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The Physiology of the Locust Ear

II. Frequency Discrimination Based upon Resonances in the Tympanum

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Summary. 1. The expected resonance frequencies of the tympanal membrane have been calculated from its dimensions, mass, and compliance. The thin part of the tympanal membrane may vibrate independently of the entire tympanum. Thus, there are at least two sets of resonances (Fig. 8).

2. The two sets of vibrations have been observed by means of laser holography (Figs. 13–15) and measured with a capacitance electrode (Figs. 16–18). The position and amplitude of the vibration patterns, the phase relationships, and the interaction of the two sets of vibration have been studied. The results are compared with the frequency sensitivity of the four groups of receptor cells.

3. The groups of receptor cells are attached to four specialized areas on the tympanum (Fig. 6). The vibrations of these areas of attachment are a maximum at the frequencies of maximum sensitivity in the receptor cells (Figs. 16 and 17). Thus, the frequency discrimination seems to be a purely physical phenomenon, based partly on the presence of the tympanal resonances, and partly on the different positions of the receptor cells on the tympanal membrane.

4. The two sets of vibrations have different spatial positions on the tympanum. The centre of the entire-membrane-vibrations is situated in one end of the membrane (Fig. 15), whereas that of the thin-membrane-vibrations is almost at the centre of the tympanum (Fig. 14). The positions of the centers of vibration are, however, not constant (Figs. 13 and 14). Different modes may have somewhat different centre positions, and these positions may change with frequency because of interactions between the two sets of resonances. Therefore, receptor cells attached to different areas on the membrane may pick up different modes of vibration. Also, the receptor cells may almost fail to respond to some modes, if their area of attachment is at a nodal circle of these modes at resonance.

Introduction

Many invertebrates can hear (review: Autrum, 1963), but very few can discriminate frequencies. In the locust ear four anatomical groups of receptor cells are attached to four specialized areas on the tympanal membrane. The frequency sensitivities of these groups are different in the *isolated ear*, i.e. a preparation consisting of the tympanum and its cuticular rim (paper I: Michelsen, 1971). In the present paper it is shown that the frequencies of maximum sensitivity in the receptor cells correspond to the expected and observed resonances of the normal modes

of vibration of the tympanal membrane. It is argued that the frequency discrimination of the locust ear is a purely physical phenomenon, based partly on the presence of the tympanal resonances, and partly on the different position of the receptor cells on the tympanum. In the following publication (paper III) the physics of the *intact* locust ear will be considered. In these papers the SI (meter-kilogram-second) system of physical units will be used.

1. Resonance and Hearing

The presence of resonance in hearing organs is not a new idea (see Whitfield, 1967). Some of the early theories (17th century) postulated the existence of mechanical resonators in the vertebrate ear; the function of these hypothetical resonators was considered to be that of magnifying a weak sound stimulus, by storing incoming sound energy over a number of cycles. Later, the idea was introduced that the resonators might have different resonance frequencies.

These thoughts found their most famous expression in the theory of Helmholtz (1863). He suggested the existence of a resonator in the cochlea, supplied by specific nerve fibers, for each subjectively distinguishable tone. The Helmholtz-theory was later abandoned, partly because of the failure to identify the resonators anatomically. Also, this and other resonance theories failed to explain the fact that in the vertebrate ear a sharp frequency discrimination is carried out together with a fine time resolution. This difficulty could, however, be overcome in the "travelling-wave theory" proposed by Békésy (review: 1960).

Recently, Huxley (1969) has revived the idea of auditory analysis by resonance. He showed mathematically that truly resonant oscillations, the position of which shifts with frequency, may after all be a possibility in the cochlea. The reason for Békésy's observation of travelling waves might, according to this view, be the artifical mechanical conditions created during the experiments. This argument seems to be valid for most experimental studies of hearing organs. The theory proposed by Huxley has been criticized by Békésy (1969, 1970).

Although the possible existence of true resonances in the cochlea is still discussed, no clear-cut example of frequency discrimination based upon the existence of selective resonances has been found so far in a hearing organ. Therefore, from a comparative and theoretical point of view the locust ear is a unique physiological preparation, which allows us to study how selective resonances in an inhomogeneous membrane can be used as the physical basis for a frequency discrimination.

It should, however, be emphasized that the anatomy and the physical properties of the locust ear are extremely different from those of the vertebrate ear. In particular, it should be born in mind that a strong

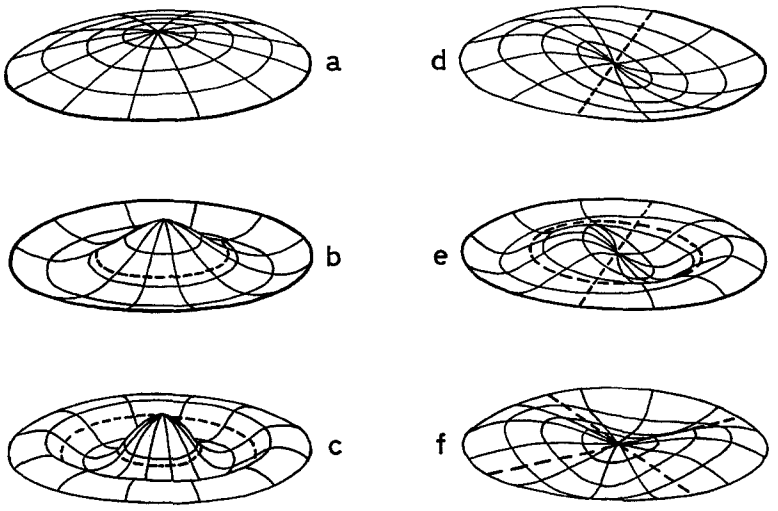

Fig. 1a–f. The first three circularly symmetrical modes of vibration in a circular membrane (a–c), and some other possible modes (d–f). The nodal lines are indicated by dotted lines. Further explanation in the text. (Redrawn from P. M. Morse: Vibration and sound. Copyright 1936, 1948 by the McGraw-Hill Book Company, Inc. Used with permission of McGraw-Hill Book Company)

mechanical coupling probably exists between the basilar membrane and the surrounding fluid, whereas in the locust ear the vibrations of the membrane are hardly influenced by the surrounding medium.

2. The Vibration of Membranes

Descriptions of the vibration of membranes can be found in most textbooks on acoustics, but for the convenience of the reader a few relevant points will be summarized. We shall consider a homogeneous membrane, fastened along a boundary circle, and acted upon by a uniform, harmonic driving force (e.g. a sound wave). The travelling velocity of transverse waves in the membrane is supposed to be much smaller than the velocity of sound waves in the surrounding medium.

At low frequencies the membrane will tend to move as a whole (Fig. 1a), and its behaviour very much resembles that of a simple driven oscillator. At very low frequencies the maximum displacement of the membrane will be almost in phase with the driving force, but as the frequency approaches the first resonance, the displacement will be delayed relative to the force. At the first resonance frequency (f_{01}) this delay is 90° (Fig. 2, *1*), and somewhat above the first resonance the instantaneous displacement of the membrane is nearly opposed to the driving force (i.e. the phase lag is about 180°).

If the frequency is increased, a circular nodal line appears at the edge and moves towards the centre. The part of the membrane around the centre has remained out of phase with the force, but the part outside the nodal circle is almost in phase with the force. The amplitude of the overall motion now increases, and a second

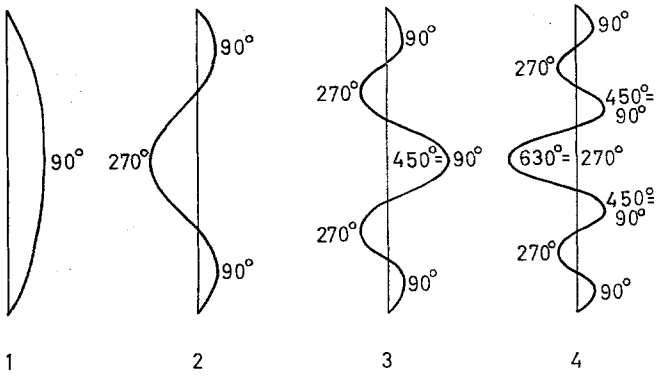

Fig. 2. The first four circularly symmetrical modes of vibration in a membrane. The approximate phase lags (between driving force and membrane displacement) are indicated at resonance for the different parts of the membrane. (*1–3* are identical to a–c on Fig. 1)

resonance is reached at a frequency (f_{02}), which is about 2.3 times f_{01}. Fig. 1b shows the membrane at the second resonance, and Fig. 2, *2*, illustrates the phase lags found at the resonance of the second mode of vibration. The movement of the membrane has now been further delayed relative to the driving force, and at a somewhat higher frequency a new nodal line will be formed, and so on (Fig. 1c shows the membrane at the resonance of the third mode of vibration, and Fig. 2 (*3* and *4*) the phase lags for the different parts of the membrane at resonance of the third and fourth mode).

In a slightly damped membrane (i.e. with a small amount of friction) the amplitude of a point on the membrane will vary a great deal over the entire frequency range. Generally, the amplitude will be a maximum at the resonance frequencies, and a minimum at a certain frequency between the resonance frequencies; but obviously this is not true for the displacement of the parts of the membrane which are at or near to a nodal circle at resonance. The variation in the overall amplitude and phase of the membrane will be fairly smooth. The amplitude and phase of individual points on the membrane, however, depend upon their position and upon the position of the nodal circles at that frequency. Thus, their variation with frequency may be rather complex. Since the receptor cells attach to small areas on the membrane, we shall consider this problem in more detail below.

It can be shown (see Morse, 1948) that if the membrane is circular, homogeneous, and acted upon by an evenly distributed force (sound wave), only these circularly symmetrical modes of vibration are to be expected. If one or more of these conditions are not fulfilled, the vibrations may be considerably more complex (Fig. 1d–f).

Methods

1. Laser Holography

Time average holograms were produced at the Division of Production Engineering, Royal Institute of Technology, S-10044 Stockholm. In the following a short description of the technique and theory of holography will be given, in order to

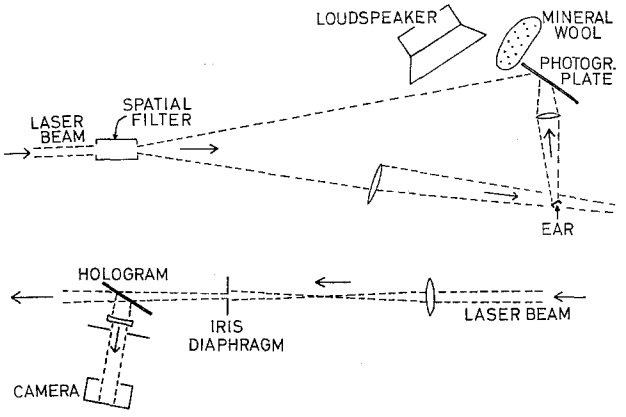

Fig. 3. The recording of the hologram (above) and reconstruction of the holographic picture (below). Explanation in the text

provide a background for an evaluation of the results. A description of the experimental technique has been published separately (Abramson, Andersson and Bjelkhagen, 1970).

The experimental set-up is illustrated in Fig. 3. The upper part of the figure shows the recording of the hologram. A laser beam, produced by a 60 mW Helium-Neon laser (Spectra Physics 125), was passed through a shutter (not shown on the figure) for 0.1–0.5 second and into a spatial filter (Spectra Physics 332). From there the light spread out, some of it reaching the photographic plate (Scientia 10E 70) directly, and some passing through a lens (+15 cm) and reaching the isolated locust ear. Some of the reflected light from the ear then passed through another lens (Meopta Belar, 75 mm) and on to the photographic plate.

Thus, the photographic plate received light both directly and by reflection from the ear. The light from these two sources interfered to produce a hologram. A loudspeaker was mounted near to the ear, but separated from the other parts (in order to avoid the transmission of vibrations). The distance from the ear to the photographic plate was 15 cm, i.e. more than half a wavelength of the lowest sound frequency used (1.8 kHz). An open cage of mineral wool, placed behind the ear and not shown on the figure, reduced spurious reflections of sound waves.

