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The Dynamics of the Middle Ear and Its Relation to the Acuity of Hearing

HARVEY FLETCHER
Columbia University, New York, New York

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The transformer action of the middle ear as measured by Bekésy is shown to be the principal cause for the low acuity of hearing for low frequencies. Because of the very low mechanical impedance across the basilar membrane at low frequencies, large acoustical pressures in front of the ear drum produce appreciable acoustical pressures across the basilar membrane. For example, at 100 cps this pressure is 30 times and at 6000 cps it is 1/10 that created across the basilar membrane.

IN the May, 1949 issue of *The Journal of the Acoustical Society*, Bekésy gave two experimental curves pertaining to the dynamics of the middle ear which have an important bearing on the acuity of hearing at various frequencies. The first one (Fig. 5 of his paper) gives the amount of fluid displaced ΔV by the round window during each cycle when tones of various frequencies throughout the audible range were impressed upon the external eardrum (membrani typani) having an acoustical pressure P_{ED}. In the curve, the values of $\Delta V/P_{ED}$ are given as ordinates and the frequency as abscissas. Similarly, in the second curve (Fig. 6 of his paper), he gives values $\Delta V/P_0$, where ΔV is again the volume of fluid displaced by the oval window and P_0 is the difference in pressure between that in the fluid just back of the oval window and that just back of the round window. In order to make these measurements, it was necessary to remove both the round window and the oval window. However, whether they are in place or whether they are removed and some artificial means is used to create the pressure difference P_0 at the two ends of the liquid column in the cochlea, the motion of the various parts of the cochlea will be the same. For a given P_0 in dynes, the velocity and displacement of the basilar membrane at every position along its length will be determined. This value of P_0 must be very nearly equal to that for the pressure across the basilar membrane at the basal end, and on what follows it will be considered equal to this pressure difference. If the acoustical pressure is impressed directly on the stapes after the oscicles have been removed, then Bekésy's measurements showed that pressures ranging from 10 P_0 at 200 cps to 1.5 P_0 at 1000 cps are required to produce a pressure P_0 across the basilar membrane at the basal end.

If the values of $\Delta V/P_{ED}$ from the Bekésy data are divided by those of $\Delta V/P_0$, then values P_0/P_{ED} are obtained. Values obtained in this way were used to give the lower curve of Fig. 1. The ordinates are expressed as db difference in pressure level or $20 \log P_0/P_{ED}$.

It is seen that when one dyne per square centimeter pressure exists in front of the eardrum, at 650 cps driving frequency, one dyne per square centimeter is created across the basilar membrane at the basal end. There is no amplification of the pressure as it passes through the mechanical amplifier of the middle ear. For driving frequencies lower than 650 cps the value of P_0 is lower than P_{ED}, so the mechanical transformer attenuates the pressure, and for frequencies higher than this value, P_0 is higher than P_{ED}, so there is amplification. Fortunately, the amplification is in the range of speech frequency. Also, this transformer action discriminates against most noises which have large acoustical pressures in the low frequency region.

It is rather surprising that for frequencies below 100 cps the attenuations are greater than 30 db. This is due to the low mechanical impedance across the basilar membrane for these low frequencies. If the containing walls and the basilar membrane were rigid and the helicotrema solidly plugged, then the impedance of the inner ear would be very large for all frequencies, and consequently under such circumstances amplifications instead of attenuations will be produced at these low frequencies. Bekésy made measurements under such conditions, and the results are given by the top curve in Fig. 1. It is seen that these values of amplification correspond to what one would expect from the mechanical constants of the middle ear. It is seen that the driving frequency must be raised to about 10,000 cps before the inner ear impedance approaches an infinite value.

As soon as the lower curve in Fig. 1 was obtained, it occurred to me that this poor transformer action of the middle ear is the cause for poor acuity of hearing at low frequencies. By means of the equations developed in my paper, "On the Dynamics of the Cochlea,"[1] one

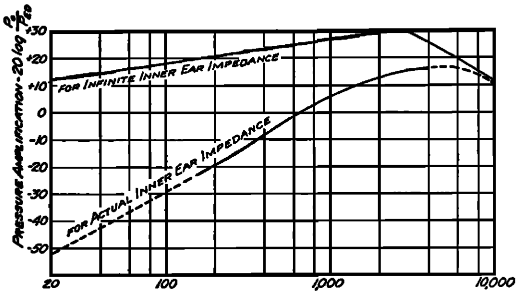

FIG. 1. Pressure amplification of the mechanical transformer of the middle ear.

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[1] J. Acoust. Soc. Am. 23, 637 (1951).

