impedance, a positive pressure being produced in the outer branch at the same time as equal negative pressure is produced in the inner branch, and vice versa.

The sources Q_j and Q'_j, on the other hand, are each applied as though the inner and outer branches were connected (approximately) in parallel.[2,5] For free-jet-edge oscillation, therefore, each produces sound pressure of the same sign in both branches. Since Q_j and Q'_j are 180° out of phase, interference results so that there is no net sound pressure produced by these sources in the normal edgetone.

The effect of replacing the inner branch with a resonant air column is to change the symmetry of the branch impedances. At the resonance frequency the branches now have impedances of approximately equal magnitude and opposite sign, being dominated by reactive components. This causes a phase inversion in the sound pressure produced by Q_j relative to that of Q'_j, so that the two sources reinforce rather than interfere with each other. The resulting monopole source, represented by the combined flow $(Q_m + Q'_j)$, is a far more efficient radiator than the edge-coupled dipole at low Mach numbers and can be counted on to dominate the field in normal organ pipe operation.

Two separate mechanisms may thus be distinguished with regard to the modes of feedback and coupling to the medium. Phasewise the two are linked by the sequence of events that take place at the trailing edge. Except for the case of transients, or for off-resonant oscillation, however, one or the other mode dominates, depending on the symmetry of the branch impedances. To avoid confusion, therefore, it would be well if the type of oscillation where pipe-mode drive and pipe-mode feedback are dominant were referred to as "pipetone" oscillation (or perhaps "organ pipe" oscillation, although this does not have the same ring of generality).

[1]John S. Rigden, *Physics and The Sound of Music* (Wiley, New York), p. 117 (1977).
[2]L. Cremer and H. Ising, Acustica 19, 143–153 (1967–1968).
[3]J. M. Coltman, J. Acoust. Soc. Am. 44, 983–992 (1968).
[4]J. M. Coltman, J. Acoust. Soc. Am. 60, 725–733 (1976).
[5]S. A. Elder, J. Acoust. Soc. Am. 54, 1554–1564 (1973).
[6]T. P. Smith III and S. A. Elder, J. Acoust. Soc. Am. 60, S121 (1976).
[7]N. H. Fletcher, Acustica 34, 224–233 (1976).
[8]N. H. Fletcher, J. Acoust. Soc. Am. 60, 481–483 (1976).
[9]N. H. Fletcher, J. Acoust. Soc. Am. 60, 926–936 (1976).
[10]R. T. Schumacher, Acustica 39 No. 4, 225–238 (1978).
[11]A. Powell, J. Acoust. Soc. Am. 33, 395–409 (1961).
[12]A. Powell, J. Acoust. Soc. Am. 34, 163–166 (1962).
[13]The work of Brackenridge (J. B. Brackenridge and W. L. Nyborg, J. Acoust. Soc. Am. 29, 459–463 (1957)) where the trailing edge is itself a resonator, seems to represent a special case. Here edge and resonant effects are merged in an interesting way. Perhaps this should be characterized as a "resonant edgetone."
[14]W. L. Nyborg, M. D. Burkhard, and H. K. Schilling, J. Acoust. Soc. Am. 24, 293–304 (1952).
[15]D. I. Blokhintsev, *ZhTF*, Vol. XV, pp. 63–70 (1945). Translated by R. D. Cooper. SLA Translation Pool No. 270 (UNR 1957).
[16]W. L. Nyborg, C. L. Woodbridge, and H. K. Schilling, J. Acoust. Soc. Am. 25, 138–146 (1953).
[17]A. Powell, *Fourth International Congress on Acoustics*, Paper 022, Copenhagen (1962).
[18]D. Bechert, "Schwingungen eines akustisch gesteurten ebenen Freistrahls," 5th *International Congress on Acoustics Liege*, Paper L35, (1965).
[19]Strictly speaking, the eddy pair constitutes a solenoidal field, so that sources can occur only in doublets, like the poles of a magnet.

