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Middle-Ear Characteristics of Anesthetized Cats*

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Ossicular motion was measured visually with stroboscopic illumination. Tonal stimulation ranged from 30 to 10 000 Hz. Up to 130 dB SPL (sound-pressure level), the motion of the stapes is predominantly piston-like, and its displacement amplitude is linearly related to sound pressure. At frequencies under 3000 Hz, the ossicles move as one rigid body; at higher frequencies, the stapes and incus displacements lag behind the malleus displacement, which suggests that the incudo-malleolar joint flexes. From measurements of stapes displacement at known sound pressures, we calculate a transfer characteristic for the middle ear with the tympanic cavities open. The effects of closing the tympanic cavities on the transfer characteristic were determined from measurements in which the electric response recorded from the round window was used as an indicator of middle-ear output. By combining these data, we obtain a transfer characteristic for the middle ear with the tympanic cavities intact. An attempt is made to compare middle-ear characteristics of cat and man.

INTRODUCTION

THE experimental work reported in this paper was primarily directed toward measuring the displacement of the stapes in response to tones of known frequency and sound-pressure level (SPL) in a living animal. If we regard stapes displacement as the output and sound pressure at the tympanic membrane as the input, then the ratio of stapes displacement to sound pressure and the phase angle between these quantities give a complete description of the transfer properties of the middle ear—insofar as the middle ear acts as a linear system. This description not only improves our understanding of the behavior of the middle ear but may also be helpful in interpreting data from other parts of the auditory system. Partly because of our desire to relate these measurements to other work on the auditory system, a large portion of which has been done on cats, we chose the cat as our experimental animal. Since we used barbiturate anesthesia, which apparently eliminated activity of the middle-ear muscles in cats,[1] our results are applicable only to conditions in which the middle-ear muscles are in a relaxed state.

Measurements of ossicular motion in human cadavers made with stroboscopic illumination were reported almost a century ago by Mach and Kessel (1874). Measurements of a middle-ear transfer characteristic were reported by von Békésy[2] in 1942, based on measurements of round-window volume displacement from temporal bones of cadavers. More recently, techniques for measuring acoustic impedance at the drum membrane[3] have improved our knowledge of the middle ear in living humans but have also raised some doubts about the usefulness of measurements made on cadavers (Zwislocki and Feldman, 1963). The first measurements of middle-ear transfer characteristics in living animals

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† During most of the period in which this work was done, J. J. G., Jr., was a National Science Foundation Cooperative Fellow. Since June 1966, he has been a Fannie and John Hertz Foundation Fellow.

[1] For recently published evidence, see Simmons (1959), Carmel and Starr (1963), Baust and Berlucchi (1964).

[2] See von Békésy (1960), pp. 429–437.

[3] For a summary of the results of this work see Zwislocki (1962).

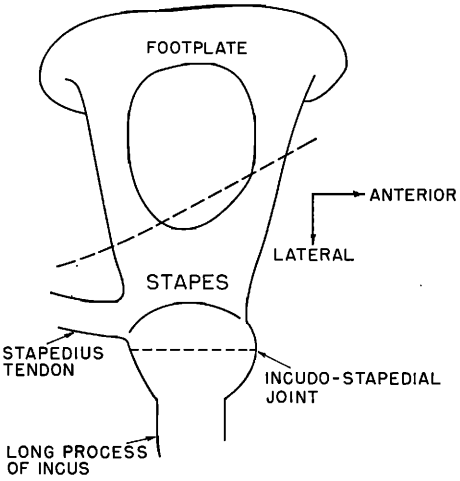

FIG. 1. Sketch (made from a photograph) of the ventral aspect of a left stapes. A portion of the ventral wall of the vestibule had been removed to expose the footplate. Normally, the petrous bone extends approximately to the dashed line so that only the lateral part of the stapes can be seen.

(anesthetized cats) were published in 1963 by Møller (1963). Our measurements were made on preparations that are virtually identical to Møller's; however, the scope of our observations differs from his in several respects.