TABLE I.

Frequency =	25	50	100	200	300	600	1000	2000	6000	10,000
$\frac{v_m}{P_{ED}}\times 10^3=$	0.033	0.17	0.25	0.55	0.75	1.6	2.7	3.9	4.2	0.70
$\frac{y}{P_{ED}}\times 10^6=$	0.21	0.55	0.40	0.43	0.40	0.41	0.44	0.31	0.17	0.01

can test this hypothesis, and it turns out to be a true one, as will now be shown.

Following the analysis given in the paper, the velocity v and displacement y are given by

$$v=j\omega y=\frac{1}{2}\frac{Pb^2}{m}\frac{1}{j[\omega-(\omega_0^2/\omega)]+(r/m)}, \quad (1)$$

where P is the pressure difference on the two sides of the basilar membrane; b is the width of the basilar membrane at the corresponding position; ω, the impressed frequency in radians per second; ω_0, the resonant frequency at the position considered; and r, the mechanical resistance of the little element. It was shown that the mass m is given by

$$m=1.75b^3 \quad (2)$$

and the value of r/m is given by

$$r/m=0.5\omega_0, \quad (3)$$

except for those positions corresponding to resonant frequencies below 200 cps. At 100 cps and 50 cps, this value was taken as $0.65\omega_0$ and $1.0\omega_0$. The maximum values of v and y are given approximately by Eq. (1) when $\omega=\omega_0$, or

$$v_m=\frac{P_m}{3.5b_m(r/m)}, \quad (4)$$

where P_m and b_m are the values of P and b at the positions where resonance occurs. The values of P_m can be obtained from the following relation.

$$P_m=\left(\frac{P_mS_m}{P_0S_0}\right)\left(\frac{S_0}{S_m}\right)\left(\frac{P_0}{P_{ED}}\right)P_{ED}. \quad (5)$$

The values of the first two factors can be read from curves given in my paper already cited, and the values of P_0/P_{ED} can be obtained from the curve in Fig. 1.

So the velocity and displacement of the basilar membrane for one-dyne pressure in front of the eardrum were calculated from these relations and found to be those in Table I.

An explanation is necessary concerning the calculation of the case for 25 cps. Since there is no position of resonance, the maximum value is obtained by replacing the factor r/m by the expression

$$\left[\left(\frac{r}{m}\right)^2+\left(\omega-\frac{\omega_0^2}{\omega}\right)^2\right]^{\frac{1}{2}},$$

which for this case $r/m=157$, $\omega=2\pi\times 25$, and $\omega_0=2\pi\times 50$. This factor then becomes 500 instead of 157.

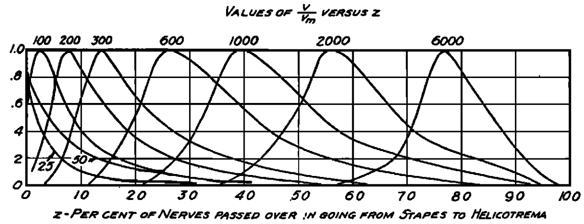

FIG. 2. Velocity amplitudes of the basilar membrane at various positions and for various impressed frequencies.

It is seen that the displacement is more nearly constant than the velocity. From 50 cps to 2000 cps, the displacement of the basilar is approximately proportional to the pressure and independent of frequency, while in this same region the velocity is approximately proportional to the frequency.

The variation of the acuity of hearing with frequency can be explained by making the following three simple assumptions. At pressure levels near those corresponding to the threshold of hearing, the number of discharges per second coming from a unit length of the basilar membrane is proportional to the following:

1. The energy of vibration or to v^2 at the position x cm from the stapes.
2. The density σ of the nerve endings at the position x.
3. The impressed frequency for frequencies below 300 cps and a constant for frequencies above 300 cps.

These are all reasonable assumptions which one might expect to hold. The last one is based on the action of auditory nerve fibers. The nerve is excited only at the maximum or minimum velocity during each cycle for frequencies below 300 cycles. Consequently, the nerve discharges are synchronized with the frequency. Therefore, they are proportional to the frequency. Above 300 cycles, due to the refractory period of the nerve, only a small increase in the rate of firing is produced by increasing the frequency so it is considered independent of frequency. Putting these assumptions into an equation,

$$N=K\frac{f}{300}\int_0^l v^2\sigma dx=K\frac{f}{300}v_m^2\int_0^{100}\left(\frac{v}{v_m}\right)^2dz, \quad (6)$$

TABLE II. Comparison of observed and calculated pressure levels for the threshold of hearing.