The lower part of Fig. 3 shows the reconstruction of the holographic picture (image). After development the photographic plate (hologram) was placed in a laser beam, which had passed a lens and an iris diaphragm. Under these conditions the hologram acts as a diffraction grating, and the wavefront reflected from the object will be reconstructed (see Pennington, 1968; Gabor and Stroke, 1969). Two pictures will be formed: a virtual image and a real image. The real image can be photographed by means of a normal camera (without a lens). In the present experiments the light from the hologram passed through a lens (–200 cm) and another iris diaphragm before reaching the camera.

If nothing moved during the recording of the hologram, the picture will look like a normal photograph (though often of bad quality). If a part of the object moved during the recording, the diffraction pattern will change. This may lead to blurred pictures, if the movement is irregular. Regular, oscillatory movements,

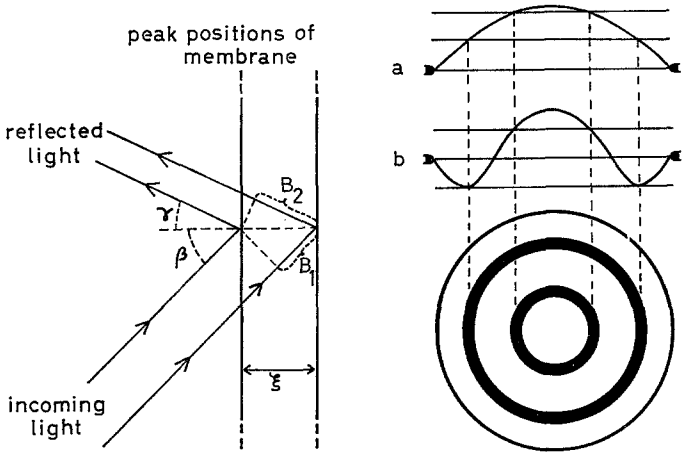

Fig. 4. *Left:* the geometry of light reflection during the recording of the holograms (see the text). *Right:* two different vibrations (*a* fundamental mode, *b* second normal mode), causing identical patterns of light and dark lines in the holographic picture (below)

however, may lead to the occurrence of fringes. Such fringes (light and dark lines) are loci of equal amplitude of vibration, corresponding to the probability density function of the motion (see Powell and Stetson, 1965; Stetson, 1970). Light reflected from the two peak positions of the oscillating membrane will interact; the intervals of peak-to-peak displacement corresponding to the occurrence of fringes depend on the wave length of laser light and on the angles of incidence and reflection of the light upon the tympanal membrane (see Fig. 4). If the peak-to-peak amplitude is ξ, and the angles of incidence and reflection are β and γ, one has

$$B_1 + B_2 = \xi \cos\beta + \xi \cos\gamma. \tag{1}$$

When $(B_1 + B_2)$ is equal to (a multiple of) the wavelength of the light (λ_1), the two reflected beams are in phase. The corresponding peak-to-peak vibration amplitude (ξ') becomes

$$\xi' = n \cdot \frac{\lambda_1}{\cos\beta + \cos\gamma} \tag{2}$$

where $n = 0, 1, 2, \ldots$.

In the present case $\beta = 45°$ and $\gamma = 30°$. The wavelength of the laser light was 0.6328 μm. Thus, normally the distance between two dark bands or between two light bands on the holograms would correspond to a difference in peak-to-peak amplitude of 0.40 μm. When the fundamental vibration is observed, one can determine the displacement of the centre simply by counting the number of rings (Fig. 4, *a*). This is, however, not the case when higher, circularly symmetric modes of vibration are observed. In such modes of vibration the concentric "bubbles" of the membrane may each give rise to one or more rings (Fig. 4, *b*). Although the nodal lines may have special contours, this is not always the case. The position of the nodal lines in the locust ear could not be determined directly from the holograms, but had to be determined with the capacitance electrode measurements.

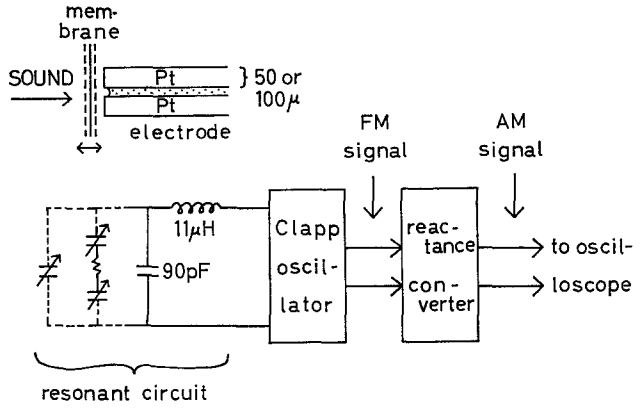

Fig. 5. The capacitance electrode (above), and the principle of the capacitance measurement (below). Explanation in the text

2. *The Capacitance Electrode*

The vibration of small areas of the tympanal membrane was measured by means of a capacitance electrode. It consisted of two platinum wires (50 or 100 μm in diameter) glued closely together with araldite for a distance of 1 cm. The wires were cut (at right angles to their longitudinal axis) and laquered with Insl-X. The free ends of the wires were connected to a capacitance transducer system (DISA 51 D 17). When the tip of this electrode was placed near to a moving membrane (Fig. 5), the (periodic) change in capacitance between the membrane and the two wires changed the resonance frequency of a resonant circuit coupled to a Clapp oscillator (DISA 51 E 02). The frequency-modulated signal was demodulated in a reactance converter (DISA 51 E 01), and the AM-signal displayed on the oscilloscope. This system makes it possible to measure periodic changes in capacitance down to 10^{-3} pF (with a small and known phase-shift) in the frequency range 0–200 kHz.

The absolute amplitude of vibration could not be estimated with this method, since the magnitude of the signal depends both on the effective size of the corresponding area of membrane, on the distance to the electrode tip, and on the electrical properties of the membrane. [The effect is probably a combination of two processes: the moving membrane changes the dielectric properties in the field between the electrode tips, but at the same time the cell layer on the membrane is conducting, so that the system can also be regarded as composed of two variable capacitances connected by an (unknown) resistor, see Fig. 5].

In order to allow the phase relationships to be measured, the isolated ear and a microphone (Brüel & Kjär 4131) were placed at the same distance from the loudspeakers (about 1.3 m). The sound signal was amplified and displayed on the oscilloscope together with the signal from the capacitance electrode system. The sensitivity of the system was sufficient to give signals with a signal/noise ratio between 1 and 10, when the 100 μm electrode was used. The signals obtained by means of the 50 μm electrode were often too small compared with the noise level. Obviously, a more sensitive system would be needed for studies on most other insect ears (a 10 times more sensitive oscillator is now under construction at DISA).

No filtering was performed, because the phase shifts in selective filters are much too drastic to allow accurate determinations of the phase relationships.

The phase difference of interest here is the difference between the driving force and the displacement of the membrane. This value could be obtained by allowing for the phase shifts in the microphone system and in the reactance converter. Furthermore, the phase difference between the sound pressure wave (measured with the microphone) and the force (acting to move the membrane) had to be calculated. In the following article (paper III) it will be shown how this figure was derived. The total uncertainty in the determination of the force-displacement phase difference depended on frequency (because the errors produced by a small difference in distance increased linearly with frequency). At "low" frequencies (1–2 kHz) the total uncertainty amounted to about $\pm 10°$; at high frequencies (15 kHz) it was about $\pm 20°$. Nevertheless, this degree of accuracy was sufficient for the present purpose.

It is relatively easy to use the capacitance electrode on plane parts of the tympanum. The attachment areas of the receptor cells, however, are so irregularly shaped that recordings were difficult. In order to interpret the results it is necessary to have an idea of the kinds of amplitude and phase relationships which can be expected from small areas on various parts of the membrane (see below). Since this method does not tell us the absolute amplitudes, the results are most easily interpreted when compared with the laser holograms (the holograms, on the other hand, do not tell us anything about the phase relationships).

The Expected Resonances

1. Properties of the Tympanal Membrane

Anatomy. The anatomy of the tympanal organ has been described in detail by several authors (Gray, 1960, gives a list of references). In the following description only the properties of relevance to the problem of membrane vibration will be considered. The tympanal membrane is bean-shaped (Fig. 6), and the dorsal end is somewhat wider than the ventral end. Typically, the membrane is 2.5 mm long and 1.5 mm at its widest. The total area is about 3 mm^2. Most of the tympanal membrane consists of cuticle (2–3 μm thick), which is covered on the inside by a layer of cells (1–2 μm thick) and by the wall of an air sac. This *thin part* of the membrane has an area of about 2.4 mm^2. In the ventral anterior corner, however, the membrane is about 8–10 μm thick. The area of this *thick part* of the tympanum is about 0.5–0.6 mm^2 (Fig. 6).

Four specialized regions with much thicker cuticle are situated between the middle of the tympanum and the anterior edge. They are the elevated process, the styliform body, the folded body, and the pyriform vesicle. The four anatomical groups of receptor cells (a, b, c and d) are attached to these bodies (Fig. 6). The areas of attachment of the a, b, and c-cells are situated at the junction of the thin and thick parts of the membrane and fairly close to each other. The d-cells, however, are attached to the pyriform vesicle 200–300 μm from the rest of Müller's organ. The thin and thick parts of the tympanum are separated by the

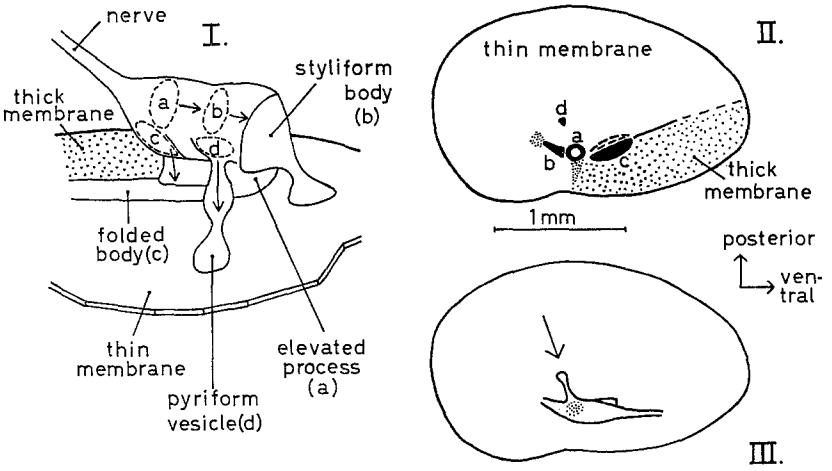

Fig. 6. The anatomy of the tympanal organ. *I* Müller's organ (right ear). The position of the receptor cells (a–d) and the attachment parts of the membrane are shown. Arrows indicate the direction of the dendrites. *II* The left ear seen from outside the animal. The dark areas indicate the areas of attachment of the receptor cells. *III* The right ear seen from the inside. The arrow indicates the visual angle of *I*

folded body and by a rod-shaped thickening in continuation of the folded body.

Mass. The mass of the tympanal membrane was determined with a microbalance (Cahn Gram Electrobalance). The membrane was cut out with fine scissors and kept in a moist chamber until the microbalance had been calibrated. The average weight of 13 tympanal membranes was 30 μg (s.d. = 1.0 μg). In three other cases, however, weights around 50 μg were found. Müller's organ in these preparations appeared swollen. The average weight of the thin part of the membrane was 7.7 μg (10 determinations, s.d. = 1.7 μg).

