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On the Dynamics of the Cochlea

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This paper is concerned with the dynamical behavior of the cochlea. It is assumed that a length of the basilar membrane which is equal to its width at each position vibrates as a unit, and that the forces exerted upon it by adjacent units are negligible compared to that exerted by the difference in pressure in the scala vestibuli and scala tympani. The boundary conditions at the stapes end is simply that the pressure difference in the two canals is equal to P_0 any desired pressure difference. However, at the helicotrema the pressure difference must be equal to that between the two ends of the capillary opening at the helicotrema.

Then from the fundamental hydrodynamical equations and the experimental constants obtained by Békésy it is shown that the speed of sound through the liquid of the inner ear may be considered infinite compared to the speed of the wave along the basilar membrane. In other words, the liquid may be considered incompressible so that the rate of liquid displacement at the oval window is equal to that at the round window, and is also equal to that produced by flexure of the basilar for frequencies above 200 cps. Below this frequency some of the liquid goes back and forth through the helicotrema.

With these assumptions, the following quantities were calculated from the fundamental dynamical equations and found to be in good agreement with the experimental results of Békésy; (a) displacement amplitudes and phases of the basilar membrane at different distances from the stapes and for different frequencies, (b) time for wave to travel from stapes to various distances from stapes, and (c) volume displacement, at various frequencies, per dyne difference of pressure at oval window and that at round window.

In this paper the dynamical behavior of the cochlea is deduced from the fundamental hydrodynamical equations and the known constants of the ear. Although the fundamental differential equation which is used is the same as that used by Petersen and Bogert[1] and Zwislocki,[2] except for a term involving the viscosity of the fluid, the interpretation of the constants and the boundary conditions are very different and therefore lead to very different results. These results give a very good agreement with those obtained experimentally by Békésy.

Since the basilar membrane is long compared to its width, it seems reasonable for calculation purposes to break its length up into small square vibrating units, the length of each unit being equal to its width. There would then be about 140 such vibrators in a 35-mm length basilar membrane. As an approximation each little element will be considered to vibrate as a piston with an area b^2 where b is the width of the basilar membrane. The forces driving each little element are the pressure differences on the two sides of the membrane multiplied by b^2 and the mutual forces exerted by adjacent elements. These latter forces will be considered negligible in comparison to Pb^2. If $\bar{y}$, then, is the average displacement across the membrane at a position x cm from the stapes end of the basilar membrane, then

$$\bar{y}=nPb^2/-m\omega^2+s+jr\omega, \qquad (1)$$

where m is the mass, s the stiffness constant, and r the mechanical resistance of the little element at this position. The factor n is a number which is probably between 0.3 and 1.0 and takes care of the fact that the edges of the element are fixed.

[1] L. C. Petersen and B. P. Bogert, J. Acoust. Soc. Am. 22, 369–381 (1950).
[2] J. Zwislocki, J. Acoust. Soc. Am. 22, 778–784 (1950).

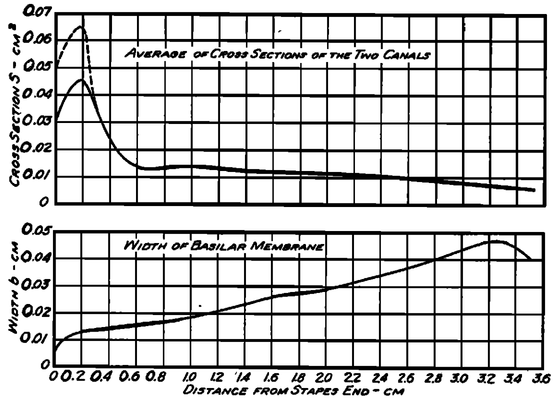

FIG. 1. Width of basilar membrane and average area of two canals for different distances from the stapes.

The problem then is to find m, s, r, and b from measurements which have been made and then find P from the fundamental differential equation.

First consider the mass m. It is the radiant mass carried by the area b^2 plus the mass of the structures carried by this area (rods of corti, etc.). It is well known that the radiant mass for such a small vibrating element in water carried by both sides of the area is $0.85b^3$ if the area were circular having a diameter b. For the equivalent square area it would be somewhat greater than this and it was taken as b^3. This is equivalent to saying that a volume of liquid extending out from the membrane a distance only equal to one-half the width of the membrane vibrates in phase with it. The basilar membrane tself, the rods of corti and other structures carried by the basilar membrane have a thickness of about one-half the width of the membrane. Also it is assumed that the density of the structure is about 1.5 so the mass of the little element itself is $0.75b^3$. Consequently,

$$m=1.75b^3. \tag{2}$$

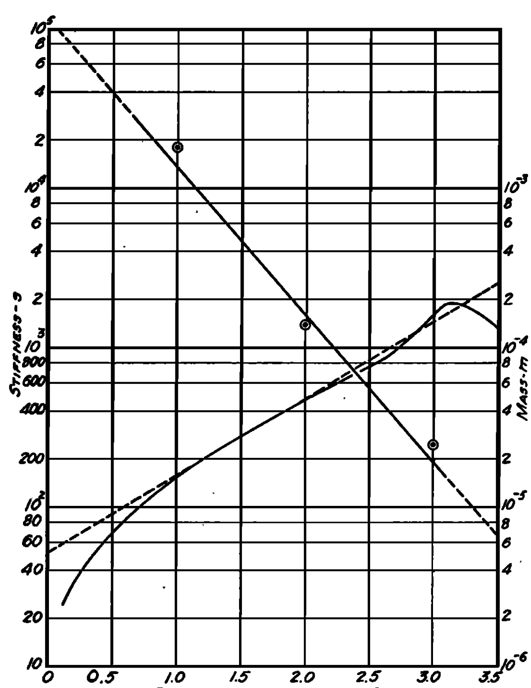

FIG. 2. Stiffness constant and mass of each little element along the basilar membrane.