	$f=$	25	50	100	200	300	600	1000	2000	6000	10,000
$20\log P_{ED}$	Calculated =	−4	−21	−35	−42	−48	−57	−67	−69	−60	−48
	Observed =	−2	−16	−30	−44	−51	−61	−63	−64	−62	−44
	Difference =	−2	−5	−5	+2	+3	+4	−4	−5	+2	−4

where N is the total number of nerve discharges per second, K is a constant, l is the length of the vasilar membrane, and $dz=\sigma dx$ is the fraction of the nerve endings passed over in going from the stapes to the position x.

It will be remembered that $f/300$ must be taken as unity for values greater than unity.

At the threshold, it would be expected that N and K would be constant for all stimulating frequencies. Therefore, $10 \log N/K$ should be a constant. Its value was taken to make calculated and observed results to give the best agreement, namely, $10 \log N/K=-87$.

Then Eq. (6) can be written

$$20 \log P_{ED}=10 \log 300/f_0 - 10 \log \int_0^{100} \left(\frac{v}{v_m}\right)^2 dz - 20 \log \frac{v_m}{P_{ED}} - 87. \quad (7)$$

The values of $20 \log P_E$ calculated from this equation are given in Table II. The values for the term

$$10 \log \int_0^{100} \left(\frac{v}{v_m}\right)^2 dz$$

were obtained from the curves shown in Fig. 2. These curves were taken from my paper, which was already cited. The values of the number σ of nerve endings per centimeter was taken from the data obtained by Guild. These values for all the frequencies lie between 5 db and 13 db, so it is unimportant in producing the observed variation of acuity of hearing with frequency. The first term of Eq. 7 causes a variation of 11 db at 25 cps to 0 db at 300 cps. The principal cause for the large variation is due to the third term which ranges from 84 db at 25 cps to 41 db at 6000 cps.

The agreement between observed and calculated results are well within the observational error.

So it is seen that the loss in acuity of hearing of a normal ear for the low frequencies is adequately explained and is due principally to the poor transformer action at these low frequencies.

If now we interpret N as the loudness in sones produced by the tone for levels near the threshold, then at the threshold level the value of $N=001$ sones. Since the value of $10 \log N/K=-87$ at the threshold level, it follows that $K=5\times 10^5$.

So, near the threshold, the loudness N in sones is given by

$$N=5\times 10^5 \frac{f}{300} \int_0^{100} v^2 dz,$$

where v is the velocity of the basilar membrane in cm/sec and z is the position coordinate or the percent of nerve endings passed over in going from the stapes to the helicotrema end of the basilar membrane.

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Recovery of the Auditory Threshold after Strong Acoustic Stimulation*

I. J. HIRSH† AND W. D. WARD
Psycho-Acoustic Laboratory, Harvard University, Cambridge, Massachusetts

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After an ear is exposed to an intense sound, the absolute threshold for many sounds is raised, usually temporarily. The manner in which the absolute threshold recovers to its normal value after such stimulation is the subject of these experiments. It is found that recovery from such auditory fatigue is not a simple monotonic process. Rather these experiments show that under certain conditions the threshold first recovers to an approximately normal value about 1 minute after the cessation of the exposure but then rises again to a higher value that reaches a maximum at about 2 minutes after the exposure. This diphasic recovery curve, with its characteristic "bounce," is found when the exposure involves sound pressure levels between 100 and 120 db and durations of the order of several minutes.

Recovery curves are shown for the auditory thresholds of clicks, bands of noise, and pure tones. Fatiguing stimuli include bands of noise and pure tones.

Two subsidiary observations are also reported. First, in many recovery curves there is evidence for a second "bounce" or rise in the threshold after stimulation. Second, after stimulation by moderate intensities the initial recovery (about 1 minute after stimulation) may demonstrate facilitation, i.e., a temporary reduction in the absolute threshold below the normal value. Qualitative observations concerning the pitch and timbre of the test stimuli and of tinnitus following stimulation are related to some of the data.

INTRODUCTION

THE term *auditory fatigue* has been applied to a wide range of experimental conditions differing mostly with respect to the duration, intensity, and frequency or frequencies in the fatiguing sound. One generalization that can be made about nearly all the many experiments on auditory fatigue is that after exposure to a sound the auditory system's threshold for certain sounds is raised temporarily, and then, unless the stimulation has been very strong, it recovers to its normal value. The amount of fatigue depends upon the characteristics of the stimulating sound and the interval between the cessation of the exposure and the measurement of the threshold.

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† Now at Central Institute for the Deaf and Washington University, St. Louis, Missouri.