These values may be compared with the calculated weights: If one assumes a specific weight of 1.2 for the cuticular part of the membrane (Jensen and Weis-Fogh, 1962) and about 1 for the cell layer, the weight of the thin membrane should be about 10.8 μg. The weight of the entire membrane is more difficult to estimate, because of the irregular shape of Müller's organ, but 40–45 μg would be an approximate estimate. This difference between the determined and estimated weights is probably due to drying of the preparation during the operation and weighting procedure: Typically, a tympanum with an initial weight of 30 μg lost about 1–2 μg of water during the first three minutes. Although the operation and determination of the weight were carried out quickly,

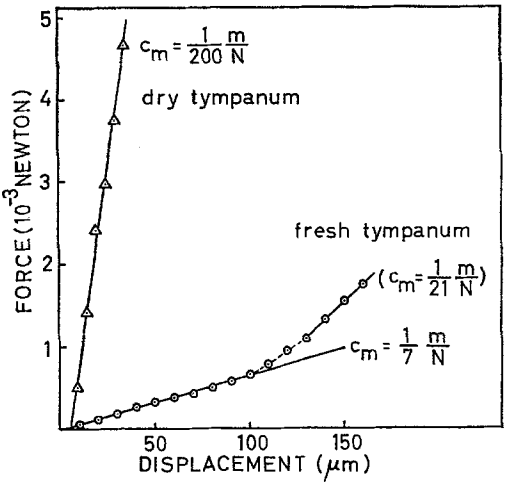

Fig. 7. A measurement of the membrane compliance (c_m). The lower curve is from a fresh tympanum, and the upper curve from the same preparation 18 hours later. Note that the compliance of the fresh membrane is almost constant for the first 100 μm displacement

the values obtained are probably somewhat too low. In the calculations performed below values intermediate between the estimated and determined weights (36 μg and 9.2 μg, respectively) will be used instead of the determined weights. Without this correction the calculated frequencies would have been about 10% higher.

Tension. The elasticity of the tympanal membrane was determined by displacing it in the perpendicular plane with the end of a metal wire. The wire had a diameter of 200 μm, and it was attached to a capacitive transducer (DISA 51 D 17) fitted with a specially made transducer plate. The capacitance transducer was mounted on a screw gauge, which could be moved in 5 or 10 μm steps. The determinations were carried out quickly in order to avoid errors due to "plastic flow" in the membrane.

The mechanical compliance (c_m) was about 0.14 m/N (12 determinations, s.d. = 0.023). In Fig. 7 the result of a typical experiment is shown. The relationship between displacement and force is approximately linear for displacements up to 50–100 μm i.e. in this range Hooke's law is obeyed, and the compliance is constant. Above this range the force increases rapidly, i.e. the compliance decreases.

The restoring force of a surface may be due to tension and/or stiffness of the surface material. In the present case (fresh tympanum, see below), the tension seems to be the dominating factor, since the compliance for the thin part of the membrane did not differ significantly from that of

the attachment areas of the receptor cells. Also, when slits were cut in the tympanum, the holes adopted the shape of a convex lens, and free tympana were quite lose. A surface whose compliance is mainly determined by its tension, is physically speaking a membrane (in contrast to a plate, in which the stiffnes is an important factor).

A considerable decrease in compliance was observed if the membrane was allowed to dry. After some hours in a dry environment the compliance may be about $^1/_2$–$^1/_{30}$ of the value for a fresh membrane (Fig. 7). This decrease in compliance is largely due to a greatly increased stiffness (cf. Herzog, 1926; Jensen and Weis-Fogh, 1962). Since a decrease in compliance will tend to shift the resonance frequencies to higher values, it is very important to keep the preparation under humid conditions during experiments.

2. The Expected Resonance Frequencies

The fundamental resonance frequency (f_{01}) in vacuum for a homogeneous membrane, fastened along a boundary circle, is given by (see Morse, 1948)

$$f_{01} = 0.383 \cdot \frac{1}{a} \sqrt{\frac{T}{\sigma}} \tag{3}$$

where a = radius (m),
T = tension per unit length (N/m),
σ = mass per unit area ($kg/m^2 = N\,s^2/m^3$).

In the present case the use of formula (3) is questionable, since the membrane is neither in vacuum, circular, nor homogeneous.

The tympanal membrane is far from homogeneous. Although the thin, homogeneous membrane constitutes more than 80% of the area, about two-thirds of the total mass is concentrated in Müller's organ. Furthermore, the presence of the four cuticular bodies in the tympanum are likely to affect its vibration. These bodies are stiff, and they cover most of the boundary between the thin and thick parts of the tympanum. The presence of this stiff boundary at the edge of the thin membrane may have the effect that *the thin membrane vibrates independently of the entire tympanal membrane*. In the calculations it is assumed that this is actually the case, and that the thin part of the membrane has a series of resonance frequencies of its own. The laser holograms show that this assumption is correct (see below).

From the area of the thin and entire membrane the probable effective radius can be estimated to 0.9 and 1.0 mm, respectively. According to Lord Rayleigh (1926) the fundamental frequency of a membrane is determined by its area rather than by its shape, but the estimate of the effective radius (a) is still uncertain. Since the vibrations take place

in air, the radiation impedance of the membrane must be considered. Thus, the mass per unit area (σ) is estimated from the mass of the membrane plus the radiation mass (see the Appendix). The membrane tension (T) can be calculated from the compliance (c_m). If the membrane is pulled evenly around its edge with a tension of T Newton per meter of edge, it can be shown (see Morse, 1948) that for a circular membrane

$$T \simeq \frac{1}{8 \cdot \pi \cdot c_m} \tag{4}$$

In the present case T becomes 0.28 N/m.

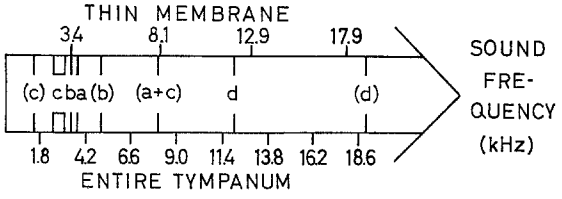

Fig. 8. The expected resonance frequencies for the thin membrane (above) and for the entire tympanum (below), compared with the preferred frequencies of the four groups (a–d) of receptor cells (centre). Letters in brackets indicate frequencies not preferred by all cells in a group

From these figures and Eq. (3) the fundamental resonance frequency (f_{01}) should be expected at about 1.8 kHz for the entire tympanum and at about 3.4 kHz for the thin part of the tympanum. In vacuum the resonance frequencies of the second, third, and fourth circularly symmetric modes are expected at 2.296, 3.599, and 4.903 times f_{01}. In air the variation of the radiation mass has to be taken into account (see the Appendix). The expected resonance frequencies of ideal membranes with size, mass, and compliance equal to that of the entire and thin tympanal membranes are listed on Fig. 8.

In Fig. 8 a few of the first resonances are indicated. There are, of course, theoretically an unlimited number of resonances, but for the higher modes the distance between the nodal lines becomes very small. The receptor cells do not attach to points on the membrane, but to stiff, cuticular bodies which occupy certain areas. Therefore, the modes of vibration are unlikely to excite the receptor cells, if the distance between the nodes is much smaller than the diameter of the attachment areas.

The resonance frequencies may be compared with the frequencies of maximum sensitivity in the receptor cells (Fig. 8). It is seen that most of the observed best frequencies are fairly close to one of the expected

resonance frequencies. On the other hand, the number of expected resonances is so large in the frequency range 1–20 kHz that a wide variety of explanations may be given for several of the observed best frequencies. The problem also arises how the receptor cells can be so selective: each group of receptor cells responds to only two or three bands of frequencies. Obviously, direct observations of the vibrations are necessary.

3. Expected Amplitude and Phase of a Point on the Membrane

In most studies of membrane vibration, special interest is paid to the average (overall) phase and amplitude of the membrane, since it is the average that determines the output from loudspeakers or microphones. In the locust ear, however, the receptor cells attach to cuticular bodies which occupy certain areas of the tympanum (Fig. 6). In the following we shall first calculate the amplitude and phase of single points on a membrane in order to obtain an idea of the kind of behaviour to be expected for the areas of attachment. Thereafter, the interaction between two vibrations will be considered.

We shall consider a homogeneous, circular membrane with physical properties (size, mass, tension, and friction) almost identical to those of the thin membrane in the locust ear. Since the friction is determined mainly by the membrane material (see the appendix), the equation of motion becomes (see Skudrzyk, 1954, p. 331)

$$T\left(\frac{\partial^2\eta}{\partial r^2}+\frac{1}{r}\frac{\partial\eta}{\partial r}\right)+\frac{F}{\pi a^2}=\sigma\frac{\partial^2\eta}{dt^2}+\frac{R}{\pi a^2}\frac{\partial\eta}{dt}\,, \tag{5}$$

where η = amplitude of displacement (m),
T = membrane tension (N/m),
r = distance from centre (m),
a = radius of membrane (m),
F = the force acting to move the membrane (N),
$\pi = 3.14159\ldots$,
σ = mass per unit area (kg/m^2),
t = time (s),
R = resistive component of membrane impedance (Ns/m).

It can be shown (Crandall, 1927) that the solution of Eq. (5) giving the displacement of a point on the membrane is

$$\eta=\frac{F\cdot(J_0(k_1 r)-J_0(k_1 a))}{T\cdot\pi\cdot a^2 k_1^2\cdot J_0(k_1 a)}\,e^{j\omega t}\,, \tag{6}$$

where $k_1^2=\omega^2\cdot\frac{\sigma}{T}\cdot\left(1-j\frac{R}{\pi a^2\omega\sigma}\right)$,
$j=\sqrt{-1}$,
J_0 = Bessel function of complex argument of order zero for cylindrical coordinates,
ω = angular frequency ($=2\pi f$),
$e = 2.71828\ldots$, base of natural logarithms.

From Eq. (6) the amplitude of vibration and the phase relations can be found for different distances to the centre. The variation of force

with frequency (see paper III) was also taken into account in the calculation of the amplitudes. (If the membrane were a part of a pressure receiver, the curves would indicate the relative velocity of vibration at different frequencies; in this case the corresponding amplitudes can be found by dividing with ω; i.e. with increasing frequency the amplitudes will decrease 6 dB per octave.) Since Eq. (6) is fairly complicated, the solutions were calculated by means of a digital computer.

The behaviour of ideal membranes was described in the introduction and illustrated on Figs. 1 and 2. The vibrations of membranes governed by Eqs. (5) and (6) differ somewhat from those of ideal membranes. The most important difference is that there are no real nodal circles on the tympanum: all parts of the tympanum (except the edge) are moving, but the amplitude of vibration is a minimum at the parts corresponding to the nodal circles in the ideal membrane. The membrane on both sides of these "relative nodal circles" is vibrating about 180° out-of-phase, but the change of phase is continuous. In contrast, in the ideal membrane the change of phase across the nodal circles is discontinuous. This difference between the ideal membrane and the tympanum is interesting, but it does not change the situation of the receptor cells very much. The receptor cells are attaching to cuticular bodies occupying certain areas on the membrane and not to infinitely small points. The presence of relative instead of real nodal lines will not cause a great difference in the vibration of the areas of attachment. Therefore, for the present purpose the nodal circles can still be treated as a reality.

Another difference from the ideal behaviour is found in the definition of resonance. In the ideal system the resonance frequencies may be defined as the frequencies at which the amplitude of vibration of the centre is a maximum; but it may also be defined as the frequencies at which the phase lag of the centre is $90° + n\,180°$ (where $n = 0, 1, 2, \ldots$). In the vibration determined by Eqs. (5) and (6) these two definitions give different resonance frequencies. When the frequency is increased at the second mode of vibration the amplitude is a maximum about 100 Hz before the phase lag reaches 270°. Here again, the deviation from the ideal behaviour has no practical significance.

In Fig. 9 the expected amplitude and phase lag at different frequencies are shown for the centre of a membrane with thin-membrane properties. The damping factor (R) was approximately that estimated from the holograms (see below). The variation in radiation mass with the mode of vibration (see Appendix) was, however, not taken into account. Therefore, the resonance frequencies are not quite identical with those indicated on Fig. 8. These curves show that the phase lag of the centre is about 90° at resonance of the fundamental mode, and that the phase lag increases about 180° for each mode (cf. Fig. 2). It is surprising that the amplitude at 5 to 6 kHz is only 3–4 times smaller than the amplitude at the first two resonances. The computed amplitude and phase curves for the centre of the entire membrane are very similar to those shown on Fig. 9. The entire membrane system is, however, about 3 times more damped than the thin membrane. The variation in vibration amplitude is therefore not so large. The amplitude of the first resonance (at 1.8 kHz) is here only 2 times larger than that at 3 kHz (cf. Fig. 15).

