agreement with observations by Békésy[15] of the phase differences of mechanical displacements. He found that in the human ear the position of maximum amplitude for a 200 cps tone was shifted toward the helicotrema by increasing the intensity, and that an increase from 1 to 3×10^{-3} cm in amplitude (about 10 db) was offset by changing the frequency by 6 percent.

Local surgical injury, such as probing with a needle through the spiral ligament, often reduced the 2π-frequency considerably. We do not know the extent of injury in these experiments, however.

In Fig. 14 are plotted the measurements of phase difference made in five typical experiments, one for each position of the exploring electrodes. The highest frequency at which the phase difference could be measured varied from one position to another. The intensity that could be employed was limited by the appearance of nonlinear distortion, presumably from the middle ear.

The relation of phase difference to frequency shown in Fig. 14 is very different at the four turns. At both I and IV it is a smooth curve, but the curvatures are in opposite directions. At Turns III the data are best described by two straight lines of slightly different slope that intersect very close to the 2π-frequency. At Turn II there is a similar "break" a little below the 2π-frequency, but the break is now in the opposite direction.

All of the curves reach the line of zero phase difference at a frequency well above zero. In other words, at these low frequencies there is no measurable phase difference between Turn I and Turn II, III (or even IV). The frequency at which the phase difference first

can be determined with considerable accuracy because they correspond to straight lines on the oscilloscope. Readings repeated at intervals during an experiment regularly agreed within 20 cps at Turn II and 10 cps at Turn III. Phase differences of π and 2π have also special theoretical interest. The averages of our values (from technically satisfactory experiments) for the frequencies giving phase differences of π and 2π are given in Table II, together with the number of experiments on which each average is based and our best estimate of the distance of the electrodes in question from the basal end of the basilar membrane. In Turn III two positions were used, "normal" and "distal." (The "normal" position was actually a little more proximal than the relative position of the electrodes in the other turns.) The "distal" position was as far apical as it was practical to drill the necessary holes into the cochlea.

The data in Table II are expressed graphically in Fig. 13. Here the position on the basilar membrane is related to the logarithm of the frequency at which a given phase is observed. The points lie very nearly on straight lines, particularly if we use Békésy's map of

[14] G. v. Békésy, J. Acoust. Soc. Am. 23, 18 (1951).
[15] G. v. Békésy, J. Acoust. Soc. Am. 19, 452 (1947).

becomes measurable varies with the position of the exploring electrodes. (Very small differences at low frequencies may be obscured by distortion of the pattern, as shown in Figs. 11 and 12.)

The frequencies at which the "breaks" occur at Turns II and III are not only very close to the 2π-frequency in each case but also very close to the frequencies of the discontinuities in the data for voltage as a function of frequency (Figs. 7 and 8). It is a reasonable assumption that all of these "breaks" and discontinuities have a common basis and represent some rather important relationship between frequency, the form or mode of movement of the cochlear partition, and the position along the partition. The possible interpretations of this transition point we shall discuss below, but in Fig. 13 are plotted our best values for these critical frequencies as a function of distance from the oval window. The "combined data" (solid points) include the value of the "2π-frequency," the frequency of the discontinuity in the relation of phase difference to frequency, and the frequency of a clear break or discontinuity in the

relation of output (voltage of the microphonic) or sensitivity (threshold) to frequency. These data are nearly identical with those for the 2π-frequency alone.