It is important to notice that the vibration of the little element depends only upon the mass of the liquid which is within one- or two-tenths of a millimeter of the surface of the membrane. So the extent of the liquid beyond this small distance does not influence the vibration except as it modifies P. In other words, the resonant characteristics are independent of the size and shape of the vessel in which the basilar membrane is immersed. This is in accord with Békésy's findings. The values of b vs x were taken as the average values taken from 25 specimens as given by Wever.[3] They are shown by the lower plot in Fig. 1. The upper part of this figure will be discussed later. In Fig. 2 the values of m vs x obtained from (2) are plotted.

Next consider the stiffness constant s. Until Békésy made his epoch-making experiments there was considerable speculation and controversy concerning the elastic properties of the basilar membrane. Many have claimed that its structure was such that only small variations in the stiffness constant for different positions along its length were possible, and therefore the so-called resonance theory must be ruled out.

Békésy measured directly this stiffness constant. He measured the deflection produced on a human basilar membrane by a hair probe. This probe was calibrated by noting that a hair fastened to its end started to bend at a definite applied force. The magnitude of this force depended upon the length of the hair. The deflection of the basilar membrane was measured with a calibrated microscope. In this way the dynes force per centimeter of deflection, which is called the stiffness constant s, was measured at three positions along the membrane; namely, 10 mm, 20 mm, and 30 mm from the stapes end. The values of s found were: at 10 mm, $s=1.8\times10^4$; 20 mm, $s=1.4\times10^3$; 30 mm, $s=2.5\times10^2$. The total length of this basilar membrane in his sample was found to be 35 mm. These values are also plotted in Fig. 2.

At the two ends the straight line chosen to fit the points is dotted indicating an uncertainty. It is to be noticed that to obtain the values plotted the force was applied over a small area near the center of the membrane. When it was applied near the edge the deflection was smaller. For about one-half the width b of the basilar membrane the deflection per dyne was approximately constant.

Before considering the mechanical resistance let us consider the resonant frequency f_0 of each little element. It is seen from (1) to be given by

$$2\pi f_0=\omega_0=(s/m)^{\frac{1}{2}}. \tag{3}$$

[3] E. G. Wever, *Theory of Hearing* (John Wiley and Sons, Inc., New York, 1949), p. 100.

The values of s and m are given in Fig. 2. If one uses the straight lines given in the plot and represented by

$$s=10^{5.07-0.94x}, \tag{4}$$

and

$$m=10^{-5.31+0.50x}.$$

Then

$$f_0=25{,}000\cdot 10^{-0.72x}. \tag{5}$$

This then gives $f_0=25{,}000$ cps at the stapes and 76 cps at the helicotrema, which it will be seen gives good agreement with observed data. This equation is represented by the straight line of Fig. 3. A somewhat better fit of the data was obtained by using the solid line which departs somewhat from the straight line at the low frequencies. The solid dots give the calculated position for maximum displacement of the basilar membrane. This position is always shifted toward the stapes from the position for the resonant frequency. The circles and crosses are two sets of experimental data by Békésy giving the positions for maximum displacement.

There is considerable uncertainty of the values of f_0 below 200 cps due to peculiar variations of the width of the basilar membrane and consequently of its stiffness in this region. However, it will be shown that the controlling factor for the response of the membrane in this region is the damping factor so these variations produce only small changes in the calculated results.

It should be emphasized that the position for these resonant frequencies remains the same regardless of the manner in which the sound is conducted to the cochlea, that is, whether it is by bone conduction, air conduction, through the stapes, or the round window, or both.

Next consider the mechanical resistance r. Again we are indebted to Békésy for values of this frictional resistance. He found that the logarithmic decrement was about the same for all positions along the membrance less than $x=2.85$ cm and was equal to 1.6. For positions nearer the helicotrema the decrement increased.

If A_2 and A_1 are two successive amplitudes

$$\log_e(A_1/A_2)=1.6=r/2mf_0$$

or

$$r=0.5\omega_0 m, \tag{6}$$

where ω_0 is equal to 2π times the resonant frequency f_0 at the position considered.

One can compute the radiation resistance of the little element to be

$$r_r=\pi^2 f^2 b^4/2c, \tag{7}$$

where f is the frequency of the impressed tone, and c the velocity of sound in water. This value of r_r lies between 10^{-4} and 10^{-6} for the audible range of frequencies. It will be seen to be negligible compared to the value given by (6). So the measured resistance does not arise from the radiation but probably from frictional sources within the membrane structure.