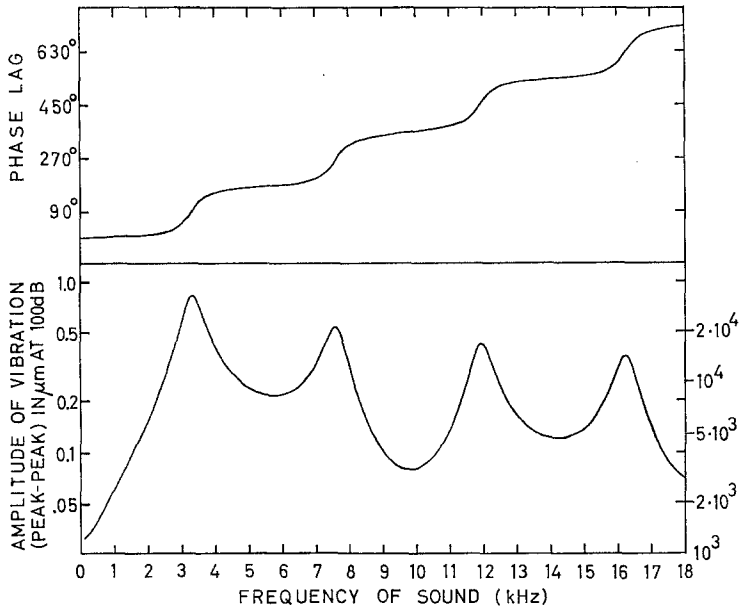

Fig. 9. Expected amplitude of vibration (below) and phase lag (above) for the centre of the thin membrane. The peak-peak amplitudes indicated in μm to the left are valid for the isolated ear at a sound level of 100 dB. The scale to the right gives the amplitudes as $\eta\,\omega/F$. The resonance frequencies are not quite correct, since the effective mass was kept constant (see the text)

The phase lags computed for points elsewhere on the membrane show an increase similar to that of Fig. 9. A decrease of about 180° in the phase lag is, however, noted each time a nodal circle passes the point in question. The variation in amplitude with frequency may be very different for different points on the membrane. In order to illustrate this difference the expected amplitudes were computed for different points on the membrane at the second mode of vibration (Fig. 10). The numbers indicate the fractional distance to the centre. It is seen that the vibration of the centre is a maximum at the resonance frequency (cf. Fig. 9). In contrast, the vibration of points with a fractional distance of about 0.44 from the centre is a minimum at the resonance frequency, i.e. these points are on the nodal circle at resonance. Also, it should be noted that parts of the membrane near to a nodal circle may show a maximum vibration amplitude at a frequency somewhat below or above the resonance frequency. This means that the frequency of maximum sensitivity in receptor cells attached to such parts does not necessarily have to be identical with the resonance frequency.

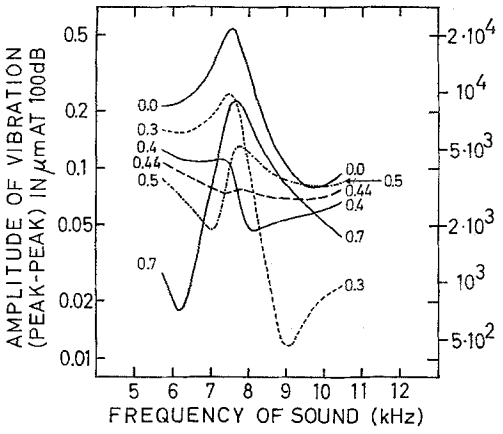

Fig. 10. The expected amplitudes at the second mode of vibration of the thin membrane. Numbers on the curves indicate the fractional distance to the centre (r/a). Note the position of the nodal circle at different frequencies

So far, we have only considered the behaviour of points on an ideal membrane with one set of vibrations. In such a system the modes follow one after the other, a new mode of vibration gradually being "born", when a new nodal circle is formed. When such a membrane is moved by a pure tone there is, of course, no possibility for any interactions between the modes, since they never exist simultaneously. It should be borne in mind, however, that the tympanum is not an ideal membrane; the attachment areas are not points on a homogeneous membrane; and there are at least two sets of vibrations.

We shall now try to obtain an idea about the expected amplitude and phase of a point on the membrane, which participates in two different vibrations (1 and 2) at the same time. If the point took part in vibration (1) only, it would be displaced with an amplitude D_1 and with a phase lag (relative to the driving force) ε_1, and similarly vibration (2) would give D_2 and ε_2. The magnitude of these displacements and their phase lags can be drawn by means of two vectors (Fig. 11). We now assume that the effect of the two vibrations can be added simply by adding the two vectors. By means of simple trigonometry one finds that

$$D_3 = \left(D_1^2 + D_2^2 + 2 D_1 D_2 \cos(\varepsilon_2 - \varepsilon_1)\right)^{1/2}, \tag{7}$$

$$\operatorname{tg}(\varepsilon_3 - \varepsilon_1) = \frac{D_2 \sin(\varepsilon_2 - \varepsilon_1)}{D_1 + D_2 \cos(\varepsilon_2 - \varepsilon_1)} \tag{8}$$

where D_3 and ε_3 are the amplitude and phase lag of the resultant vibration of the point in question.

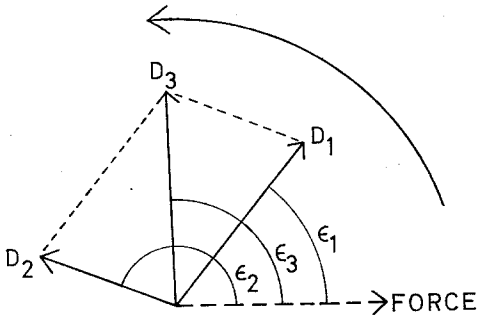

Fig. 11. The addition of two simultaneous vibrations (1 and 2). The displacement (D) and phase lag (ε) are drawn as vectors. D_3 and ε_3 indicate the resultant vibration

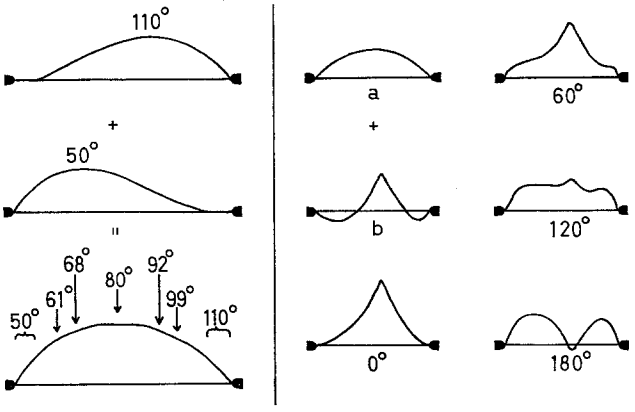

Fig. 12. Simple examples of the addition of two vibrations by means of Eqs. (7) and (8). *Left:* Different phase lags of the two components result in a gradual change in phase over the membrane. *Right:* The addition of the vibrations a and b may result in very different vibrations depending on the phase lags of the components (numbers on the four resultant vibrations indicate the difference in phase between the centers of a and b)

In Fig. 12 these equations have been used to calculate the amplitude and phase of some resultant vibrations. At left, two vibrations with different phase lags are added. The phase lags of the resultant vibration are changing gradually over the membrane. At right, the vibrations a and b have been added. In this example the difference in phase lag between the two vibrations has been varied. It is seen that very different resultant vibrations are obtained at various differences in phase between the component vibrations.

Naturally, these examples are over-simplifications. In the tympanal membrane both amplitude and phase of the component vibrations vary with frequency. At most frequencies the difference in phase between the component vibrations remains relatively constant. Around the resonance frequencies, however, both amplitude and phase change rapidly. Note that the addition of the two vibrations may lead to the formation of an "artificial nodal line" (Fig. 12, right).

The Observed Vibrations

1. Properties of the Tympanal Resonances

In the preceding paragraphs the expected vibrations have been calculated on the assumption that the tympanal membrane behaves as an ideal membrane. It is obvious that the entire tympanum is very far from being homogeneous, and that the thin part of the membrane (although fairly homogeneous) is not circular. The most surprising feature of the vibrations, as observed by means of laser holography and the capacitance electrode, is how well they follow the predicted behaviour. There are, of course, several minor deviations between the predicted and the observed vibrations, but the overall impression is that of a general agreement.

The following description of the vibration patterns in the isolated ear is based on a total of 68 holograms (of 7 different preparations) and a total of about 1500 measurements with the capacitance electrode (53 preparations). All experiments were done within one hour after the removal of the ear. In the laser experiments the preparation was covered with humid filter paper between the exposures.

The best correlation with theory is found for the resonance frequencies; in fresh preparations most resonance frequencies deviate less than 10 per cent from the expected values. It is, however, difficult to give exact measurements for the resonance frequencies, since there is some variation between the preparations. Also, somewhat higher values were found at the end of the experiments, if the preparation had been allowed to dry. The effect of drying was relatively moderate (about 10–15 per cent increase in the resonance frequencies during the first hour), but obviously the drastic increase in the stiffness illustrated in Fig. 7 is a warning against experiments of longer duration. The variation between the preparations and the effect of drying seems to be sufficient to explain the variation observed in the recordings from single receptor cells (paper I).

The most surprising deviation from theory is that the spatial position of the centre of vibration is not constant. In an ideal membrane the centre of vibration should be located at the geometrical centre of the

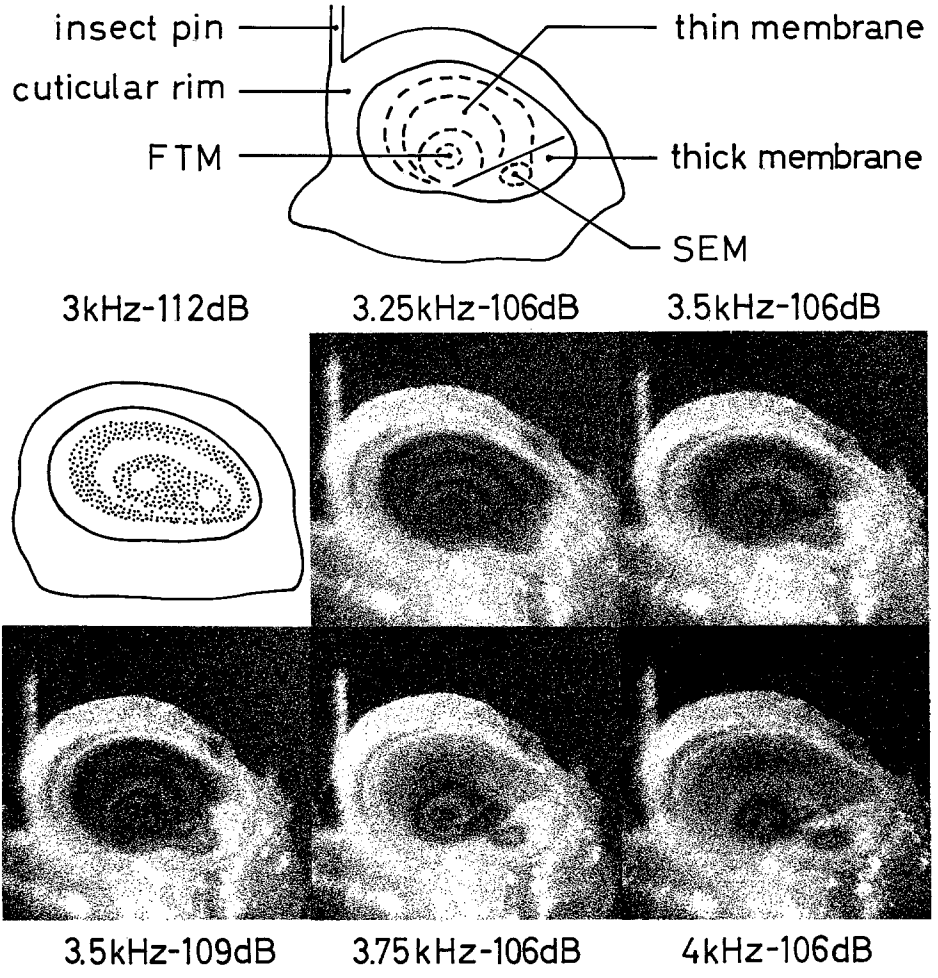

Fig. 13. Holographic pictures of the vibrations in the frequency range 3–4 kHz. *Above:* The orientation of the isolated ear, and the approximate positions of the centers of the fundamental mode of the thin membrane (FTM) and of the second mode of the entire membrane (SEM). *Below:* The vibration patterns; the dark and light lines on the pictures are loci of equal amplitudes of vibration (see Fig. 4). Note the concentration of the FTM vibration, when the frequency is varied from 3 to 3.75 kHz. (The 3 kHz vibration pattern has been drawn from a holographic picture of bad technical quality. This picture was from another preparation)

membrane. In the tympanal membrane, however, the centers of vibration are not at the geometrical centre, and their positions differ for different modes of vibration. The centers of all the modes of vibration of the