9. THE TIME LAG OF THE TRAVELING WAVE

The time of travel of a given wave along the cochlear partition was measured directly, both for pure tones and for tone-pips. The tone-pip has the advantage that there is no ambiguity as to which are the corresponding waves at different positions. The outputs from different pairs of electrodes were connected to separate oscilloscopes. Simultaneous reference markers (timing pulses) were introduced into all channels by capacitative coupling to the input leads to the cathode-follower preamplifiers. The pulses were derived from the second stimulating circuit of the Grass square-wave stimulator that was used to generate the tone-pips. The delay circuit in the stimulator made it a simple matter to synchronize the markers as desired with the sweep and with the tone pips. Sample oscillograms are shown in Fig. 15. The long delay of the low frequency tone-pips in reaching the apical turn is obvious. Many measure-
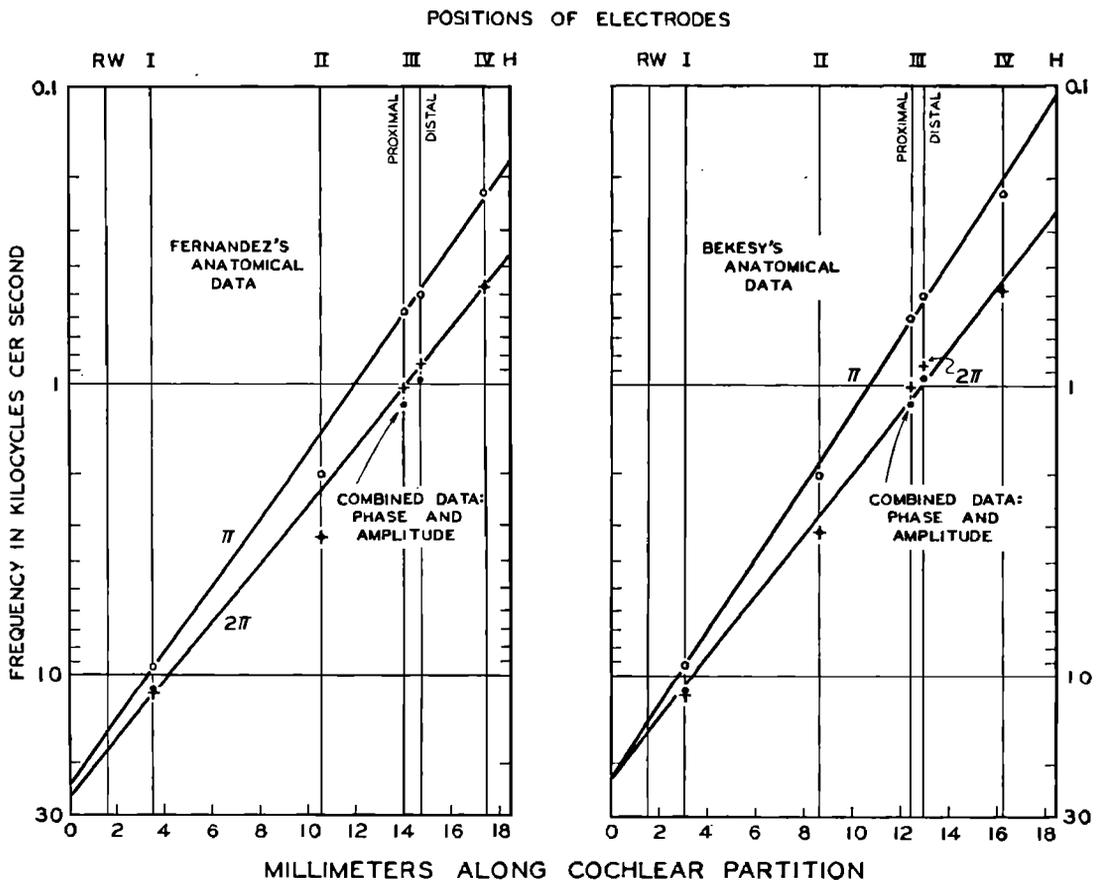
POSITIONS OF ELECTRODES

FIG. 13. Data from Table II. The distances along the cochlear partition are measured from the extreme basal end of the basilar membrane. RW indicates the usual position of our most basal pair of electrodes close to the round window. H indicates the helicotrema. Circles indicate frequencies at which the phase shift is π, crosses the frequencies at which it is 2π. The dots represent the averages of all of our data from phase shift (2π) and from discontinuities in phase-shift functions (Fig. 14) and in relative output functions (Figs. 7 and 8). The only experiments rejected were those which were technically unsatisfactory or which yielded no clear discontinuities in the relevant data. The lines were fitted by eye.
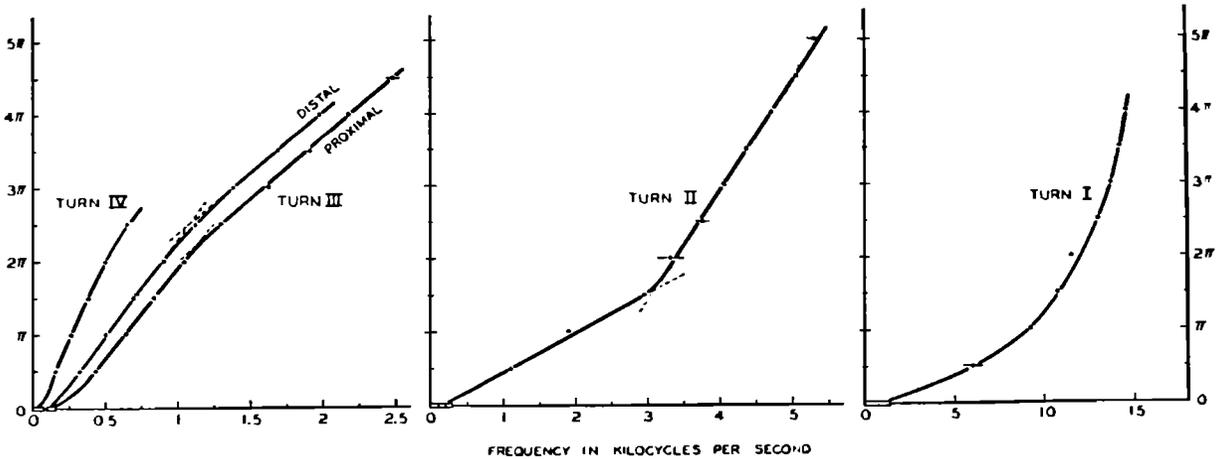
PHASE DIFFERENCES OF THE COCHLEAR MICROPHONICS

FIG. 14. Phase differences between the outputs of electrodes at various positions. Turns IV, III and II are referred to Turn I; Turn I is referred to position 'RW.' In each experiment the sound-pressure level was adjusted to hold the output from Turn I constant. It was about 80 to 90 db re 0.0002 microbar according to the 1-cc coupler calibration of our sound system. The frequency scales are all linear but are chosen to fit the data. Short horizontal lines represent zones of uncertainty due to distorted wave forms.

ments were made from such oscillograms and from similar oscillograms using pure tones.