For positions nearer the helicotrema than $x=2.85$ the increased resistance is no doubt due to the liquid moving back and forth in the helicotrema. To obtain an estimate of this for the little element adjacent to the helicotrema at the position $x=3.5$ cm one proceeds as follows. If an alternating force $\mathfrak{F}e^{j\omega t}$ is impressed upon this element while the others are held at rest then a pressure P will be created on the two sides of the helicotrema. If the helicotrema is considered a small capillary of length Δl and cross section πa^2 where a is the radius then it can be shown[4] that

$$P=\left(j\omega\frac{4}{3}+\frac{8\eta}{a^2}\right)\frac{V_c}{\pi a^2}\cdot\Delta l, \tag{8}$$

where η is the coefficient of viscosity of the liquid in the ear and V_c volume velocity of the fluid in the small capillary representing the helicotrema. But the volume velocity in the capillary is the same as the volume

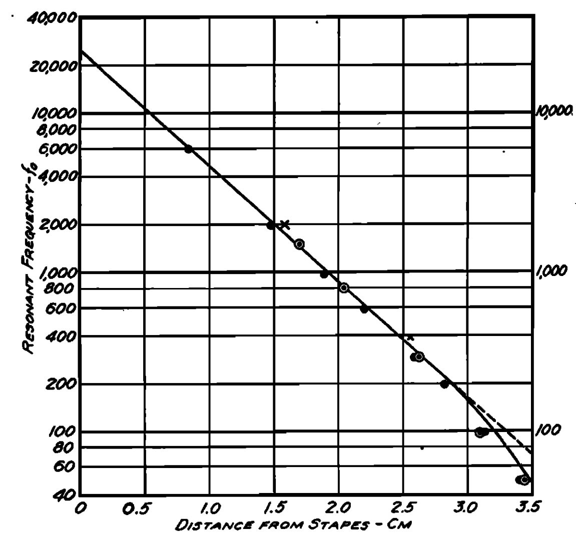

FIG. 3. Resonant frequency of each little element of basilar membrane.

displacement due to the little element or

$$\bar{v}b^2=V_c, \tag{9}$$

where $\bar{v}$ is average velocity of the element. It is given by

$$\bar{v}=(\mathfrak{F}-Pb^2)/j(m\omega-s/\omega)+r. \tag{10}$$

Combining (8), (9), and (10) one obtains

$$\mathfrak{F}/\bar{v}=j\omega\left(m+n\tfrac{3}{4}\cdot\frac{b^4}{\pi a^2}\cdot\Delta l\right)-j\frac{s}{\omega}+r+\frac{8\eta\pi}{(\pi a^2)^2}\cdot\Delta l b^4. \tag{11}$$

This shows that the mass has been increased by $(3/4)(b/1.75)(\Delta l/\pi a^2)m$. If Δl is taken as 0.1 and πa^2 as 0.0025 then this reduces to $0.8m$, or the mass has been increased by a factor of 1.8. This shows that the action

[4] L. E. Kinsler and A. R. Frey, *Fundamentals of Acoustics* (John Wiley and Sons, Inc., New York, 1950), p. 241.

of the helicotrema has the effect of adding mass to the little elements near the helicotrema.

If the dotted line in Fig. 2 is adopted for the effective mass then this increase in mass has already been added.

Equation (11) also shows that the added resistance

$$\Delta r=(8\eta\pi b^4/(\pi a^2)^2)\cdot\Delta l. \qquad (12)$$

Using the same values as used above and with $\eta=0.02$ then Δr is equal to $8000\, b^4$ or $\Delta r/m=183$. The value of ω_0 for this last resonator obtained from (3) is 477 and so r/m obtained from (6) is 238. The value of r/m then is increased by a factor of 1.8. So for calculation purposes the values of r/m were taken as shown in Table I. This damping varies from sample to sample depending upon the dimensions of the helicotrema and width of the basilar membrane.

Values of the mechanical constants r, m, and s for the little element at each position are now available. It remains then to find the value of P at each position, then the value of $\bar{v}$ can be calculated for each position. To do this turns out to be rather complicated.

TABLE I. Damping constants for the little elements along the basilar membrane.

$x=3.5$	3.4	3.3	3.2	3.1	3.0	2.9	2.8	2.7
$\frac{r}{m}=430$	470	500	540	570	610	645	755	890
$\omega_0=477$	560	630	786	920	1080	1290	1510	1780
$\frac{r}{m}\frac{1}{\omega_0}=0.9$	0.83	0.80	0.68	0.62	0.56	0.5	0.5	0.5

One can get a notion of what is taking place by the following consideration. First let us assume that the canal walls and basilar membrane are unyielding and the cross section is uniform and that the round window is a pressure release so that the pressure at this position falls to zero. The equations representing this condition show that the amplitude of the acoustical pressure difference falls linearly from the oval window to the helicotrema for frequencies below 5000 cycles per second. The situation is the same as for a stretched string fixed at one end and moved sinusoidally up and down at the other end. As long as the string is short compared to the wavelength being propagated the whole string moves up and down in phase with the driving force. For 10,000 cycles however, for a 7-cm tube of water, the length of the tube is one-half wavelength so resonances would occur giving rise to amplitudes much larger than the driving amplitude.

This pressure distribution builds up quickly (order of 10^{-5} second) because the time it takes the walls and basilar membrane to yield is of the order of 10^{-2} second for the 100-cycle position to 10^{-4} for the 10,000-cycle position. The first time is the time for sound to travel 7 cm in water and the second time that for the little element to build up to $\frac{2}{3}$ of its maximum amplitude. So during this period of reaching the steady state the elements near the oval window build up to their maximum first, then successive elements build up as one goes from there toward the helicotrema. This then produces a traveling wave along the basilar membrane very different from the acoustic wave going through the liquid and greatly modifies the initial pressure distribution. The fundamental equation governing the motion of the liquid and membrane will now be developed.