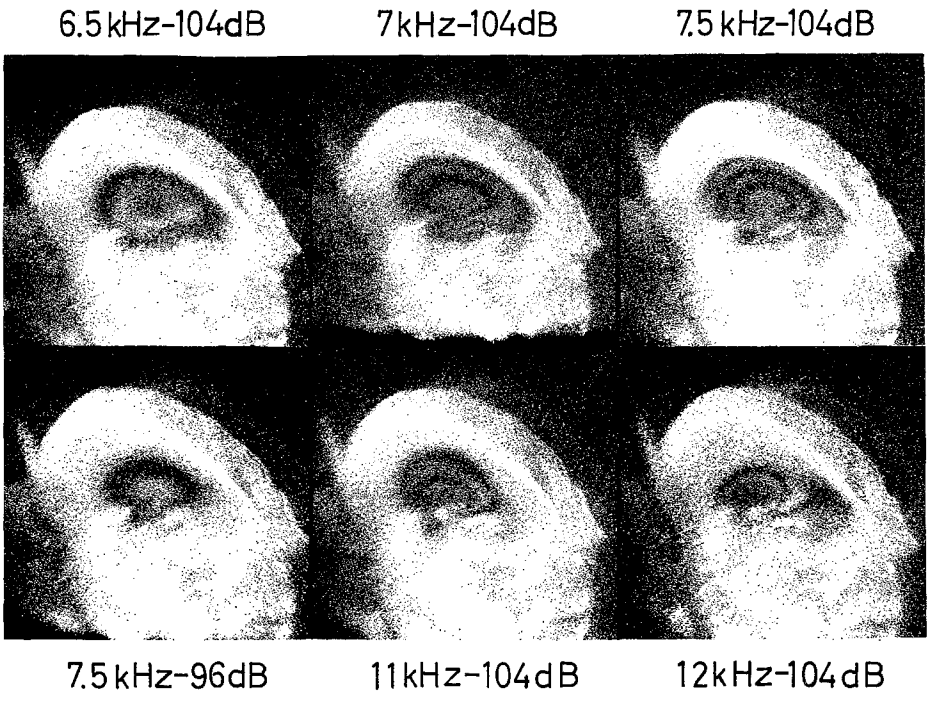

Fig. 14. Holographic pictures of the second and third mode of vibration of the thin-membrane system. The orientation of the isolated ear is similar to Fig. 13. The three upper pictures show the increasing amplitude of vibration as the second resonance frequency (8 kHz) is approached. The pictures at 11 and 12 kHz show the concentration of the area of vigorous vibration as the third resonance frequency (13 kHz) is approached

entire membrane are located in the thick-membrane-end of the tympanum; but the centre of the first mode is at the thin membrane (Fig. 15), whereas the centers of higher modes are in the thick membrane.

The centers of vibration of the *thin*-membrane system are located nearer to the geometrical centre of the tympanum (Figs. 13 and 14). Here again, the position of the centre is not constant; at some frequencies the centre of vibration is at the geometrical centre of the thin membrane (Fig. 14); at other frequencies it is at the area of attachment of the a- and b-cells, i.e. near the edge of the thin membrane (Fig. 13). This may seem surprising, but because of the peculiar shape of the thin membrane (Fig. 6) the area of attachment of the a- and b-cells is in fact both at the edge of the thin membrane and near to its centre.

This difference in the spatial position of the two sets of vibrations is also evident from the measurements with the capacitance electrode.

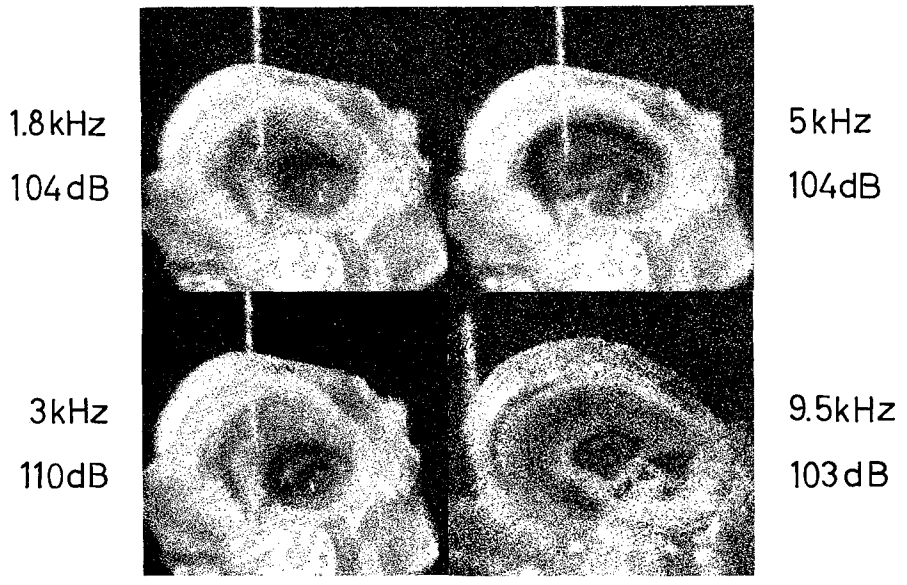

Fig. 15. Holographic pictures of vibration patterns in the isolated ear. *Left:* The fundamental mode of the entire-membrane system. Note that the centre of vibration is in the thick-membrane corner of the tympanum. *Right:* Two unexpected patterns of vibration (see the discussion). In three of the pictures the insect pin is also seen on a part of the membrane. In fact, the pin was behind the membrane, and reflected light was transmitted through the membrane

When the electrode is placed at the thick-membrane-end of the membrane, the phase lag and the variation in amplitude are close to those expected for the entire-membrane system. In the opposite end of the membrane, however, the values are close to those expected for the thin-membrane system.

The behaviour of the membrane between the two centers of vibration is determined by both vibrations (see above). In the larger part of this "zone of interaction" the final vibration is determined mainly by the vibrations of the thin-membrane system. This is not surprising, since the damping of the thin membrane is about three times less than that of the entire membrane (see below). Thus, above 3 kHz the amplitude of vibration of the thin-membrane system is normally larger, and consequently this system will tend to "dominate" the entire-membrane system. Some of the interactions will be described in detail below, since the attachment area of some receptor cells is in the "zone of interaction" between two vibrations.

A surprising feature of some of the tympanal vibrations is their spatial concentration. It was mentioned above that the vibrations of the entire membrane have their centre in the thick-membrane-end of the tympanum. Although these vibrations are derived from the entire tympanum, vigorous movement may be restricted to a very small area (SEM on Fig. 13). This is also true for some of the thin-membrane vibrations, e.g. the fundamental mode at 3.75–4 kHz (FTM on Fig. 13) and the third mode at 12 kHz (Fig. 14).

The Vibration at Different Frequencies. On the holograms at 1.8, 2, and 2.5 kHz the fundamental mode of the entire membrane (FEM) covers a fairly large part of the thick-membrane-end of the tympanum. At 3 kHz the FEM may still be the only vibration seen (Fig. 15), but in some preparations and at high intensities the fundamental mode of the thin membrane (FTM) can also be seen (Fig. 13). The capacitance electrode experiments show how these vibrations interact (see below: c-cells).

In the frequency range 3.25 to 4.5 kHz the vibrations are dominated by the FTM. The second mode of the entire membrane (SEM) is now restricted to a small area on the thick membrane. The FTM-vibration may be fairly uniform over the membrane (3.25 kHz on Fig. 13), but generally it is spatially concentrated (Fig. 13). Therefore, it is not surprising that the FTM seldomly causes a clear maximum of vibration in the capacitance measurements. These vibrations are discussed below (a- and b-cells).

At 5 kHz the holographic picture may be very similar to that at 4 kHz (Fig. 13), but in one preparation the picture of Fig. 15 was obtained. The nature of this vibration is discussed below.

At 6.5 to 8.5 kHz the vibration is dominated by the second mode of the thin membrane (Fig. 14). This vibration is well suited for detailed measurements with the capacitance electrode, since its interactions with the entire-membrane vibrations seem to be minimal. The position of the nodal circle at different frequencies could be determined by placing the electrode at different positions on the membrane and gradually increasing the sound frequency. If the distance between the electrode and the centre was more than about half the radius, a sudden decrease in phase could be observed at a certain frequency below the resonance frequency. At the same time the amplitude of vibration was a minimum. At a distance of about half the radius this drop in phase and amplitude occured near to the resonance frequency (see Fig. 17). Near the center both the phase lag and the amplitude increased without interruption. These experiments confirmed the impression gained from the holograms: the position of the second mode is almost symmetric on the thin membrane. This is in contrast to the fundamental and third modes, which are very askew. The experiments also agree reasonably well with the behaviour predicted from physical theory (Fig. 10), but since the tip of the electrode was not comparable to a point, the changes of phase and amplitude were not as dramatic as expected.

At 9.5 kHz (Fig. 15) an unexpected vibration exists on a very limited area of the membrane (see the discussion). At this frequency one can also see another vibration on the holographic picture (Fig. 15); this vibration is located at the thick-membrane end of the tympanum, and probably it is the fourth mode of the entire membrane.

At 11 to 14 kHz the third mode of the thin membrane can be seen on the holograms (Fig. 14) and measured with the capacitance electrode (see below:

d-cells). At higher frequencies, however, the vibrations become too complex to be resolved by the present technique.

2. The Damping Factor and the Tuning of the Receptor Cells

In general, friction has very little influence in determining the resonance frequency, and it has therefore been neglected in the calculations of resonance frequencies performed above. The amplitude of vibration, however, is markedly influenced by the friction of the system. The friction can be divided into external and internal friction. The external friction (indicated as R_r = the resistive component of the radiation impedance) is equal to the resistance to the motion which the surrounding air manifests. In the appendix it is shown that the external friction can be neglected for the isolated membrane. Thus, we shall only consider the contribution of the internal friction (indicated as R = the resistive component of the membrane impedance).

The magnitude of R determines the amplitude of vibration at resonance, and it also determines the degree of tuning to the resonance frequency. The degree of tuning is often expressed by the "Q of the system". Q is the number of cycles required for the amplitude of motion to reduce to $1/e^{\pi}$ of its original value (approximately 0.043), when the driving force stops.

In a *simple oscillator* (mechanical or electrical) Q can be found from the tuning to the resonance frequency (f_0) by means of the expression

$$Q = \frac{f_0}{f_2 - f_1} \tag{9}$$

where f_1 and f_2 are the frequencies below and above f_0, at which the response of the system is 3 dB down relative to the response at the resonance frequency. The relationship between R and Q is given by

$$Q = \frac{1}{R \cdot \omega_0 \cdot c_m} = \frac{\omega_0 \cdot m}{R} \tag{10}$$

where ω_0 = angular frequency at resonance ($= 2 \cdot \pi \cdot f_0$),
c_m = the compliance,
m = the mass.