The time delays for pips and for pure tones were in complete agreement within the accuracy of the method. The time lag was also calculated from the measurements of phase difference by means of the Lissajous figures. Typical examples, based on the data given in Fig. 14, are shown in Fig. 16. Here it is clear that the time lag at a given position is not constant. It rises
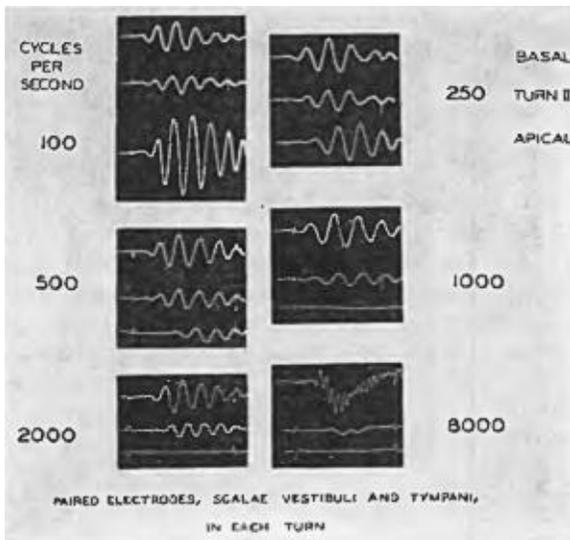

FIG. 15. Simultaneous oscillograms from Turns I, II, and IV taken with tone-pips of various frequencies. The maximum amplitude in the basal turn (100 cps) is 270 μv (peak-to-peak). The amplification is the same for Turns I and II but is 10 db less for Turn IV. Note the long delay at Turn IV of the first wave of the group at 250 and 500 cps. The electrical markers are simultaneous in all channels. The displacements of the base line in Turns I and II (8000-cps tone-pip) are due to the "summating potential."[a]

to a maximum at about the 2π-frequency at Turns IV and III and then falls again. At Turn II the rising branch of the curve shows an inflection, and the maximum (at about 4π) is not clear. At Turn I the time lag is still increasing rapidly at 4π. In spite of these differences in detail it is very clear that in general the time lag is much the greatest at Turn IV and it diminishes progressively to very small values at Turn I. The interpretation of the family of curves shown in Fig. 16 is difficult, but the trends shown are very consistent from one experiment to another.

A simpler relationship is shown in Fig. 17. Here the time lag for a 750-cps pure tone was measured directly at the various electrode positions and the best smooth curve was drawn by eye to the resulting points. The increase of time lag with distance is clear. The corresponding curve for velocity in meters per second is also shown.

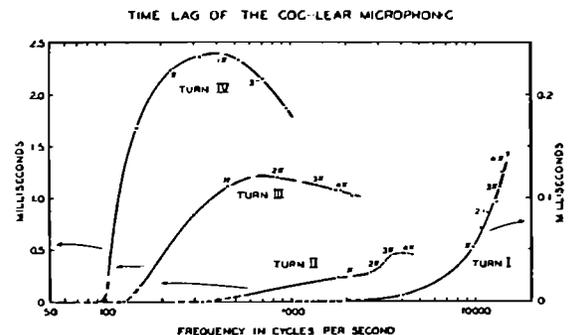In Table III are collected our best estimates for the

FIG. 16. Time lag of the cochlear microphonic at the several positions, calculated from the data shown in Fig. 14. Note that the time scale at the left applies to Turns IV, III, and II and the expanded scale at the right to Turn I. The small numerals indicate the phase shift in multiples of π at the various frequencies.
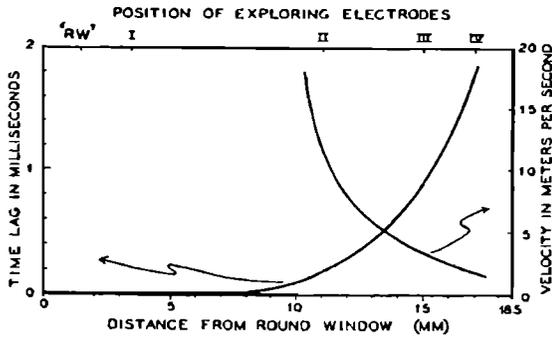
FIG. 17. Time lag and phase velocity for a steady tone of 750 cps. The original data were obtained as simultaneous oscillograms with electrical time markers superimposed. The positions of the exploring electrodes are based on Fernández' anatomical data.

time lag at each of the exploring positions, measured in each case for the frequency that showed a phase difference of π at that position. The reference point was always Turn I (3.5 mm from the basal end) except for Turn I itself which was referred to the 'RW' position (1.5 mm). The average velocity to each point in question has very little meaning because the velocity is changing so rapidly beyond the first turn. It is of the order of magnitude of 100 m/sec in the first turn for all frequencies below 5000 cps and slows down to not more than 2 m/sec in the fourth turn for tones near 500 cps.