We measured ossicular displacements visually with stroboscopic illumination by a method that is quite similar to that of Mach and Kessel (1872, 1874). Although measurements can be made more quickly and more sensitively with capacitive-probe systems,[4] probes have not yet been made small enough to measure *stapes* displacement without removing part of the cochlea. Visual measurements of stapes displacement can be made without altering the cochlea; the visual method also gives an immediate indication of the character of the motion (e.g., rotation or translation).

I. METHOD

A. Preparation of the Animal

Adult cats usually weighing from 1½ to 2½ kg were anesthetized by intraperitoneal injection of Dial (75 mg/kg). A tracheal cannula was inserted. Physiological saline (20–50 cc) was injected subcutaneously, and penicillin (100 000 units) was given intramuscularly. The rectal temperature was monitored and maintained at 37±1°C by intermittent use of a heating pad.

From a ventral approach most of the ventral and lateral surface of one auditory bulla was uncovered. The bulla was opened and the bony septum removed. The chorda tympani nerve was cut, and the styloid projection[5] bent posteriorly so that the incudo-stapedial joint and the ventro-lateral part of the stapes could be seen (Fig. 1). The stapes was sprayed with small particles of silver, which served as discrete points for displacement measurements.[6] In some cases during the experiment, it was necessary to aspirate fluid that collected in the bottom (dorsal surface) of the middle-ear cavity.

To check the sensitivity of each ear, electrical responses to clicks were recorded from a wire placed near the round window. The threshold for detecting the N_1 response component was determined for every animal (except Cat 10). Data from ears with thresholds more than 10 dB above the median have not been included in this report. The resulting range of threshold is from 10 dB below (the lowest obtained) to 10 dB above the median.

In a few instances, we observed apparently spontaneous contractions of the stapedius muscle. The head of the stapes was abruptly pulled posteriorly, while the incus remained relatively stationary and the articulating surfaces of the incus and stapes slid across each other in an anterior–posterior direction. In some of these cases, a light stroking on the inside of the pinna evoked both a twitch of the pinna and a stapedius contraction. When these contractions were observed, or if by other signs (e.g., a withdrawal reflex when pinching a toe) we judged the animal to be lightly anesthetized, an additional dose of 20–40 mg Dial was given. This invariably eliminated the stapedius contractions.

B. Acoustic System (See Fig. 2)

The external auditory meati were cut off approximately 5 mm from the skull. An ear bar on one side held a probe-tube assembly in place so that one end of the tube was within a few millimeters of the drum membrane. A condenser microphone monitored the sound pressure at the other end of the probe tube. The probe-tube assembly was similar to that described by Kiang.[7] The sound source (a Jensen Hypex DD-100) was connected by a tube $\approx$2 cm long to the probe-tube assembly. The input to the power amplifier was varied with a step attenuator in 1-dB steps. When the cat's ear was replaced by a rigid cavity, this system could produce tones from 30 to 10 000 Hz with SPL's of up to 150 dB SPL[8] with no gross distortion apparent in the sound-pressure waveform displayed on an oscilloscope. When the system was terminated by a cat ear, however, distortion was often apparent at SPL's of less than 150 dB.

The SPL at the tympanic membrane was computed from: (1) the root-mean-square output of the microphone amplifier, (2) the gain of the microphone-amplifier system (3) the absolute sensitivity of the micro-

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[4] Møller (1963); von Békésy (1960), pp. 53–57; Fischler, Frei, Rubinstein, and Spira (1964); Hoeft, Ackerman, and Anthony (1964).

[5] For a drawing of the anatomy of this region, see C. E. Blevins (1964).

[6] See von Békésy (1960), p. 38.

[7] See Kiang (1965), p. 5.

[8] All SPL's are given in decibels *re* 0.0002 dyn/cm^2.