The quantities S_1, u_1, p_1 will refer to the cross-sectional area, the fluid velocity parallel to the length of the canal, and pressure at the point x in the scala vestibuli. Similarly, the letters S_2, u_2, and p_2 will refer to similar quantities in the scala typani.

Consider an elemental box in the scala vestibuli which is Δx long and has the cross section S_1. It will contain a mass equal to

$$S_1\rho\Delta x,$$

where ρ is the density of the fluid in the inner ear. The rate that the mass occupying this little element is changing is equal to the rate that the liquid flows through the cross section at x minus the rate that it flows through the cross section at $x+\Delta x$ minus the rate it flows out at the bottom due to the bending of the basilar membrane. Putting these statements into mathematical language gives the continuity equation,

$$S_1/\rho\delta\rho/dt+\delta(S_1u_1)/\delta x+\bar{v}b=0, \qquad (13)$$

where $\bar{v}$ is average velocity across the element and directed from the scala vestibuli to scala tympani. The force pushing this elemental mass along the canal in the direction x away from the stapes is equal to

$$-\delta(S_1p_1)/\delta x\cdot\Delta x.$$

This is opposed by the inertial force of the small mass in the element plus the frictional forces.

It can be shown[5] that this leads to the force equation

$$-(\delta(S_1k_1)/\delta x)=j\rho\omega QS_1\bar{u}_1. \qquad (14)$$

Where, in general,

$$1/Q=[1-(2J_1(Ka)/KaJ_0(Ka))] \qquad (15)$$

the symbols J_0 and J_1 indicating bessel functions of the zero and first order, a the radius of the canal, and

$$K^2=-(j\rho\omega/\eta) \qquad (16)$$

and where now $\bar{u}$ is the average velocity over a cross section of the canal. This value of Q reduces to the one used earlier if S_1f is small compared to unity or

$$Q=4/3-j0.08/Sf \qquad (17)$$

and reduces to

$$Q=1+0.14/(Sf)^{\frac{1}{2}}(1-j), \qquad (18)$$

when Sf is large compared to unity.

[5] See reference 4, p. 20.

It is well known that in a fluid medium

$$\delta\rho/\delta t=(j\omega/c^2)p_1, \tag{19}$$

where c is the velocity of sound waves in the medium. Equations (13), (14), and (19) can be combined to give for the steady state

$$\frac{1}{Q_1}\frac{\partial^2(S_1p_1)}{\partial x^2}+k^2S_1p_1-j\rho\omega b\bar{v}=0. \tag{20}$$

A similar equation holds for the scala tympani using subscript 2 and reversing the sign of $\bar{v}$ or

$$\frac{1}{Q_2}\frac{\partial^2(S_2p_2)}{\partial x^2}+k^2S_2p_2+j\rho\omega b\bar{v}=0. \tag{21}$$

It is difficult to handle these two equations unless it is assumed that $S_1=S_2=S$ at each position x and consequently $Q_1=Q_2=Q$. This will be assumed and the value of S taken as $(S_1+S_2)/2$. These are the values of S plotted in Fig. 1.

Anatomical measurements indicate that this assumption is approximately true except within 2 or 3 mm of the stapes where S_1 becomes many times S_2. So for all regions except this one near the stapes the value of S for calculations is taken as the average values of S_1 and S_2 from three samples given by Wever in his book and are shown by the solid line in Fig. 1. Below $x=0.3$ the dotted line was estimated to be more nearly the value of S to use.

Subtract (21) from (20) and substitute

$$(p_1-p_2)S=SP=Ye^{j\omega t}. \tag{22}$$

The result is

$$\frac{1}{Q}\frac{\partial^2 Y}{\partial x^2}+k^2Y-2j\rho\omega b\bar{v}=0. \tag{23}$$

But the value of $\bar{v}$ is $j\omega\bar{y}$ and $\rho=1$, so from (1)

$$2j\omega b\bar{v}=2uP/1.75F \tag{24}$$

where

$$F=1-\left(\frac{f_0}{f}\right)^2-j\frac{r}{m}\frac{1}{\omega}. \tag{25}$$

So our fundamental differential equation becomes

$$\frac{1}{Q}\frac{\partial^2 Y}{\partial x^2}+\left(k^2-\frac{2n}{1.75SF}\right)Y=0. \tag{26}$$

When $Q=1$ this reduces to the same equation as used by Petersen and Bogert and Zwislocki.

The wave constant k^2 is equal at 10,000 cps to 0.18 and proportional to the frequency for other driving frequencies.

The value of n was taken as $\frac{1}{2}$ so the value of $1/1.75SF$ becomes as high as 120. Therefore k^2 is usually negligible. This means that for the wave travelling down the membrane the fluid may be considered incompressible.