Figure 10 reveals another important point concerning time lag in the cochlea. At a given point the time lag for different frequencies is not the same. This fact is implicit in the complicated relationships shown in Fig. 16, but it appears at a glance in the oscillograms of the mixture of 1000- and 350-cps tones. The time relations between the two have changed from Turn I to Turn II. (The oscillograms in Fig. 10 were taken *simultaneously* on three adjacent oscilloscopes.) We may summarize this situation by saying that the ear is a "dispersive medium," meaning that it conducts traveling waves of different frequencies at different velocities. This is in addition to the proposition illustrated in Fig. 17 that waves of a given frequency travel with different speeds over different parts of the cochlea.

10. EFFECTS OF VARIOUS PROCEDURES UPON THE SPACE-TIME PATTERN OF THE MICROPHONIC

We have conducted a number of experiments designed to clarify the manner in which the space-time pattern

TABLE III. Time lag and velocity.

Electrodes		Distance mm		Frequency (π)	Delay	Average Velocity m/sec	
Reference	Exploring	F[a]	B[b]	cps	msec	F[a]	B[b]
RW	I	2.0	1.5	9,300	0.054	37	28
I	II	7.0	5.5	2,030	0.25	28	22
I	III P	12.5	10.8	595	0.84	15	13
I	III D	13.2	11.3	495	1.01	13	11
I	IV	17.0	16.8	227	2.2	7.7	7.6

[a] See reference 5.
[b] See reference 15.

of the cochlear microphonic is determined. They consist chiefly of procedures that might be expected to interfere with the transmission of a traveling wave up the cochlear partition.

(A) Blocking the Cochlear Duct

The simplest and most perfect way to hinder the propagation of a vibratory wave along the cochlear duct is to block the duct with bone wax. Two pairs of electrodes were placed in the cochlea, one in the third turn and the other in the basal turn, and, just as in the previous experiments, the amplitude and the time-lag of the microphonic were examined with either tone-pips or pure tones. Then a large hole, approximately 200 microns diameter, was drilled through the bony wall of the cochlea in the second turn, leaving the spiral ligament and the endosteum intact. This procedure alone scarcely affected the amplitude or phase of the microphonic at all. Then bone wax was forced into this hole until the cochlear duct seemed to be entirely blocked by the wax. The pattern of the microphonic was again examined with sound stimuli applied to the ear through the external auditory meatus. The blocking of the cochlear duct in the second turn did not significantly affect the microphonic response of the basal turn for either high or low frequency sounds. The size of the action potential in response to high frequency (8000 cps) tone-pips also remained unaffected. The microphonic response from the third turn, however, was always greatly reduced by this procedure. The reduction for low frequency (500 cps) tone-pips generally amounted to 30 db or slightly more.

This result indicates that the vibratory wave we are observing by means of its accompanying electrical potential does not propagate along the bony wall of the cochlea. It propagates along the fluid medium in the two scalae or along the cochlear partition or both.

(B) Holes in Scala Vestibuli and/or Tympani

After the normal pattern of the microphonic response was recorded with one pair of electrodes in the third turn and the other pair in the basal turn, a fairly large hole was made in the bony wall of scala vestibuli of the second turn. The hole was generally 140 to 180 microns wide and 300 to 800 microns long lengthwise of the scala vestibuli. The intensity of sound stimulus required to get the original amplitude of microphonic was now 3 or 4 db greater than before at both pairs of electrodes and for all frequencies. But if the response at the basal turn was brought to its original level by increasing the sound intensity slightly, the phase-difference and the amplitude of the third turn response were practically the same as those observed before the hole was made. (The reduction in the relative amplitude of the third turn response was less than 2 db, if any.)

In other experiments a hole about 40 to 60 microns wide and 100 to 200 microns long was made in the

bony walls of scala tympani and a much larger hole in scala vestibuli of the second turn. Perilymph flowed out of the two holes and accumulated in the bulla until both openings were under the surface of the perilymph. We hoped that this procedure would produce an effective acoustical short-circuit in the second turn. (The electrodes were placed in the third turn, but in such positions that the fluid accumulated in the bulla did not reach the small holes in which the electrodes were inserted.) We were surprised to find that this drastic operation did not appreciably affect the microphonic response except when a part of the scala media seemed to be damaged seriously by the surgical operation.

In a number of other experiments, the upper electrodes were placed in the most distal accessible region of the third turn, and a hole or holes were made on the proximal part of the accessible third turn region, either in scala vestibuli or tympani or both. In all cases we found very little or absolutely no detectable change in the relative amplitude or phase of the microphonic.

In one experiment we tried to enlarge the hole in the scala tympani of the second turn and accidentally broke down about 200 microns of the bony partition between the basal turn (scala vestibuli) and the second turn (scala tympani). In this experiment also the change in the amplitude of the third turn response (with the basal turn response adjusted to its original level) was very slight. There was practically no change for frequencies below 800 cps. The phase-difference as a function of frequency also remained practically unchanged.

These observations can be explained by assuming either (1) that the release of the pressure wave (which may travel along the fluid medium in the two scalae) through the holes is not sufficient to cause a detectable change in the relative amplitude of the cochlear microphonic, or (2) that the vibratory wave is carried solely by the solid structures of the cochlear partition. The size of the hole made in the scala vestibuli of the second or third turn was in many cases larger than the cross-section area of the scala at that region. In the scala tympani we could not make a hole larger than the cross section of the scala at that position, but its area was greater than that of the scala tympani near the helicotrema. The acoustical short-circuiting effect of these holes should be greater than that of the helicotrema. These results therefore support the view that the vibratory wave travels along the cochlear partition and not along the fluid medium in scala vestibuli and scala tympani.