Stiffness gradient along the basilar membrane as a basis for spatial frequency analysis within the cochlea

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Stiffness z of the basilar membrane of the house mouse against a displacement by sound was calculated from data on width and thickness of the membrane. Three functions of the kind $\log_{10} z = ax + b$ were obtained which equally express the stiffness change in dependence on the locus x on the basilar membrane. These functions were compared with the one for frequency representation. The result is that the spatial distribution of displacement maxima for frequencies and of stiffness follows the same kind of place-dependent functions over a large portion of the basilar membrane. From this it can be concluded empirically that the frequency and stiffness (calculated from width and thickness of the basilar membrane) scales along the cochlea are generally proportional to each other and that stiffness is a dominant factor for the determination of the locus of the displacement maximum for a given frequency.

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INTRODUCTION

The frequency-dependent displacement of the basilar membrane by traveling waves is the principle basis for frequency resolution within the cochlea of mammals. The mechanical properties of cochlear fluid spaces and membranes change between base and apex with the ef-

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fect that the displacement maxima for different frequencies are orderly spread along the basilar membrane with high frequencies represented near the base and low frequencies near the apex. Many, sometimes complicated mathematical models of cochlear mechanics have been proposed (see, e.g., Dallos, 1973; Geisler, 1976), which often build upon v. Békésy's (1960) measurements of volume displacement and elasticity gradients along the cochlea.

In the present paper it will be shown that spatial frequency analysis based on frequency-dependent displacement maxima of the basilar membrane correlates with a function of changing width and thickness of the basilar membrane along its major part. Width and thickness are basic anatomical measures which can be determined without greater difficulties. However, their influence on the displacement pattern of the basilar membrane and on frequency representation has not yet been quantitatively demonstrated.

I. METHODS

Width and thickness were measured in nine cochleas of the house mouse, Mus musculus (outbred strain NMRI) with a resolution of one measurement per 0.1 mm [total length of the basilar membrane, 6.84 mm (Ehret and Frankenreiter, 1977)]. The insert to Fig. 1 shows that the basilar membrane of the mouse is divided into two parts, pars pectinata (d_1, w_1) and pars tecta (d_2, w_2). Both parts can be clearly distinguished from about 2 mm from the apex down to the base. The thickness of pars pectinata increases monotonously from the apex up to about 1 mm from the base, while the thickness of pars tecta increases somewhat irregularly from 2 mm from the apex to about 1 mm from the base; the width of both parts decreases from the apex to the base (Ehret and Frankenreiter, 1977).

For calculating stiffness z of the basilar membrane one has to consider its mode of displacement. It has been demonstrated (Ehret and Frankenreiter, 1977) that a displacement of the basilar membrane of the mouse happens as a motion at three hinge points (arrows in the insert to Fig. 1) without any flexion of pars pectinata and pars tecta (cf. Steele, 1973, mode II). This is true from about 2 mm from the apex almost down to the basal end.

The stiffness against a displacement at the three hinge points is proportional to the stiffness of the material at the hinges, inversely proportional to the total width w of the basilar membrane, and in addition depends on w_1/w_2. If $w_1 = w_2$ then the largest displacement should occur for a given pressure, and the stiffness is smallest. In the mouse w_1 is always larger than w_2, and it follows that the stiffness increases with increasing difference between w_1 and w_2. Thus z is proportional to w_1/w_2. The stiffness of the material at the hinges can be assumed to be proportional to the thickness d_1 of the basilar membrane. Iurato (1962) showed that numerous radially running filaments which often are arranged in bundles are important components of the basilar membrane. In pars pectinata two strata of filaments are separated by a "cottony" ground substance. At the hinge
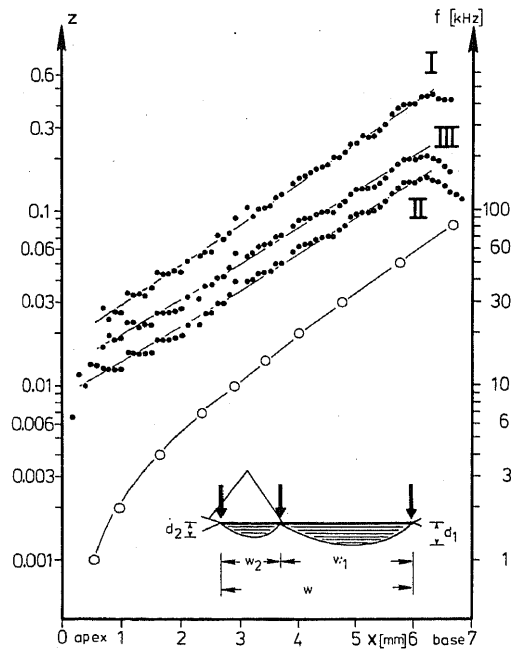