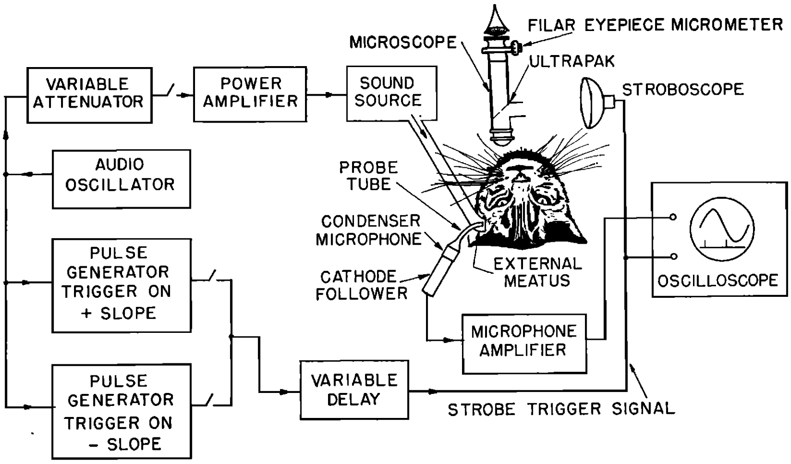

Fig. 2. Schematic drawing of the experimental equipment.

phone at the probe tube, and (4) a measured correction for the probe tube.

C. Optical System

The sinusoidal signal that supplied the input for the acoustic system also triggered two pulse generators whose outputs were adjusted to be a half-cycle apart. After passing through a variable delay unit, these two pulse trains were used to trigger the stroboscope (General Radio 1531-A Strobotac). If only one of the pulse trains was turned on, the "strobe" flashed once each cycle; if both were on, the strobe flashed twice each cycle. A pulse generator was included in the system, which prevented triggering of the strobe above its specified maximum rate (600/sec). Hence, at frequencies above 300 Hz, the strobe flashed every $n/2$ cycles (n odd) when both switches were on.

The strobe reflector was fitted with a condensing lens that directed the light into the "ultrapak" of a Leitz monocular microscope. The ultrapak system illuminates the field of the microscope through an arrangement of a mirror and lenses that are concentric with the main optics of the microscope. It was possible, in most cases, to bring an 11× objective lens (lens to object distance ≈ 5 mm) into focus on the stapes. (The objective was heated electrically to prevent condensation of moisture on the lens.) The ocular lens was a filar eyepiece micrometer with a magnification of 12.5. By addition of a vernier scale, the position of the hairline could be read to an accuracy corresponding to 0.042 μ in the focal plane of the microscope with the 11× objective.

Since the hairline could be set over a point most accurately when the particle diameter was approximately equal to the hairline width, we ground the silver particles (between two pieces of paper) to obtain a large number of particles $\approx 2\,\mu$ in diameter. (The thickness of the hairline was equivalent to 1.7 μ with the 11× objective.) The particles were scraped off the paper with a hypodermic needle and sprayed onto the stapes.

The "fine-focus" control on the microscope was calibrated so that we could measure distances along the optical axis by reading the position of the control when certain parts of the field were in focus.

D. Procedure for Measuring Phase Angle and Direction of Displacement

With a tone on, the middle ear was illuminated twice each cycle. The observer varied the delay of the strobe flashes while he observed a small silver particle. If the SPL was high enough, each small silver particle appeared as two spots (Fig. 3). By varying the delay of the trigger pulses, the observer adjusted the two spots for maximum separation or for minimum (no) separation. The resulting delay was read from an oscilloscope by a second experimenter. Our standard procedure was to repeat the adjustments for maximum and minimum five times each. In general, the difference between the average readings for maximum and minimum separation was $90° \pm 4°$. For subsequent measurements, the delay was set for maximum separation at a value determined from an average of these readings. With the timing set at this value, the eyepiece of the microscope was rotated and the hairline adjusted until it intersected both spots. The direction of the displacement in the focal plane was read from a protractor which had been fitted to the eyepiece. This setting was done twice for each frequency and was usually repeatable within $\pm 2°$.

Since the smallest silver particles that could be clearly seen were a few microns in diameter, separation into two spots did not occur for peak-to-peak displacements of less than a few microns. In these cases (almost all measurements above 3000 Hz), displacement direction could not be measured and phase was determined