(C) Hindrance of Movement of the Cochlear Partition

A completely reversible change in the phase-difference and amplitude distribution of the cochlear microphonic was obtained by pressing the region of stria vascularis with a strand of guinea pig hair after the bony wall

over the scala media had been removed. The upper electrodes were placed in the distal end of the accessible third-turn region, a round fenestra, 300 to 500 microns in diameter, was made in the middle of the turn. This procedure alone slightly elevated the "threshold" for high frequency tones without affecting the "threshold" for low frequency tones. When the region of the stria vascularis was pressed with the smooth flexible hair, the ratio of the amplitude of microphonic from the third turn to that from the basal turn was reduced appreciably, by 6 db or more. This effect was reversible, i.e., when the pressure applied to the scala media was released, the amplitude rapidly returned to normal. The extent of this reversible reduction in the microphonic from the upper turn depended upon the frequency of sound. The higher the frequency the greater was the reduction.

A reversible reduction in the microphonic was also produced by the introduction of a nichrome-steel wire (20μ) into scala media. A small hole, approximately 30 microns diameter, was made in the bony wall over the middle of the stria vascularis of the proximal part of Turn III. This did not alter the microphonic response at the distal part of the same turn. The wire was introduced through the hole to a depth of about 250 microns from the surface of the bone. This procedure reduced not only the response from that particular area, but also the responses from beyond the hole. When the wire was withdrawn, the response of the third turn usually recovered to its original value. Escape of endolymph from the hole was slight and the condition of the cochlea remained unchanged for several hours after this manipulation.

On about a dozen preparations, attempts were made to press the basilar membrane from beneath, with nichrome-steel wire or a thread of hair, through a hole made in scala tympani. This procedure always caused an appreciable change in the phase and amplitude of the microphonic recorded from the particular region where the pressure was applied. But at the same moment there was in most cases no change in the phase or amplitude of the microphonic recorded from the distal side of this region. (The distance between the hole and the distal electrodes was generally 1 mm, measured on the outer wall of the cochlea.) When the pressure on the basilar membrane was made stronger, the microphonic recorded from the distal side was reduced, but this change was generally irreversible and progressive, undoubtedly due to injury of the scala media. In two out of a large number of trials, we obtained a reversible reduction in the microphonic from the distal side, but this observation could not be reproduced very readily, and we could not be sure that the pressure was actually limited to the basilar membrane.

We believe that this series of observations furnishes very strong evidence that mechanical vibration travels along the solid structures of the cochlear partition by virtue of their elasticity and stiffness.

(D) Destruction of the Cochlear Partition

A complete surgical destruction of the scala media between the basal and third turn of the cochlea caused a progressive loss of microphonics in all parts of the cochlea. The immediate effect of such a destruction with a needle or a scalpel is similar to that of hindering the movement of the scala media with a wire or a hair. The reduction in the amplitude of the third turn response is greater for middle-frequency tones than for low frequency tones, and the dependence of the phase-difference upon the frequency becomes more pronounced. In these experiments we do not know just how much of the structural continuity of the cochlear partition was destroyed by the operation, and hemorrhage inside the cochlea may have contributed to the change in the pattern of the microphonic response.

(E) Acoustic Driving at the Third Turn

A hole approximately 130 microns in diameter was made in the bony wall over scala vestibuli of the third turn at the distal end of the accessible region. A glass tube of about 3-mm bore drawn to a capillary tip of about 100-microns diameter was inserted. The perilymph flowed into the capillary for less than a millimeter. The other end of the glass tube was connected to a PDR-10 receiver by means of a coupler and a flexible rubber hose. Two pairs of electrodes had been placed in the proximal end of the third turn and in the basal turn. For tone-pips of 500 and 1000 cps, the time-lag of the third turn response and the ratio of the amplitude here to the response of the basal turn was practically the same as in the usual experiment with sound stimuli applied by way of the oval window. In other words, the response from the third turn lagged behind that from the basal turn by the length of time shown in Fig. 16. (For frequencies higher than 2000 cps, we could not obtain measurable responses from the third turn.) When the glass capillary through which the sound was delivered into the third turn was placed not in the hole but on the bony wall of the cochlea there was no measurable response in any part of the cochlea. This indicates that the sound wave actually entered the scala vestibuli of the third turn from the glass capillary by way of the fluid in the tubing, not by bone conduction.

Our interpretation of this result is as follows. We assume the cochlear fluids to be practically incompressible and the bony walls rigid. The displacement of fluid by the sound wave at the opening of the capillary tube must therefore result almost instantaneously in volume-displacement of fluid at the various openings of the cochlea, namely oval window, round window and the narrow gap between the glass capillary and the edge of the hole in the third turn. The displacement of the round window should be associated with a *simultaneous* displacement of the cochlear partition.