FIG. 1. Three curves (I–III) show the dependence of stiffness of the basilar membrane [after Eqs. (1)–(3) and (6), left ordinate] on the locus on the membrane (abscissa). The regression lines follow Eqs. (7)–(9). The curve with the open circles demonstrates the frequency representation on the basilar membrane of the mouse after Eq. (10) (frequency, right ordinate). The insert shows a diagram of a radial section through the basilar membrane of the mouse, indicating the measured widths and thicknesses and the three hinge points (arrows), where a movement of the basilar membrane occurs.

points the ground substance is reduced and the strata coincide (also Engström, 1955). A thickening of the basilar membrane is based on an increase in the number of filaments and the mass of ground substance (Iurato, 1962). It follows that the thicker the basilar membrane the more filaments can be assumed to run through the hinges, which means an increase in stiffness. The relation among stiffness, width, and thickness of the basilar membrane can be summarized by the equation

$$z = k_1(d_1 w_1 / w w_2) \quad \text{(Curve I)} . \tag{1}$$

The term w_1/w_2 is rather constant along the basilar membrane of the mouse so that it can be included into the proportionality factor, with the result

$$z = k_2(d_1/w) \quad \text{(Curve II)} . \tag{2}$$

Furthermore, w can be replaced by w_1

$$z = k_3(d_1/w_1) \quad \text{(Curve III)} . \tag{3}$$

The relation among stiffness, width, and thickness of the basilar membrane can be calculated on the basis of another consideration including, however, the condition of no flexion of pars pectinata and pars tecta. The displacement amplitude at the hinge point between both parts increases on a constant pressure with increasing extensibility of the basilar membrane in radial direction. The extensibility can be characterized by Poisson's ratio μ, which is the ratio between the transverse con-

traction and linear (in this case radial) expansion (Bergmann and Schaefer, 1970);

$$\mu = -\frac{\Delta d/d}{\Delta w/w}$$

or

$$\mu = \sim w/d \ . \tag{4}$$

Stiffness (z) would be proportional to $1/\mu$, and substituted in Eq. (4):

$$z \sim d/w \ . \tag{5}$$

If d in Eq. (5) is replaced by d_1, the thickness of pars pectinata, the final equation follows:

$$z = k_4(d_1/w) \quad \text{(Curve II)} , \tag{6}$$

which corresponds to the previously derived Eq. (2).

II. RESULTS AND CONCLUSIONS

In Fig. 1 three stiffness[1] functions (calculated from the original data from Ehret and Frankenreiter, 1977) according to Eqs. (1)-(3) and (6) are plotted against the length of the basilar membrane. The proportionality factors k_1, k_2, k_3 (k_4) were always set equal to 1, which can be done without changing the shape of the curves. Regression lines $(r = \text{correlation coefficient})$ were drawn in all three cases and are excellent approximations to the data points except near the base of the basilar membrane, where z becomes rather constant. The regression lines follow the equations:

Curve I: $\log_{10}z = 0.23x - 1.8, \quad r = 0.9977 , \tag{7}$

Curve II: $\log_{10}z = 0.21x - 2.1, \quad r = 0.9962 , \tag{8}$

Curve III: $\log_{10}z = 0.21x - 1.9, \quad r = 0.9930 , \tag{9}$

where x is the distance on the basilar membrane from the apex. The slopes of all three regression lines differ very little so that all three curves represent the same relation between stiffness and locus on the basilar membrane.