The values of Q for frequencies 50, 100, 200, and 600 cps are $1.28-j.18$, $1.2-j.12$, $1.1-j.10$, and $1.06-j.06$, respectively. In the range where Q differs appreciably from unity there is considerable uncertainty in the value of $(r/m)(1/\omega)$. So for calculation purposes the value of Q was taken as unity. Also the value of k^2 was taken equal to zero. So Eq. (26) reduced to

$$\partial^2Y/\partial x^2=Y/1.75SF. \tag{26A}$$

To solve this equation by numerical integration consider that $1.75SF$ is constant and equal to its value at $x=x_1$ for the interval between $x=x_1$ to $x=x_1+\Delta x_1$. Then Eq. (26A) integrates into

$$Y=1.75SF(\Delta x)^2/2+C_1\Delta x+C_2, \tag{27}$$

where C_1 and C_2 are constants of integration. At $\Delta x=0$, $Y=Y_1$ and $\partial y/\partial x=m_1$. Therefore

$$Y=Y_1+m_1\Delta x+(1/1.75SF)((\Delta x)^2/2), \tag{28}$$

where m_1 is the slope of the curve Y *vs* x at $x=x_1$ and Y_1 is the corresponding value of Y. Now let

$$Y=A+jB, \tag{29}$$

and

$$1/1.75SF=R+jX. \tag{30}$$

Then Eq. (28) is equivalent to the two equations involving only real quantities

$$A_2=A_1+\frac{\Delta A_1}{\Delta X_1}\Delta X_2+(RA-XB)\frac{(\Delta X_2)^2}{2} \tag{31}$$

and

$$B_2=B_2+\frac{\Delta B_1}{\Delta X_1}\Delta X_2+(RB+XA)\frac{(\Delta X_2)^2}{2}. \tag{32}$$

The process of numerical integration then is to start with initial values of A_1, B_1, $(\Delta A/\Delta X)_1$, and $(\Delta B/\Delta X)_1$. From these values calculate the values A_2 and B_2 for a a step ΔX from (31) and (32). Then

$$A_2-A_1=\Delta A_2=(\Delta A_1/\Delta X_1)\Delta X_2 +(RA-XB)((\Delta X_2)^2/2), \tag{33}$$

and consequently the new slope is $\Delta A_2/\Delta X_2$ or equal to the old slope plus $(RA-XB)(\Delta X_2/2)$.

Thus one proceeds step by step from one end of the membrane to the other and obtains values of A and B corresponding to each position x.

The boundary conditions at the stapes are for $x=0$

$$S_0P_0=(A_0+jB_0)e^{j\omega t}, \tag{34}$$

where P_0 is the difference in pressure in the scala vestibuli at the stapes from that in the scala tympani at the round window and S_0 the cross-sectional area of the stapes, or

$$P/P_0=(A+jB/A_0+jB_0)(S_0/S). \tag{35}$$

This equation then enables one to find P both in

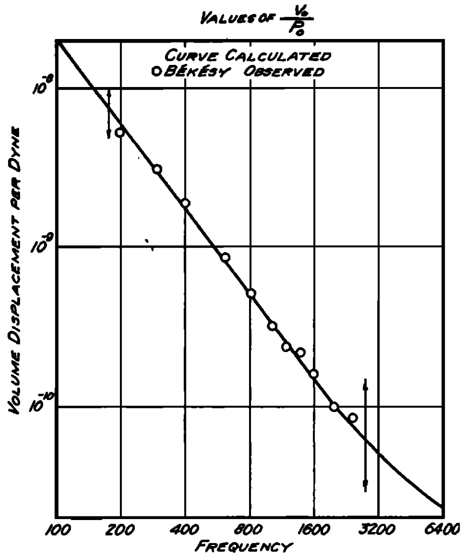

FIG. 4. Volume displacement per dyne pressure at the stapes.

magnitude and phase for any value of x since A and B are known for each value of x.

To find the boundary conditions at the helicotrema one proceeds as follows. The volume displacement V_1 of liquid along the scala vestibuli at any position x is given by (14) as

$$-(\partial(S_1p_1)/\partial x)=j\rho\omega Q_1(\partial V_1/\partial t). \tag{36}$$

Similarly for the scala tympani

$$-\partial(S_2p_2)/\partial x=j\rho\omega Q_2(\partial V_2/\partial t). \tag{37}$$

Near the helicotrema

$$(\partial V_2/\partial t)=-(\partial V_1/\partial t).$$

So Eqs. (36) and (37) combine into

$$-(\partial(P_cS_c)/\partial x)=2j\omega\rho Q_c(\partial V_c/\partial t), \tag{38}$$

the subscript c indicating values in the two canals at $x=3.5$ cm, the position of the helicotrema.

Now consider the helicotrema as a small capillary Δl cm long and having a cross-sectional area S_H. Apply (14) to this small capillary and there results

$$-\partial(S_HP_H)/\partial x=j\rho\omega Q_H(\partial V_1/\partial t). \tag{39}$$

The volume rate going through the helicotrema is equal to the volume rate going along the canals or

$$(1/2Q_c)(\partial(P_cS_c)/\partial x)=(1/Q_H)(\partial(S_HP_H)/\partial x)$$
$$=-(1/Q_H)(S_HP_H/\Delta l), \tag{40}$$

or the boundary conditions at the helicotrema where $s=3.5$ cm are given by

$$\partial(A_1+jB_1)/\partial x=-\frac{2}{\Delta l}\frac{Q_c}{Q_H}\frac{S_H}{S_c}(A_1+jB_1). \tag{41}$$

An estimate of S_H and S_c and Δl gave 0.0025 cm^{-2}, 0.006 cm^{-2} and 0.1 cm. Using these values and taking Q_c/Q_H equal to unity then Eq. (41) gives the two conditions that must hold at the helicotrema

$$(\partial A/\partial x)_1=-8A_1, \tag{42}$$

$$(\partial B/\partial x)_1=-8B_1. \tag{43}$$

It is convenient to start the calculation at the helicotrema in which case each step Δx is negative. So if one starts with $A_1=1$, $\Delta x=-0.05$, and $B_1=0$, then the initial increments

$$\Delta A_1=(\partial A_1/\partial x)_1\Delta x=+0.4$$

and

$$\Delta B_1=(\partial B/\partial x)_1\Delta x=0.$$

Starting with these values will yield values of A_0 and B_0 at the stapes. These can then be scaled down to fit any desired conditions there.