(Wever and Lawrence[16] showed that an acoustic stimulus applied through a hole in the apex could be canceled by a tone of the same frequency, properly adjusted in phase and amplitude, delivered through the external auditory canal.) The spatial pattern of the immediate displacement evidently does not depend on whether the sound wave is applied at the oval window or in the third turn.

It would be natural to suppose that the time at which the immediate displacement reaches its maximum amplitude will differ at different points along the cochlea by no more than half a cycle. This immediate displacement is followed by a traveling wave, due not to the difference in pressures in the fluid across the partition but to the stiffness and elasticity of the partition itself as it is moved in the immediate displacement. This wave travels in its usual direction and at its usual speed regardless of the place at which the acoustic energy is delivered to the cochlear fluids. The direction of its normal travel does not depend on the place at which the sound energy is delivered, but on the gradients of width, stiffness, mass, and other physical properties along the cochlear partition. In the basal turn the partition has greater stiffness and less mass and in consequence responds to the external driving force more quickly and reaches its maximum displacement sooner than in other places. This earlier movement tends to drag the more apical segments along with it, and thus to initiate a true traveling wave, in the sense of Wever and Lawrence,[16] as opposed to a mere phase lag between neighboring but independent elements.

11. DISCUSSION

(A) Relation to Studies of Mechanical Movement

Our present observations confirm qualitatively the corresponding observations by Békésy[16] made by quite different methods. The existence of phase differences as well as differences in amplitude of the movement in different parts of the cochlea seems established beyond the possibility of a doubt. A full interpretation of our results requires, however, a better understanding of the origin of the cochlear microphonic and its relation to the movement of the cochlear partition. Our study of this problem is now almost complete and the results will be reported in a later paper.

We know that the cochlear microphonic is a linear function of sound-pressure level over a wide range of frequency and intensity (Sec. 4). Békésy has shown[17] that the microphonic is related to displacement and not velocity or acceleration. The trend of Békésy's curves for the space pattern of displacement as a function of frequency differs from the trend of our curves for the voltage of the cochlear microphonic. Békésy's curves

[16] E. G. Wever and M. Lawrence, Proc. Nat. Acad. Sci. 38, 133 (1952).
[17] G. v. Békésy, J. Acoust. Soc. Am. 23, 29 (1951).

show a gradual rise from a small displacement in the basal turn to a maximum with a somewhat steeper fall toward the apex. The position of the maximum depends on the frequency. Our data (cf. Fig. 9) do not suggest a clear maximum in the voltage of the cochlear microphonic but rather a long plateau that extends all the way to the round window.

The basis of this difference is not yet quite clear. It is true that our Figs. 5, 6, and 8 all indicate that the sound-pressure level necessary to produce a given voltage of cochlear microphonic is from 10 to 20 db less for Turns II and III than for Turn I (provided we consider only the low tones and the range of intensity over which the output of the upper turns is a linear function of the sound-pressure level). At a few low frequencies Turn IV also is more sensitive than Turn I even though the use of a reference electrode at the helicotrema probably reduces considerably the fraction of the actual potential that is recorded. The voltages measured at the other turns are also undoubtedly modified by the differences in cross-section area of the cochlear canal and in the width of the basilar membrane.

In spite of these uncertainties the large voltage of the cochlear microphonic recorded from the first turn in response to low frequencies of stimulation suggests strongly that a given displacement of the basilar membrane may not produce the same flow of local electrical current (and consequent differences of potential at the recording electrodes) in different turns of the cochlea. It is possible that the microphonic may be more nearly proportional to the curvature of the basilar membrane or possibly to tension in some particular elements of the cochlear partition than it is to the displacement.

(B) Relation to "Frequency-Maps" of the Cochlea

Many investigators have related frequency to position along the cochlear partition. This relation is the central feature of all "place theories" of hearing. Usually it is the position of maximum displacement that is considered. Several such "maps" have been summarized by Steinberg,[18] and by Békésy and Rosenblith.[19]

Our present Fig. 13 constitutes another such map, but in this case it is the phase difference, not the maximum amplitude, that is represented as a function of position. The trend is roughly similar to most of the previous maps, but close comparison is impossible until we know what phase difference exists at the position of maximum amplitude. A phase difference of $\pi/2$ seems plausible, or perhaps π. Possibly the critical point that gives its local sign to the pattern of excitation is the "break" (cf. Fig. 7), which is closely associated with the

[18] J. C. Steinberg, J. Acoust. Soc. Am. 8, 176 (1937).

[19] G. v. Békésy and W. A. Rosenblith, "The mechanical properties of the ear," Handbook of Experimental Psychology (John Wiley and Sons, Inc., New York, 1951), S. S. Stevens, edition, Chapter 27, pp. 1075–1115.

2π-phase difference. We cannot yet decide among these alternatives.