These equations do not apply to the higher modes of membranes, but they are almost valid for the fundamental mode of vibration, if some corrections are made: The values of c_m, m, and R cannot be used directly in the equations for simple oscillators (see Morse, 1948). Thus, the value of f_0 for the thin membrane calculated from Eq. (10) is about 4 kHz, as compared with the 3.4 kHz found by means of Eq. (3). Therefore, if the determined value of c_m is used in Eq. (10), the effective mass used should be about 1.38 times the real mass. Similarly, the value of R used in Eq. (10) will depend on the part of the membrane considered, because the membrane—unlike a simple oscillator—does not vibrate with a uniform amplitude of motion. It can be shown (see Skudrzyk, 1954, p. 333) that the value of R calculated from the amplitude of the centre of vibration is about 0.43

times the value to be used for the calculation of Q by means of Eq. (10). The real, physical R, however, has to be calculated by means of Eq. (6).

In the following, the values of Q estimated from the tuning of the receptor cells will be compared with the values expected from the amplitude of vibration observed on the holograms. The cells are primary receptor cells, and there is probably no lateral interaction between them. Therefore, the tuning of their threshold curves are likely to reflect the tuning of the vibration of their areas of attachment. The amplitude of vibration can be obtained from the holograms. The force, however, has to be estimated by means of indirect methods. In the following article (paper III) the force acting to move the tympanum in the isolated ear is calculated by comparing the sensitivity of the isolated ear with that of an operated, semi-intact ear.

The average value of (the physical) R for the thin membrane, derived from 14 holograms, was $5 \cdot 10^{-5}$ Ns/m. In contrast, the entire membrane is more damped: the average value of R (8 holograms) was $16 \cdot 10^{-5}$, i.e. about 3 times larger than for the thin membrane. The expected values of Q for the fundamental modes of vibration of the thin and entire membrane calculated by means of Eq. (6) are about 4.7 and 2.8, respectively.

The fundamental resonance of the entire membrane is expected (and observed) at approximately 1.8 kHz (see above). The c-cells have been found to respond at about 1.5 kHz (see paper I), and the Q of their tuning curves is about 3. The vibrations recorded around 1.8 kHz by means of the capacitance electrode also have Q-values around 3 (Fig. 16). Thus, the degree of tuning of these receptor cells is approximately what one would expect, if they were responding to the fundamental mode of the entire membrane.

The fundamental resonance of the thin membrane is expected at approximately 3.4 kHz. Responses of the a- and b-cells have been found very near to this frequency (at 3.74 and 3.46 kHz, respectively; see paper I). In the a-cells the average value of Q is about 3, whereas in the b-cells it is about 6. From the amplitude of vibration a Q-value of 4.7 was expected, so it is not possible to use the value of Q to determine which of these groups are responding to the fundamental mode of the thin membrane. The Q-values are, however, certainly of the right order of magnitude.

The effect of friction can be regarded as a resisting force, opposing the movement of the membrane. In textbooks it is normally considered proportional to the velocity of the movement, and this assumption has also been made in Eq. (5). In practice, however, this is not always true. The experiments show that in the present case the assumption is not far from being correct: The values of R calculated from the holograms and from the capacitance electrode measurements are in the same order of magnitude as the Q values of the receptor cells. The former measure-

ments were performed at sound levels about 40–60 dB higher than those needed for the determination of the tuning of the receptor cells.

It was mentioned above that the value of Q tells us how rapidly a vibration dies out, when the driving force stops. Similarly, the time required to reach steady-state after the onset of a driving force also depends on the damping of the system. If the damping is small, energy can be stored over a number of cycles, and the vibration gradually increases to steady-state magnitude. Consequently, the ear will be very sensitive to continuous sound around one of the resonance frequencies. On the other hand, the cost of this high sensitivity is a poor time resolution. The sound signals of grasshoppers consist of short, pulsed sounds with broad frequency spectra (Dumortier, 1963). Thus, the ear must be able to respond to pulses of a few cycles duration. It can be shown (see Deutsch, 1967) that—as far as physics is concerned—a Q value of 3 is the optimum for the reception of three cycle bursts of sound. In the locust ear the time resolution of one group of receptor cells (c) is much poorer than that of the other groups. The reason for this difference is probably neural, since the c-cells also respond more slowly to long pulses than do the other groups (Michelsen, 1966).

The Q values reported for the mammalian ear differ as widely as do the opinions about their importance for time resolution in the different theories of hearing (resonance-versus travelling wave-theories). Physical measurements of the vibration of the basilar membrane show Q values around 1.6–2.5 (Békésy, 1960; Johnstone and Boyle, 1967; c.f. Tonndorf and Khanna, 1968). In contrast, measurements of the system impulse response (Möller, 1970) and of tuning curves for individual units in the cochlear nerve (Evans, 1970) indicate Q-values about 10 times larger than those determined by means of physical methods.

It was mentioned in the introduction that an important argument against the occurrence of resonances in the vertebrate ear is the existence of a sharp frequency discrimination together with a fine time resolution in the same sound receptor. The weight of this argument depends upon how much of the frequency analysis is due to mechanical factors (see Möller, 1970). If a substantial part of the frequency discrimination is due to lateral inhibition, then the time resolution should not be compared with the frequency discrimination of the intact auditory system, but only with the part due to mechanical factors. It is interesting that the mechanical tuning of the basilar membrane—as measured with physical methods—is not sharper than that of the locust ear (see above). Since the locust ear is a true resonance system, it would be interesting to compare the time resolution, which has been obtained in this ear, with that of vertebrate ears. Such studies are in progress.

3. The Selectivity of the a- and b-Cells

The sensitivity of the a- and b-cells is a maximum at 3.74 and 3.46 kHz, respectively (paper I: table). In the frequency range 3–4 kHz a very dramatic change in the vibration pattern can be observed on the holograms (Fig. 13). Around 3 kHz the vibration is still governed by the entire-membrane vibration (Fig. 15), but at high intensities (Fig. 13), is can be seen to co-exist with the fundamental mode of the thin membrane (FTM). Note, that at 3 kHz the FTM is almost at the centre of the tympanum. Fig. 13 shows what happens, as the frequency is increased:

At 3.25 kHz the FTM is the dominating vibration. At 3.5 kHz almost the same picture as at 3.25 kHz is observed, but the amplitude of membrane displacement has decreased somewhat. The second mode of vibration of the entire membrane (SEM) is apparent on the thick part of the tympanum. At 3.75 kHz the FTM is more concentrated, and the amplitude of the SEM has increased (Fig. 13). At 4 kHz approximately the same picture is seen, but the amplitude of the FTM has decreased further. At higher frequencies the amplitude of vibration decreases even further, and the centre of the thin membrane vibration moves towards the centre of the membrane.

The a- and b-cells are attached to the elevated process and the styliform body, respectively. The space between these cuticular bodies is filled with a thin mass of cells, and the areas of attachment are also very close to each other. It is therefore not surprising that the best frequencies are very similar. The difference between their best frequencies was just significant ($P = 98\%$), but the difference for other response parameters was highly significant (paper I, table).

The Q-factor of the b-cells is about two times greater than that of the a-cells. Nevertheless, the a-cells are about 5 dB more sensitive than the b-cells. This is surprising, since—assuming that both responses were due to fundamental modes—a sharper tuning would mean a smaller R and thus a larger amplitude of vibration [see Eq. (10)]. Therefore, from their tuning one would expect the b-cells to be about 6 dB more sensitive than the a-cells. The experimental results, however, show that the opposite is true. Furthermore, the best frequency of the b-cells (3.46 kHz) is closer to the resonance of the FTM than is the best frequency of the a-cells (3.74 kHz). Here again, one would expect the b-cells to be more sensitive than the a-cells.

The holograms (Fig. 13) show a very concentrated vibration in the a-cell area of attachment at frequencies around 3.75 kHz. Thus, a probable explanation for the large sensitivity of the a-cells is that they are situated at the centre of this vibration. If this is true, then the attachment area of the b-cells is some hundred μm from the centre of vibration. Thus, the relative sensitivities become understandable if one assumes that the a-cells are responding to the combined effect of the FTM and the outer "bubble" of the SEM, and that the b-cells respond to the FTM only.

It should be emphasized, however, that the experimental results obtained so far do not tell us whether this explanation is correct. The spatial resolution on the holograms is not good enough to allow an accurate estimate of the position of the 3.75 kHz vibration. The results obtained with the capacitance electrode in this area vary rather much, but most amplitude curves resemble that shown on Fig. 16, *III*. Unfortunately, the tip of the capacitance electrode is too large to allow the

fine details in the vibration of these adjoining attachment areas to be resolved (the more sensitive oscillator mentioned above will probably allow smaller electrodes to be used in future experiments).

4. The c-Cells: Interaction of the Fundamental Modes

The c-cells may have up to three frequencies of maximum sensitivity: 1.5 kHz, 2.5–3 kHz, and 8 kHz (see paper I, Fig. 8). The response at 8 kHz is probably due to the second mode of the thin membrane (see above). The response at 1.5 kHz is sometimes absent. All cells, however, respond maximally around 2.5–3 kHz, but this response does not correspond to any of the expected resonances. In the following, it will be shown that the response at 1.5 kHz is due to the fundamental mode of the entire membrane, and that the response at 2.5–3 kHz is caused by the interaction between the fundamental modes of the entire and thin part of the tympanum.

The vibrations of the entire tympanum seem to have their centers in the thick-membrane-end of the tympanum (see above). No receptor cells attach directly to this area, but the attachment area of the c-cells (the folded body) forms a part of the boundary between the thin and the thick parts of the tympanum (Fig. 6). Thus, it would not be surprising if the c-cells were specialized in picking up some of these vibrations. It was shown above that the degree of tuning of the c-cells to 1.5 kHz is approximately what one would expect, if they were responding to the fundamental mode of the entire tympanum.

When the capacitance electrode is placed close to the folded body, the variation in the relative amplitude of vibration in the frequency range 1 to 4 kHz may be an almost true copy of the response curve of the c-cells. Furthermore, different types of vibration have been found in different recordings; these types include an almost pure 1.8 kHz response with very little tendency towards a maximum at 2.5–3 kHz (Fig. 16, *I*), a 3.4 kHz response with only a small tendency towards a maximum at 1.8 kHz (Fig. 16, *III*), and a gradual series of intermediate types (Fig. 16, *II* illustrates a typical example). All these types of vibration have also been observed in the response of single c-cells (paper I). The most common type of response in the c-cells were identical to type II or intermediate between type II and type III (see paper I, Fig. 7), but cell responses like type I or III have occasionally been observed.

Thus, it is possible to record vibration patterns which correspond to the observed patterns of frequency sensitivity in the receptor cells. The nature of these vibrations can be seen from the phase relationships. In the 1.8 kHz response (Fig. 16, *I*) the variation of the phase lag (from driving force to membrane displacement, see above) is almost equal to

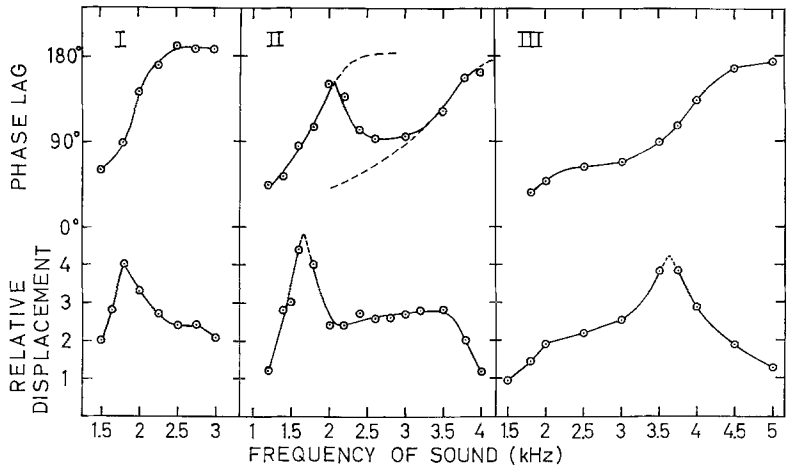

Fig. 16. Variation in amplitude and phase lag measured with the capacitance electrode placed close to the folded body (c-cells). *I* and *III* are extreme types which almost correspond to the fundamental modes of the entire and thin membrane, respectively. *II* is an intermediate type. Further explanation in the text

that expected for the resonance of a fundamental mode (see above): The phase lag is about 90° at the frequency of maximum vibration, and the curve has approximately the slope and shape expected. Also, the upper values are around 180°. Thus, the amplitude- and phase-measurements support the conclusion already reached from calculation, tuning, and holography that the 1.8 kHz response is due to the fundamental mode of the entire membrane.