It is obvious that Eq. (38) can also be applied to conditions at the stapes or

$$-\frac{\partial(S_0P_0)}{\partial x}=2j\omega PQ_0\frac{\partial V_0}{\partial t}=-2\omega^2PQ_0V_0,$$

or taking ρ and Q_0 equal to unity

$$V_0=\frac{1}{2\omega^2}(m_{A0}+jm_{B0})e^{j\omega t}, \tag{44}$$

where m_{A0} and m_{B0} are the values of the slopes giving A *vs* x and B *vs* x at the position $x=0$. Békésy made measurements of V_0 per dyne or

$$\frac{V_0}{P_0}=\frac{S_0}{2\omega^2}\frac{(m_{A0}+jm_{B0})}{A_0+jB_0}. \tag{45}$$

In Fig. 4 are shown results calculated by this equation and the values measured by Békésy.[6] The solid curve is calculated and circles observed. It is seen that the calculated and observed results are in excellent agreement. Indeed the agreement is too good since the statistical error due to sampling as given by Békésy is

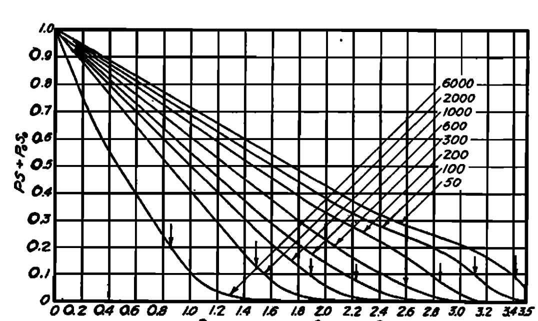

FIG. 5. Distribution of pressure in the inner ear due to various driving frequencies.

[6] G. v. Békésy, J. Acoust. Soc. Am. 21, 233–245 (1949).

indicated by the arrows. At the higher frequencies it is about a factor 5 and at the lower frequencies a factor of 2 or 3. The calculated phase difference varied from 0.84π to 0.92π and agrees with Békésy's result, that is, V_0 lags P_0 by about 0.9π, within the observational error. The values of SP/S_0P_0 from (35) were calculated and are shown in Fig. 5. The vertical arrows on these curves indicate the position for the maximum displacement of the basilar membrane as calculated below.

The displacement of the basilar membrane per dyne pressure difference between that of the oval window and that at the round window is given by

$$\frac{\bar{y}}{P_0}=-\frac{S_0}{Q_x}\frac{(R+jX)}{2b\omega^2}\frac{(A+jB)}{(A_0+jB_0)}. \qquad (46)$$

The displacement $\bar{y}$ per unity volume displacement at the stapes is given by

$$\frac{\bar{y}}{V_0}=-\frac{1}{Q_xb}\frac{(R+jX)(A+jB)}{m_{A0}+jm_{B0}}. \qquad (47)$$

Equation (46) shows that the displacement $\bar{y}$ per dyne varies inversely as the square of the frequency and the other quantities in (46) vary slowly with frequency. Likewise (47) shows the displacement $\bar{y}$ per unit displacement of the stapes varies slowly with frequency.

$$\bar{y}/y_m=((R+jX)(A+jB)/(R_m+jX_m)(A_m+jB_m))\times(b_m/b) \qquad (48)$$

where the values with subscript m are the values which produce a maximum displacement. Calculations from this equation give the curves shown in Fig. 6. The circles and crosses are from one set of data by Békésy and the squares are from another set published at an earlier date. The phase angles given in the upper plot by

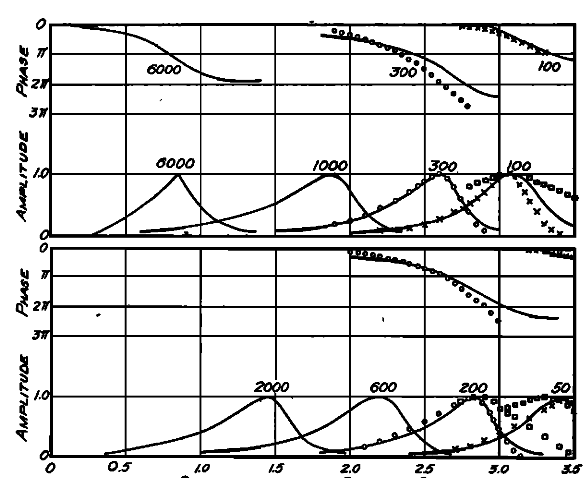

FIG. 6. Amplitude and phase of the vibration of the basilar membrane at various distances from the stapes.