(C) Relation to Physico-Mathematical Theories of Cochlear Dynamics

Our new data provide interesting tests for physico-mathematical theories of the motion of the cochlear partition. Most of the recent treatments of this problem (Ranke,[10] Zwislocki,[11] Peterson and Bogert,[12] and Fletcher[13]) are based on essentially the same concepts. The differences among them consist chiefly in the particular approximations which were made to permit actual evaluation of the problem. The fundamental equation describing the motion of the cochlear partition derives from the three following partial differential equations:

Equations of continuity

$$\frac{\partial(S_1u_1)}{\partial x} = B\frac{\partial y}{\partial t} = -\frac{\partial(S_2u_2)}{\partial x}. \qquad (1), (2)$$

Equation of motion of the membrane

$$M\frac{\partial^2 y}{\partial t^2} + R\frac{\partial y}{\partial t} + Ky = -(p_1-p_2)B + T\frac{\partial^2 y}{\partial x^2} - U\frac{\partial^4 y}{\partial x^4}. \qquad (3)$$

Equations of motion of the fluid in the two scalas

$$\rho\frac{\partial(S_1u_1)}{\partial t} + F_1u_1 = -\frac{\partial(S_1p_1)}{\partial x}, \qquad (4)$$

$$\rho\frac{\partial(S_2u_2)}{\partial t} + F_2u_2 = -\frac{\partial(S_2p_2)}{\partial x}. \qquad (5)$$

The symbols follow those used by Fletcher[13] and are explained in full in the appendix.

The equations of continuity, (1) and (2), are based upon the conservation of mass of the fluid during the motion of the fluid and the partition. We assume from the outset that the fluid in the cochlea is incompressible. This we consider legitimate because we know from our experiments that the actual motion of the cochlear partition is a far slower process than the propagation of a sound wave in water.

The equation of motion of the partition is a symbolic expression of the statement that the forces driving each small element of the cochlear partition are, first, the pressure differences on the two sides of the partition multiplied by the area of the element and, second, the mutual forces exerted by the adjacent elements. The two last terms represent respectively the force due to longitudinal tension in the membrane and that due to its longitudinal stiffness considered as a beam. The third term, Ky, is a conservative term representing energy stored by the stiffness of the partition and proportional to the displacement. The second term, $R(\partial y/\partial t)$, is a dissipative term expressing frictional (or viscous) losses.

The equations of motion of the fluid state that the longitudinal acceleration in an elementary "box" (of cross section S_1 or S_2 and length Δx) multiplied by the mass of the fluid is equal to the force exerted by the difference in pressure on the two sides of the box minus the dissipative frictional term that expresses the losses due to the viscosity of the fluid.

The problem is to solve these simultaneous differential equations under appropriate boundary conditions. Unfortunately the equations are complicated and no completely rigorous solution has been obtained. It is necessary, therefore, to introduce reasonable approximations that will lead to a practical solution. We do not offer any explicit form of the solution which can be obtained when a particular set of approximations are made. We simply draw from these differential equations several qualitative conclusions which help us visualize the motion of the cochlear partition under various conditions.

It is easy to see that Eq. (3) describes a transverse wave, the speed of which depends in general upon the frequency of the driving force. When the term, $T(\partial y^2/\partial x^2)$, predominates over the last term, $U(\partial^4 y/\partial x^4)$, the speed first falls as the frequency increases and then reaches a steady level. When $U(\partial^4 y/\partial x^4)$ is much greater than $T(\partial^2 y/\partial x^2)$, a low frequency wave should always travel faster than a high frequency wave. This transverse wave traveling along the cochlear partition appears in pure form only when the driving force, $(p_1-p_2)B$, is localized in a region of the cochlear partition near the stapes.

An entirely different type of wave equation can be derived from the simultaneous differential equations stated above when we make the approximation $T=U=0$. Replacing the operator $\partial/\partial t$ with $j\omega$ and combining the equations, we then obtain

$$\frac{\partial^2(p_1-p_2)}{\partial x^2}=\frac{2\rho B^2}{MS}\left\{\frac{1-j(F/S\omega\rho)}{1-(\omega_0/\omega)^2-j(R/M\omega)}\right\}(p_1-p_2). \quad (6)$$

This equation is essentially the same as the one derived by Fletcher[13] (Eq. (26a)). We actually followed Fletcher in making the approximation $S_1=S_2=S$ and $T=U=0$. (See appendix for definition of symbols.) This equation is also substantially the same as those derived by Zwislocki,[11] and by Peterson and Bogert.[12]

Based upon these qualitative considerations, we shall speak of three different "forms of motion" that take place in the cochlea. Two of these forms may appear simultaneously in different parts of the cochlea and the third may be superimposed on and fused with each of the other two. Our problem is not either—or, to decide which single form of motion best describes the observed facts, but to determine under what conditions, if ever, one form of motion becomes dominant and under what conditions, if any, any one of the three forms can be neglected.

(D) The Three Forms of Motion of the Cochlear Partition

(1) *Direct driving* of the partition by the sound wave is the motion which occurs when the hydrostatic pressure in the cochlea varies simultaneously along the region of the cochlear partition under consideration. The difference in this pressure across the partition, (p_1-p_2), drives each element of the partition in vibration (perpendicular to the plane of the partition). Some of the elements, by virtue of their mass, M, and their stiffness, K, may resonate to the driving force. This "form of motion" is a "resonance theory" in the sense of Wever and Lawrence.[16] One feature of this form of motion is that the difference in phase between two different places of the cochlear partition driven "directly" should be less than π. This form of motion can occur in its pure form either (a) under the condition that all the frictional and mutual forces are negligible and the (circular) driving frequency (ω) is higher than the resonance frequency (ω_0) in the region of the cochlear partition under consideration (Eq. 6, the case in which the coefficient of (p_1-p_2) is real and positive), or (b) when the frequency of sound is so low that the whole length of the cochlear partition under consideration is shorter than about one-fourth of the wavelength of the "traveling" wave.