From the calculations one should expect the next resonance above 1.8 kHz to be the fundamental vibration of the thin part of the tympanum at 3.4 kHz. Consequently, at this frequency the parts of the tympanum near to the centre of the thin-membrane-vibrations should have a phase lag of about 90°. In some recordings close to the folded body (Fig. 16, *III*) this is almost true. The tympanal membrane in the thick-membrane-end, on the other hand, should probably be more influenced by the entire-membrane-vibrations and thus have a phase lag of about 230° at 3.4 kHz. The membrane between the two centers of vibration can be expected to have intermediate phase lags (see above).

In principle, this is confirmed by the capacitance electrode measurements: In the recordings shown in Fig. 16, *II*, the variation in phase lag in the frequency range 1 to 4 kHz is approximately what might be expected for a point situated between the two centers of vibration. At low frequencies (around 1.8 kHz) the variation of phase and amplitude

is governed by the fundamental mode of the entire tympanum (cf. Fig. 16, *I*). Around 3.4 kHz the behaviour is mainly determined by the fundamental mode of the thin membrane (cf. Fig. 16, *III*). Between these frequencies, a dramatic change of phase is observed, corresponding to a gradual shift in the relative "influence" of the two vibrations on this part of the tympanum.

During the interaction in the frequency range 2–3 kHz, the amplitudes of the two individual vibrations are added to produce a fairly constant amplitude of vibration (Fig. 16, *II*). It is interesting that the 3.4 kHz vibration does not produce any peak in the amplitude. Also, the amplitude decreases markedly around 4 kHz. At this frequency the fundamental mode of the thin membrane is interacting with the second mode of the entire tympanum (see above: a- and b-cells). This interaction seems to produce a vigorous vibration of the a-cell area of attachment (elevated process), but a decrease of the vibration amplitude at the folded body (c-cell area of attachment).

Thus, the addition of vibrations from the two sets may lead to both larger and smaller amplitudes than those expected for the individual vibrations. This is not surprising, since the amplitude of the resultant vibration depends on both the amplitudes of and the phase difference between the two components. In a second-mode-vibration the membrane on the two sides of the nodal circle is vibrating totally out of phase. The addition of a fundamental mode may therefore produce quite opposite effects with respect to resultant amplitude. Unfortunately, from the present recordings it is not clear where the nodal line of the second mode of the entire tympanum is situated on the membrane. Further studies are needed on this problem.

5. The d-Cells and the Position of the Third Mode

The amplitude- and phase-relationships illustrated in Fig. 17, left, were recorded in most preparations, when the capacitance electrode was placed close to the attachment point of the d-cells (the pyriform vesicle, see Fig. 6). The amplitudes are a maximum at 13 kHz, i.e. at the expected resonance frequency of the third mode of the thin membrane. This frequency is near the best frequency of the d-cells (12 kHz, range 10–14 kHz). The amplitude is a minimum around 8 kHz (resonance frequency of the second mode of the thin membrane). In this frequency range the d-cells are rather insensitive (see paper I: Fig. 10). The reason for this behaviour is that the area of attachment of the d-cells is close to the nodal circle of the second node at resonance. This can be seen, if the capacitance electrode is moved to other positions near the pyriform vesicle. The position of the nodal circle is also in reasonable agreement with the position expected from Eq. (6).

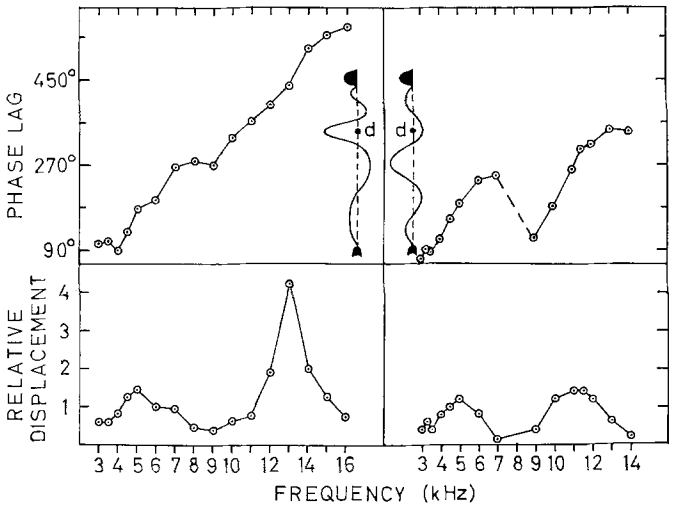

Fig. 17. Amplitude and phase measured with the capacitance electrode close to the pyriform vesicle (d-cells). *Left:* the normal case; the third mode (at 13 kHz) is so askew that its centre is at the d-cell area of attachment. *Right:* a more symmetric vibration; the pyriform vesicle is not at the centre of vibration. Note the decrease in phase at the passing of the nodal circle

It is seen from Fig. 2 that in the ideal membrane this position would correspond roughly to a maximum of vibration at the third mode, namely to the part of the membrane between the two nodal circles of the third mode. The phase-relationships, however, show that this is not true (Fig. 17, left): At 13 kHz the displacement is delayed about 90° with respect to the driving force, and not 270° as one would expect (see Fig. 2). Also, it is apparent from Fig. 17 that a 360° phase-shift is observed when the frequency is varied from about 3 kHz (approximately first mode of the thin membrane) to 13 kHz (third mode). This result can only be understood, if the d-cells respond to the movements of the centre of the third mode (and not to the "bubble" between the two nodal circles), see Fig. 17. Thus, the position of the third mode is very asymmetric. Although the technical quality of the holograms was not too good in the frequency range around 13 kHz, they do show that the maximum of displacement is centered approximately at the attachment area of the d-cells (Fig. 14).

The position of the area of attachment of the d-cells is unique, since normally the d-cells avoid responding to the second mode by being near the nodal circle at resonance, but at the same time they pick up the largest amplitude of the third mode by attaching to its centre and not to the membrane between the nodal circles.

In a few preparations, however, the third mode was probably not so askew. In these cases (Fig. 17, right) the d-cells were picking up the middle "bubble" of the third mode instead of the centre, and the amplitude of vibration was relatively smaller (assuming the 5 kHz response to be constant). Note the decrease in phase, which indicates the passing of the inner nodal circle.

Thus, in electrophysiological recordings one should expect to find a reduced sensitivity to high frequencies in some of the preparations. This was in fact observed by Popov (personal communication, 1968), who noticed that the low-frequency optimum was much more stable than the high-frequency optimum in recordings from semi-isolated ears. The difference in physical parameters, causing the different vibrations in the two groups of preparations, remains to be determined.

The fundamental mode of the thin membrane (at 3.4 kHz) is centered at the a-cell area of attachment (see above). Apparently, this vibration is so localized that it hardly affects the d-cells. On the other hand, the pyriform vesicle of the d-cells is set into vibration by the 5 kHz vibration. The nature of this vibration will be discussed below.

Discussion

1. The Mechanism of Frequency Discrimination

These results show that one should expect the thin part of the tympanum and the entire tympanum to resonate at certain frequencies (Fig. 8). Direct observations of the vibration patterns show that the actual vibrations behave almost as expected. The spatial position of the vibrations is, however, different for the two sets of vibrations. Furthermore, the positions are not constant.

In paper I it was shown that the four groups of receptor cells in the locust ear have different frequency sensitivities. The length of the sound pulses used in these experiments was 100 msec. From the damping of the tympanal membrane one may expect steady-state vibration to be reached within a few msec. Thus, it is reasonable to compare the sensitivities measured in the receptor cells with the vibration of tympanal membranes exposed to continuous sound. The use of relatively high sound intensities in laser holography and measurements with the capacitance electrode was permissible, since both the compliance and friction seem to be linear in the range of vibration amplitudes considered (see above). The selectivity of the receptor cells may be explained as follows:

The a-cells respond mainly to frequencies around 3.7 kHz. At their best frequency the basic mode of vibration of the thin membrane interacts with the second mode of the entire tympanum. As a result, the former mode concentrates around the attachment area of the a-cells

(Fig. 13). The a-cells may also respond to the second mode of the thin membrane (8 kHz).

The b-cells respond to the fundamental mode of vibration of the thin membrane (3.4 kHz). Their attachment area is some hundred μm from that of the a-cells, and they are probably not subjected to the most vigorous vibration of the first mode. They are therefore not as sensitive as the a-cells. Some b-cells also have a small second maximum around 5 kHz. The nature of the 5 kHz vibration is discussed below.

The c-cells generally respond around 2–3 kHz. Some c-cells also respond to the fundamental mode of either the entire tympanum (at 1.8 kHz) or the thin membrane (at 3.4 kHz), but others do not. The response of the c-cells seems to be determined by the interaction of the two fundamental modes of vibration (Fig. 16). Some c-cells may also respond to the second mode of the thin part of the tympanal membrane (8 kHz).

The d-cells respond predominantly to the third (13 kHz) and fourth (18 kHz) mode of vibration of the thin part of the membrane. Their attachment area on the thin membrane is near the nodal circle at resonance of the second mode, but in most preparations it is at the centre of the third mode (Fig. 17, left).

It can be concluded that the frequency discrimination in the locust ear is a purely physical phenomenon, based partly on the presence of the two sets of vibrations, and partly on the different anatomical position of the groups of receptor cells. The strongest stimulation of the receptor cells is found at the frequencies of maximum vibration of their areas of attachment on the tympanum. Normally, these frequencies are the resonance frequencies, but because of the interaction between the vibrations, this is not always true (a- and c-cells). Apparently, the selectivity of the groups of receptor cells has three different causes:

The vibrations of the entire tympanum have their centers in the thick-membrane-end of the tympanum. Consequently, only the group of cells which are attached to this area (the c-cells) respond directly to some of these vibrations. Although most of these resonances do not stimulate the receptor cells directly, they may still play an important role as "modulators" for the "dominating" thin-membrane vibrations.

A probable result of this interaction is the change of spatial position observed both in the entire-membrane vibrations and in the vibrations of the thin membrane system. The most surprising feature here is that the vibrations are extremely localized. For example, the spatially concentrated first mode of the thin membrane, which causes a vigorous movement of the a-cell attachment area (Fig. 13), hardly affects the attachment areas of the three other groups.

Finally, the groups of receptor cells may have their attachment area near one or more nodal circles (at the corresponding resonances). This principle is well illustrated in the d-cells (see above). The interaction between two vibrations may also create an "artificial nodal line", if the two vibrations oppose each other. This may be the reason for the decrease in the response of the c-cells around 4 kHz (see above).

Thus, according to this view the frequency sensitivity of a receptor cell is determined by the vibration of its area of attachment on the membrane, and not by any frequency preference of the receptor cell itself. The dynamic properties of the receptor cells, on the other hand, are probably of neural origin (cf. Nakajima and Onodera, 1969). In the locust ear two different types of adaptation have been found (Michelsen, 1966); the c-cells respond more slowly than the other cells. It is remarkable that, although the attachment of the c-cells to a more damped membrane should, in theory, allow them to have a better time resolution than the other cells, the opposite is in fact true.