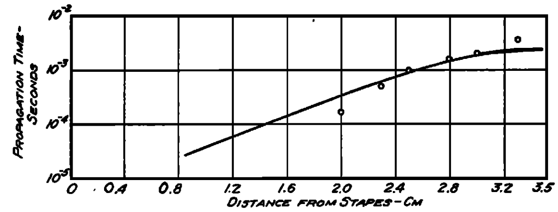

FIG. 7. Propagation time of wave traveling along basilar membrane.

the solid line are calculated from

$$\theta=\tan^{-1}\frac{X}{R}+\tan^{-1}\frac{B}{A}-\tan^{-1}\frac{B_0}{A_0}-\pi, \qquad (49)$$

for all cases except for 100 cps and 50 cps. This phase angle is the difference in phase between $\bar{y}$ and P_0 as shown by (46) or the displacement $\bar{y}$ per dyne is given by

$$\bar{y}=\frac{S_0}{2b\omega^2}\left(\frac{(RA-XB)^2+(RB+XA)^2}{A_0^2+B_0^2}\right)^{\frac{1}{2}}\cdot\cos(\omega t-\theta). \qquad (50)$$

The value of $\tan^{-1}(X/R)$ is equal to π at $x=0$ so θ is equal to zero and $\bar{y}$ is in phase with the pressure at the stapes. The calculated phase angles shown in Fig. 6 for 50 cps and 100 cps are taken from (54) simply because the calculated results agree with the observed ones. They show the phase between displacement of stapes and displacement of membrane at position x for these two frequencies. If θ is plotted the two curves for phase are shifted downward 0.9π. The difference in phase will be the same for $\bar{y}$ *vs* P_0 or $\bar{y}$ *vs* V_0, and it is my understanding that this is what Békésy observed.

The time for the wave to travel from stapes to any position x should be the same as the phase difference between maximum V_0 and maximum $\bar{y}$ divided by ω or

$$\tau=\frac{\tan^{-1}(X_m/R_m)-\pi+\tan^{-1}(B_m/A_m)-\tan^{-1}(m_{B0}/m_{A0})}{\omega}, \qquad (51)$$

where the subscripts m refer to values which make $\bar{y}$ a maximum. Calculations from (51) give the solid curve in Fig. 7. The circles are data observed by Békésy. The measured time was that taken from the instant the stapes was struck to the time when a noticeable deflection of the basilar membrane occurred at the point observed. For example, for 200 cps $x_m=2.84$, $X_m=117$, $R_m=61$, $B_m=0.73$, $A_m=00$, $m_{B0}=2.9$, and $m_{A0}=-1.5$. Therefore,

$$\tau=(116-180+90-117/360\times 200)$$
$$=1.23\times 10^{-3}\text{ second}$$

and this is the time for the wave to travel from stapes to $x=2.84$ cm.

Since it has been shown that the fluid may be con-

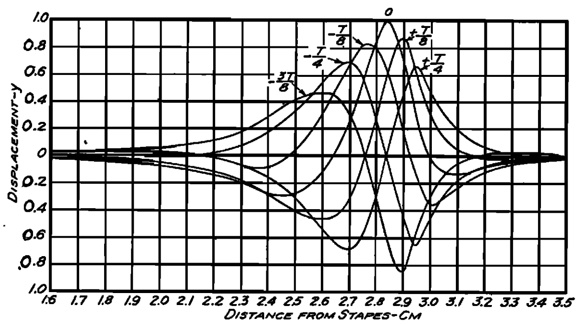

FIG. 8. Shape of basilar membrane during vibration at times which are successively $\frac{1}{8}$ of a period apart.

sidered incompressible, the volume displacement V_0 would be the same as the total displacement of the membrane provided nothing goes through the helicotrema. The pressure curves in Fig. 5 show that this should hold for frequencies above 200 cps. Therefore

$$V_0=\int_0^{3.5} b\bar{y}dx, \tag{52}$$

and these two quantities must be in phase. For example, for 200 cycles, V_0 leads $\bar{y}_m$ by 89° as seen from the above calculation. Consequently, the maximum displacement produced by entire membrane occurs about $\frac{1}{4}$ period before the y_m occurs. This is illustrated by the curves shown in Fig. 8 which shows a plot (for 200 cps) of

$$(\bar{y}/y_m)\cos(\omega t-\theta) \tag{53}$$

for times which are $T/8$ and $T/4$ and $3T/8$ before $t=t_m$ the time when $\bar{y}_m$ occurs and for times which are $T/8$ and $T/4$ after $t=t_m$ where T is the period of vibration.

The area under each curve which is above the zero line minus the area under the zero line is proportional to the integral in (52). These areas are plotted against time in Fig. 9 and it turns out to be sinusoidal as it should be. Also this diagram helps to make clear the meaning of the travel time τ. It is interesting to note that when $\bar{y}$ becomes a maximum, the total displacement of liquid due to the basilar is almost zero for this case of $f=200$ cps.

It has been shown that the calculated results are all

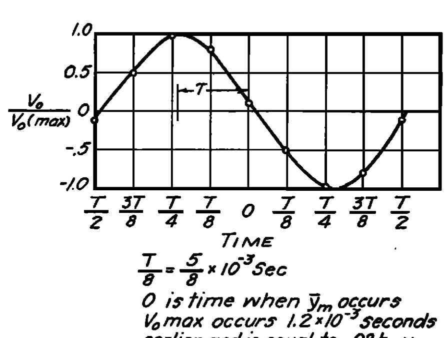

FIG. 9. Variation with time of the total displacement of the basilar membrane.

in excellent agreement with the experimental results which seem to justify the assumptions made in deriving the equations. However, there is yet one comparison between calculated and observed results which shows larger differences than any noted above. It is the absolute values of $\bar{y}_m/V_0$ given from Eq. (47) which are given by

$$1/b\left(\frac{(RA-XB)^2+(RB+XA)^2}{m_{A0}{}^2+m_{B0}{}^2}\right)^{\frac{1}{2}}$$

where R, X, A, and B correspond to values giving $\bar{y}$ a maximum value. These values are shown in Table II. The observed values are from 3 to 8 times larger than the calculated ones. As a check on the calculated value for 200 cps, Eq. (48) was used as follows. It can be

TABLE II. Volume displacement at the oval window divided by maximum displacement of the basilar membrane for different driving frequencies.