These curves have to be compared with the frequency representation function on the basilar membrane of the house mouse. This function was derived from psychophysical masking experiments (Ehret, 1975, 1976) and is also presented in Fig. 1. This function follows the equation

$$f = 3350 \times (10^{0.21x} - 1) , \tag{10}$$

which simplifies for values of $x \geq 2$ mm, when the term -1 plays a subordinate role, to

$$f = 3350 \times 10^{0.21x} . \tag{11}$$

Equation (11) can be transformed into Eq. (12), which is directly comparable to Eqs. (7)-(9):

$$\log_{10}f = 0.21x + \log_{10}3350 . \tag{12}$$

It is evident that the slope factor 0.21 of Eq. (12) equals the slopes in Eqs. (8) and (9), and it is very close to that of Eq. (7).[2] This means that stiffness calculated from the width and thickness of the basilar membrane depends on the locus on the basilar membrane just in the same manner as the displacement maxima

for frequencies. The conclusion follows that stiffness of the basilar membrane as calculated from width and thickness [Eqs. (1)-(3) and (6)] seems to be a crucial factor in the determination of the locus for the maximum displacement of the basilar membrane at a given frequency.

One can combine Eqs. (7)-(9) with Eq. (12) by substituting the term $0.21x$ and obtain generally

$$f = cz , \tag{13}$$

which is the expression for the proportionality between frequency representation and stiffness. Equation (13) is valid for $2 \leq x \leq 6.2$ mm. Near the apex and at the absolute base of the cochlea of the mouse other factors like the mass and viscosity of fluids and the helicotrema near the apex seem to have a considerable influence. Equation (13) expresses an empirical relation derived from experimental data which are independent from each other. Although the physics underlying Eq. (13) may be complicated, the stiffness scale and the frequency scale show the same kind of gradual variation along a large portion of the basilar membrane which is an indication for a causal relationship.

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[1] Stiffness Z, which is the reciprocal of elasticity, is physically defined as the ratio of force and displacement $(Z = F/\Delta l)$. The displacement amplitude Δl, however, is inversely proportional to the "anatomical" stiffness z defined in this paper $(\Delta l \sim 1/z)$, and when this is substituted in the above equation it follows that $Z \sim Fz$, showing that physical stiffness and anatomical stiffness are proportional to each other. Thus stiffness from the width and thickness of the basilar membrane is an adequate measure of the true physical stiffness of the system.

[2] Comparing the slopes of the functions in Fig. 1, one has to consider that the shown curve for frequency representation follows Eq. (10) with the term -1 included. Thus the actual slope of this curve between 2 mm and the base is steeper than indicated by Eq. (12) and equals the slope of curve I [Eq. (7)].

Békésy, G. v. (1960). *Experiments in Hearing* (McGraw-Hill, New York).

Bergmann, L., and Schaefer, C. (1970). *Lehrbuch der Experimentalphysik, Vol. 1. Mechanik, Akustik, Wärme* (de Gruyter, Berlin).

Dallos, P. (1973). *The Auditory Periphery* (Academic, New York).

Ehret, G. (1975). "Masked auditory thresholds, critical ratios, and scales of the basilar membrane of the house mouse (*Mus musculus*)," J. Comp. Physiol. 103, 329-341.

Ehret, G. (1976). "Critical bands and filter characteristics in the ear of the house mouse (*Mus musculus*)," Biol. Cybern. 24, 35-42.

Ehret, G., and Frankenreiter, M. (1977). "Quantitative analysis of cochlear structures in the house mouse in relation to mechanisms of acoustical information processing," J. Comp. Physiol. 122, 65–85.

Engström, H. (1955). "The structure of the basilar membrane," Acta Oto-Rhino-Laryngol. Belg. 9, 531–542.

Geisler, C. D. (1976). "Mathematical models of the mechanics of the inner ear," in Handbook of Sensory Physiology, Vol. V/3, Auditory System, Clinical and Special Topics, edited by W. D. Keidel and W. D. Neff (Springer, Berlin–Heidelberg–New York).

Iurato, S. (1962). "Submicroscopic structure of the membranous labyrinth III. The supporting structure of Corti's organ (basilar membrane, limbus spiralis and spiral ligament)," Z. Zellforsch. Mikrosk. Anat. 56, 40–96.

Steele, C. R. (1973). "A possibility for sub-tectorial membrane fluid motion," in Basic Mechanisms in Hearing, edited by A. R. Møller (Academic, New York).