During the recordings from single receptor cells an abnormal unit was found in the anatomical region of the c-cells. The frequency sensitivity of this cell was similar to that of a typical c-cell (paper I, Fig. 7, left), but it had an a-cell type of adaptation. This observation can be explained by assuming that, during the ontogeny, an a-cell had attached itself to the c-cell part of the tympanum. Thus, the frequency sensitivity would be determined by the area of attachment, whereas the adaptation would remain identical to the a-cell type.

The frequency discrimination in the locust ear is not very sharp compared to that of vertebrate ears. It should be noted, however, that the vibration of the tympanum is so complex above 3 kHz that it is possible—for a given sound frequency—to find a point on the membrane which has a maximum of vibration at that frequency. Thus, a much better frequency discrimination might have been obtained, if more groups of receptor cells had attached to the tympanum.

2. Some Unsolved Problems

The present study can only be regarded as the first step towards an understanding of the mechanism of frequency discrimination in the locust ear. A number of uncertain points and unsolved problems have been neglected in the main part of the paper in order not to make the description more complicated than necessary. Two problems will be discussed here: Are there other vibrations than those expected for the ideal membrane? And, to what kind of vibration are the receptor cells subjected?

Irregular Vibrations. In general, the vibrations of the tympanum can be regarded as composed of two sets of circularly symmetric modes. It was mentioned in the introduction that, in an ideal membrane acted

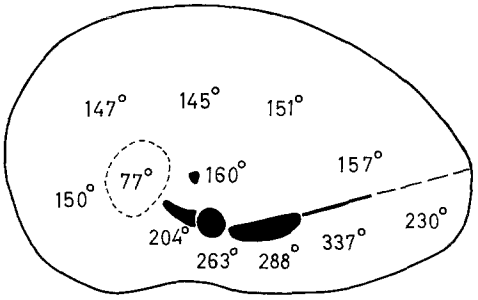

Fig. 18. The variation in phase lag over the membrane at 5 kHz. The values are the average of about 150 measurements from 5 different preparations. Further explanation in the text

upon by a uniform force (sound wave), only the circularly symmetric vibration patterns can be expected. The tympanal membrane is, however, not homogeneous or circular, so it is possible that other types of vibration occur. In the present study at least one vibration was observed, which does not fit into the calculated series of vibrations.

At 9.5 kHz an unexpected vibration has been observed on the holograms in the area between the centre of the membrane, the folded body (c-cells), and the pyriform vesicle (d-cells), see Fig. 15. It can also be recorded by means of the capacitance electrode. The phase lag at the 9.5 kHz peak was about 270°. Apparently, this vibration is restricted to a very small area of the membrane, and it does not seem to affect the receptor cells. At the frequencies around 9.5 kHz several irregular vibrations can be expected (see Morse, 1948). The nature of this vibration remains unknown.

In most recordings with the capacitance electrode from the thin membrane one of the maxima in the amplitude of vibration was found around 5 kHz (Fig. 17 shows typical examples). Also, some b-cells have a small second sensitivity maximum around 5 kHz (paper I, Fig. 6). At this frequency the thin-membrane system should be changing from the first (3.4 kHz) to the second (8 kHz) mode, and the entire-membrane system should be between the second (4.2 kHz) and the third (6.6 kHz) mode. Thus, the amplitude of vibration should be relatively small in both systems. Nevertheless, an amplitude maximum is often observed.

The holographic pictures made at 5 kHz differ very much. One of them was almost identical to the 4 kHz vibration shown in Fig. 13; i.e. the centers of vibration were at the a-cell area and at the thick membrane, respectively. Another picture is shown in Fig. 15. In this case the centers are nearer to the geometrical center of the tympanum. The amplitude of the 5 kHz vibration on Fig. 15 is approximately what one would expect from the computed values (Fig. 9).

The phase lags observed at 5 kHz differ rather much over the membrane (Fig. 18). At the thin membrane values around 150° are observed, whereas the thick membrane has phase lags up to about 340°. These values are the average of about 150 measurements on 5 preparations, and they are near to the expected phase lags (170 and 340°, respectively). In two preparations an area with phase lags around 80° was observed on the thin membrane near to the b-cells.

Thus, both the amplitude and phase lag are near to the expected values for the circularly symmetrical vibrations. The only unexpected finding is the area of 80° phase lag. The most probable explanation for the observed amplitude maximum and the response of the b-cells is that the centre of the thin-membrane vibration (which at 3–4 kHz is at the a-cell area) is moving towards the centre of the tympanum at 5 kHz. Therefore, the capacitance electrode (and the receptor cells attaching to the thin membrane) will record a maximum of amplitude, although the thin-membrane vibration should be a minimum at 5 kHz!

The only resonance expected for the thin-membrane system around 5 kHz is that of the simplest irregular vibration (d on Fig. 1) at 5.4 kHz (see Morse, 1948). In this vibration there should be a nodal line across the membrane, and the membrane on each side of this nodal line should vibrate out of phase. The addition of a weak "d-vibration" and the circularly symmetric modes might give a vibration pattern as that seen on Fig. 15. This "explanation" is, however, only a guess. Further observations are needed to solve the problem.

Excitation of the Receptor Cells. The technique used here was sufficient to demonstrate the presence of the vibration patterns of the membrane, but it did not allow a detailed study of the vibration of the attachment areas. It may, however, be useful to speculate about some of the problems which remain to be solved in future experiments:

In the above description the excitation of the receptor cells has been said to be determined by the vibration of their attachment areas on the membrane. In general, this may be true, but it should be borne in mind that the cell bodies are situated in a mass of cells, Müller's organ (Fig. 6). The anatomy of the receptor cells and their (indirect) attachment to the cuticular bodies are extremely complex (see Gray, 1960). The excitation of the receptor cells is likely to be determined by the displacement of the dendrites *relative* to the rest of the cells. Therefore, it is important to know whether the mass of cells in Müller's organ can be set into vibration by the movements of the tympanum.

The attachment parts of the tympanum have been referred to as "areas", but (except for the pyriform vesicle) they are certainly not simple thickenings of the cuticle (see Schwabe, 1906). The styliform body has the shape of an hour-glass, which is fastened to a plate at the membrane-end. The shape of the hollow elevated process is often described as that of a cup, but in fact it bends at some distance from the tympanal membrane. Finally, the folded body is a surprisingly large and complicated, folded thickening of the membrane. It would not be surprising if these complicated structures have a function in the transmission of the vibrations to the receptor cells.

I should like to express my most sincere thanks to O. Juhl Pedersen M. Sc. and Knud Rasmussen M. Sc. (The acoustics Laboratory, The technical University of Denmark) for their invaluable help on the physical problems. Without their continuous advice during the years this investigation could not have been carried out.

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Appendix

The Radiation Impedance

The vibration of the tympanum, caused by a given sound wave, is determined mainly by the properties of the membrane. However, the air will react against the movement. The contribution of this interaction can be measured as a radiation impedance. At "low" frequencies the radiation impedance may be represented by a combination of a mass and a frequency-dependent resistance. Therefore, interactions between the membrane and the air will affect both the resonance frequencies and amplitude of vibration. An exact calculation of the radiation impedance is difficult. For the circular plate surrounded by an infinite baffle the radiation impedance for different modes of vibration have been calculated by Lax (1944). A similar approach can be made for the membrane, but in the present case the membrane is unbaffled, and no exact formula exist for this case. However, the order of magnitude of the radiation impedance can be estimated by means of some simple models.

The radiation impedance (Z_r) of the unbaffled membrane may be estimated by computing that of a spherical dipole source with the same radius as the membrane. It can be shown (see Morse, 1948) that

$$Z_r = R_r + j X_r \simeq \frac{16 \cdot \pi^5 \cdot \varrho \cdot f^4 \cdot a^6}{3 c^3} + j \cdot \omega \cdot \frac{2\pi \cdot \varrho \cdot a^3}{3} \tag{11}$$

where R_r = radiation resistance (Ns/m),
X_r = reactance component of Z_r (Ns/m) = ωm_r, where
m_r = radiation mass (kg),
$j = \sqrt{-1}$,
$\pi = 3.14159\ldots$,
f = frequency of sound (s^{-1}),
a = radius of membrane (m),
c = velocity of sound (approximately 344 m/s),
ϱ = density of air (approximately 1.2 kg/m^3),
ω = angular frequency ($= 2\pi f$).

It is apparent from Eq. (11) that the reactive component of the radiation impedance is given by half the mass of a volume of air equal to that of the equivalent dipole source. In the present case one finds $m_r = 2.5\ \mu g$ for $a = 1$ mm.

The value calculated by means of the spherical dipole-model may be compared with the value estimated for a plane, unbaffled, circular disk moving as a rigid piston. It can be shown (Wiener, 1951; Beranek, 1954) that in the size and frequency range considered here,

$$m_r = 0.85 \pi \varrho a^3. \tag{12}$$

From this equation one finds $m_r = 3.2\ \mu g$ for $a = 1$ mm. This result is fairly close to that found above (2.5 μg). When compared with the weight of the thin part of the tympanum (about 9.2 μg), the radiation mass is far from negligible.

The radiation mass calculated by means of these models may be used for the first mode, where all parts of the membrane vibrate in phase. At present no formula exist for computing the exact radiation mass at higher modes of vibration of the unbaffled membrane, but it seems safe to assume that it will be considerably smaller than that for the first mode. If one considers a spherical sound source of n-th order at "low" frequencies ($\omega a/c < 1$, i.e. $f < 50$ kHz for $a = 1$ mm), the radiation mass is approximately given by (Morse, 1948)

$$m_r = \frac{3M}{(n+1)(n+2)} \tag{13}$$

where $M = \varrho\, 4\pi a^3/3 =$ the mass of the equivalent volume of air. Using this model and $a = 1$ mm, the radiation mass becomes 2.5, 1.0, 0.5, and 0.3 μg for the first four modes, respectively [for $n = 1$ the expression is identical to Eq. (11)]. Approximately the same reduction was found by Lax (1944) for plates surrounded by infinite baffles. Although these models are not valid for the present case, the same degree of reduction has been used in the calculations above. The error introduced is minimal.

The mass per unit area (σ) is estimated from the mass of the membrane plus the radiation mass. Since the latter depends upon the order of the vibrational mode, the total effective mass must be calculated for each mode. It was mentioned above that the membrane behaves as a simple, driven oscillator at frequencies up to the first resonance frequency, but that certain corrections are necessary in order to fit the measured membrane parameters to the equations for simple oscillators. If one calculates the equivalent membrane impedance for "low" frequencies (see Morse, 1948), one finds an effective mass of 1.38 times the total mass of the membrane [and an effective stiffness of 8π times the membrane tension, cf. Eq. (4)]. Therefore, when the real mass and the radiation mass were added, the latter was reduced by 1/1.38. It is not quite clear whether this reduction is permissible also for higher modes, but here again the error introduced is minimal.

From formula (11) it is seen that whereas the resistive component (R) of the membrane impedance (Z) is normally considered to be independent of frequency, the resistive component (R_r) of the radiation impedance (Z_r) increases with the fourth power of frequency. Using $a = 1$ mm and $f = 10$ kHz, one finds $R_r = 5 \cdot 10^{-7}$ mks mechanical ohms (Ns/m). At 20 kHz R_r becomes $8 \cdot 10^{-6}$ Ns/m.

The magnitude of R_r derived for a plane, unbaffled, circular disk moving as a rigid piston is given (Beranek, 1954) by

$$R_r = 0.19 a^6 \varrho\, \omega^4/c^3. \tag{14}$$

The value obtained by means of this equation is about 5 times smaller than that calculated from Eq. (11).

It has been shown above that the resistive R of the membrane is about $5 \cdot 10^{-5}$ Ns/m for the thin membrane (where $a = 0.9$ mm) and $16 \cdot 10^{-5}$ Ns/m for the entire tympanum (where $a = 1$ mm). Thus, even at 20 kHz (where the thin membrane is vibrating in its fourth mode, and the value of R_r therefore probably should be reduced, see Lax, 1944) the magnitude of R_r is at least 10 times smaller than R. For the present purpose it therefore seems safe to neglect the radiation resistance.

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