	Values of $V_0/\bar{y}$	
f	Calc	Obs
100	2.4×10^{-3}	20×10^{-3}
200	1.4×10^{-3}	12×10^{-3}
300	3.1×10^{-3}	10×10^{-3}
600	2.0×10^{-3}	8×10^{-3}
1000	2.0×10^{-3}	6×10^{-3}
2000	1.0×10^{-3}	5×10^{-3}
6000	1.5×10^{-3}	···

written as follows:

$$V_0=y_mb_m\times\int_0^{3.5}\left(\frac{(RA-XB)^2+(RB+XA)^2}{(R_mA_m-X_mB_m)^2+(R_mB_m+X_mA_m)^2}\right)^{\frac{1}{2}}\times\cos\left(\theta-\frac{\pi}{2}\right)dx,$$

where

$$\theta=\tan^{-1}(RB+XA/RA-XB)-\tan^{-1}(R_mB_m+X_mB_m/R_mA_m-X_mB_m).$$

The integral was found by graphical means to be 0.083. Therefore,

$$V_0/y_m=0.041\times0.083=3.4\times10^{-3}.$$

This is closer to the observed value of 12×10^{-3} but the difference is still large.

One can deduce from the curve of y/y_m derived by Békésy from his data.[7] The value of V_0/y_m is as follows:

$$V_0=\bar{y}_m\int_0^{3.5} b\frac{\bar{y}}{y_m}dx.$$

[7] G. v. Békésy and W. A. Rosenblith, "The mechanical properties of the ear." In S. S. Stevens (Editor), *Handbook of Experimental Psychology* (John Wiley and Sons, Inc., New York, 1951), Fig. 36, p. 1100.

The integral was found by graphical means to 2×10^{-3}. The curve of y/y_m which was used had a phase of $\pi/2$ ahead of the one where y comes to maximum. There may be an uncertainty of a factor 2 in the calculated results as a result of the size of step used in the numerical integration and $m_{A0}+jm_{B0}$ which is a factor in Eq. (54) depends upon the last step in this process. Also Békésy gives the statistical variation of V_0 as a factor 2 to 5. This uncertainty more than covers the difference observed but still one should look for a reason not yet apparent to explain this difference, since the agreement seems so good for all of the other relations.

APPENDIX. List of symbols and their meanings

A, B	real and imaginary parts of Y.
a	radius
b	width of the basilar membrane
C_i	constants of integration
c	velocity of sound in water
$\mathfrak{F}$	=force
F	$=1-\left(\frac{f_0}{f}\right)^2-j\frac{r}{m}\frac{1}{\omega}$
f	frequency of impressed tone
f_0	resonant frequency of an elementary unit of the membrane
J_i	bessel functions of order i
K	$=(1-j)(\rho\omega/2\eta)^{0.5}$
k^2	wave constant $(=\omega^2/c^2)$
Δl	length of helicotrema
m	mass of an elementary unit of the membrane
m_1	slope at x_1 of function relating Y to x
n	constant between 0.3 and 1.0 (for edge effects of elementary units)
P	pressure difference on the two sides of the membrane
P_e	pressure between scala tympani and scala vestibuli at helicotrema
P_H	pressure across the helicotrema
P_0	pressure on the membrane at the stapes
p_1	pressure at point x in the scala vestibuli
p_2	pressure at point x in the scala tympani
Q	$=\left(1-\frac{2J_1(Ka)}{KaJ_2(Ka)}\right)^{-1}$
R	real part of $1/1.75SF$
r	mechanical resistance of an elementary unit of the membrane
r_r	radiation resistance of an elementary unit of the membrane
S	average of S_1 and S_2; cross sectional area
S_e	average cross-sectional area of canals at helicotrema
S_H	cross-sectional area of helicotrema
S_0	cross-sectional area of stapes
S_1	cross-sectional area of scala vestibuli
S_2	cross-sectional area of scala tympani
s	stiffness of an elementary unit of the membrane
T	period of vibration
u_1	fluid velocity parallel to length of scala vestibuli
u_2	fluid velocity parallel to length of scala tympani
$\bar{u}$	average fluid velocity over a cross section of the canal
V_e	volume velocity of fluid in helicotrema
V_0	volume displacement of liquid at stapes
V_1	volume displacement of liquid in scala vestibuli
V_2	volume displacement of liquid in scala tympani
$\bar{v}$	average velocity of an elementary unit of the membrane
X	imaginary part of $1/1.75SF$
x	distance from stapes in centimeters
Y	amplitude of quantity SP which is varying sinusoidally with time
$\bar{y}$	average displacement across membrane at x cm from the stapes
η	coefficient of shear viscosity of liquid in the ear
ρ	density of liquid in the ear
τ	propagation time of wave along the basilar membrane
ω_0	angular frequency of resonance of an elementary unit of the membrane

Note: A paper "On the dynamics of the middle ear and its relation to the acuity of hearing," which is a continuation of this paper, will appear in the March issue of this journal. A summary of the results will appear in my paper published in the December number of *Physics Today.*