(2) A *surface wave* is the form of motion described by Eq. (6) when the coefficient of (p_1-p_2) is not a positive real number. This form of motion has been discussed extensively by Zwislocki and others. This surface wave can be generated without significant mutual forces between neighboring elements. This wave travels along the partition mediated primarily by the pressure difference across the partition. It can cause phase differences greater than π between two positions in different parts of the cochlea.

The motion of the cochlear partition may differ in form in different parts of the cochlea. Equation (5) tells us that if the absolute values of the imaginary terms in this equation are much smaller than unity the spread of the pressure difference along the cochlear partition takes place quite differently according to whether the driving frequency (ω) is greater than or less than the resonant frequency (ω_0). Of course, the resonant frequency is very different at the apex from what it is at the round window, and in general the audio-frequencies lie between these two values. This means that the spread of pressure difference along the partition should take place differently in different parts of the cochlea for one and the same frequency (ω). Suppose the frequency corresponds to the resonant frequency of a point in the second turn. Then in the third turn where $\omega>\omega_0$ a direct driving of the type (a) mentioned above may take place. In the basal turn, however, where the resonant frequency (ω_0) is much greater than the driving frequency (ω), either a surface wave or a direct driving of the type (b) should occur.

(3) The third "form of motion" is an *elastic wave* that depends on the mutual forces between adjacent elements in the cochlear partition. The pressure differences across the partition, whether delivered directly (first form) or as a surface wave (second form), set the cochlear partition in motion according to Eq. 3. Suppose, as an approximation, that over a certain range of frequencies the driving force, $(p_1-p_2)B$ in Eq. (3), is restricted to a region of the cochlea near the stapes. Then the more distant parts of the partition will carry a transverse wave described by the equation

$$M(\partial^2 y/\partial t^2)+R(\partial y/\partial t)+Ky$$
$$=T(\partial^2 y/\partial x^2)-U(\partial^4 y/\partial x^4). \quad (7)$$

This transverse wave depends solely upon the solid structure of the partition and not upon the difference in the hydrostatic pressure across the partition. In this respect it differs from the second form of wave motion described above. Our failure to modify the pattern of the actual wave in the cochlea (observed by the electrical means) by producing an "acoustical short circuit" supports our view that this third form of motion cannot be neglected in considering the actual motion in the cochlea. When the driving frequency is high and the wavelength short, the elastic waves should become prominent because the effects of the "mutual forces" in the partition depend on the curvature of the structures along the partition.

It is our present opinion that the amazing complexity of the phase and amplitude patterns of cochlear motions can be understood, at least qualitatively, in terms of the three different types of motion: direct driving, surface waves, and transverse elastic waves.

APPENDIX

Table of Mathematical Symbols and Notations

B: width of the basilar membrane (a function of x).

F_1: coefficient for the frictional force acting upon an elementary box of fluid in scala vestibuli in its longitudinal motion.

F_2: similar value of the fluid in scala tympani.

F: average of F_1 and F_2.

K: coefficient for the elastic force acting upon the cochlear partition.

M: mass of the cochlear partition per unit length.

p_1 and p_2: pressure at point x in the scala vestibuli and tympani, respectively.

R: coefficient for the frictional force acting on the cochlear partition.

S_1, S_2: cross-section area of the scala vestibuli and scala tympani, respectively.

S: average of S_1 and S_2.

T: longitudinal tension of the cochlear partition.

U: coefficient for the shear force acting upon the cochlear partition.

u_1, u_2: average longitudinal velocity of the fluid in scala vestibuli and tympani, respectively.

x: distance along the cochlear partition.

y: average displacement of the cochlear partition at point x.

t: time.

ρ: density of the fluid.

ω: 2π times the frequency of the sound.

ω_0: $(K/M)^{\frac{1}{2}}$, namely 2π times the resonance frequency at point x.

Dimensions of the Cochlea (Guinea Pig)*

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Measurements have been made under the microscope of many structures in the cochlea of the guinea pig and the results plotted graphically as a function of position along the cochlea. The structures measured are the spiral lamina, Rosenthal's canal, the basilar membrane (length, width and thickness), the channels and windows of the cochlea (cross-section area) and the hair cells (angles of orientation).

INTRODUCTION

THE dimensions of the structures of the cochea and the way in which they vary as a function of position along the cochlea have long been a matter of interest because of their bearing on the dynamics of

the cochlea.[1] More recently they have become important also for calculations of the probable distribution of electrical current flow and potential fields within the cochlea.[2] Wever[3] has published many useful measurements on the human cochlea. The present study was undertaken to supply similar data for the guinea pig,

[1] H. Fletcher, J. Acoust. Soc. Am. 23, 637 (1951).
[2] G. v. Békésy, J. Acoust. Soc. Am. 23, 18 (1951).
[3] E. G. Wever, *Theory of Hearing* (John Wiley and Sons, Inc., New York, 1949).