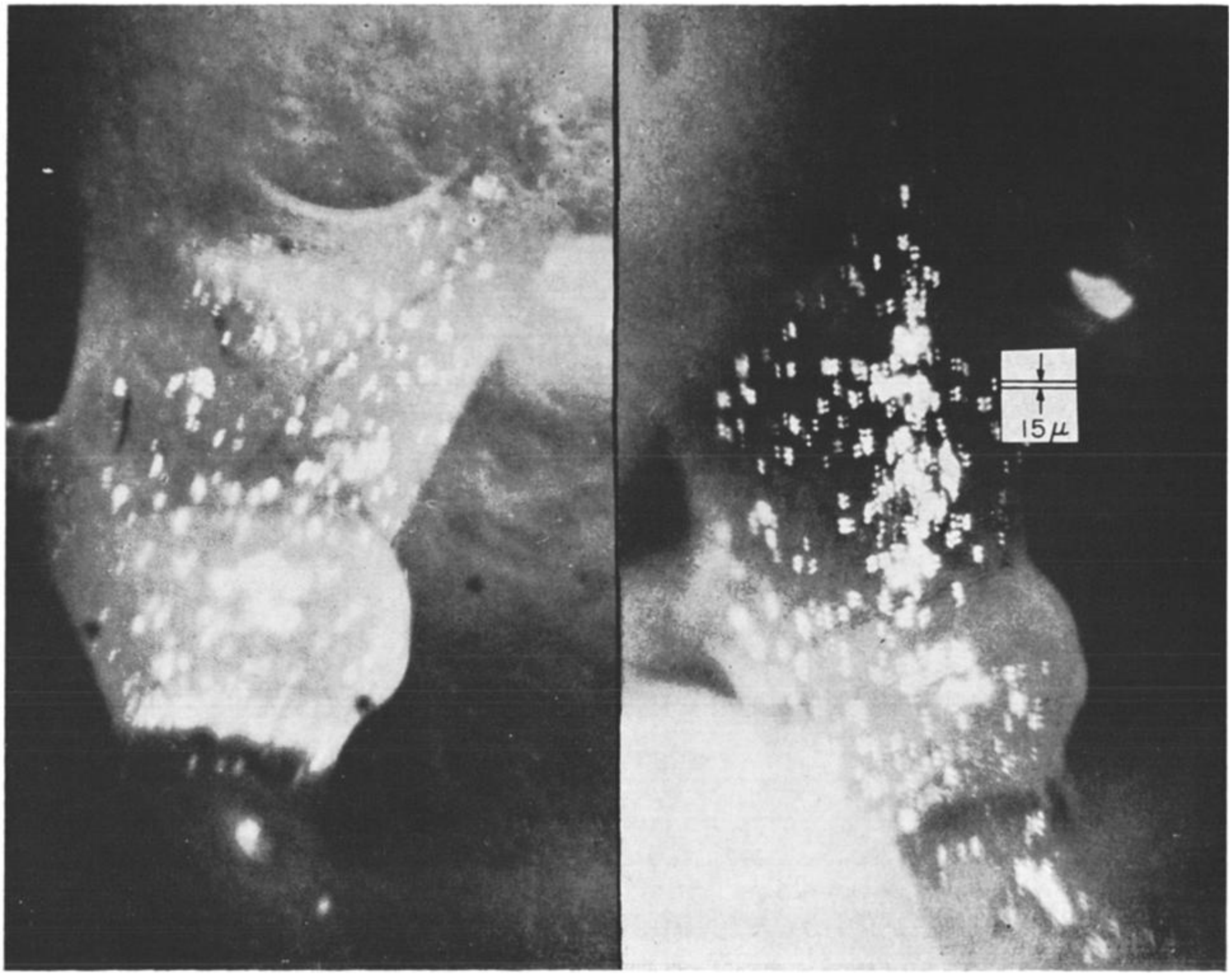

FIG. 3. Photographs of the stapes illustrating its appearance when illuminated twice each cycle. *Left*: Microscope Orientation 1. In this picture, the orientation of the stapes is similar to that of Fig. 1. *Right*: Microscope Orientation 2. View from a more anterior position. Note that the small light spots (e.g., the two at the left ends of the 15-μ calibration lines) occur in pairs that are separated by the peak-to-peak displacement amplitudes. SPL: 140 dB. Frequency: 300 Hz (Cat 32).

by the following method. The hairline was oriented perpendicular to the direction of motion that had been determined with larger displacements (i.e., at lower frequencies). With the strobe flashing *once* each cycle, the hairline was placed next to or partially over a silver particle. By manipulating both the variable delay and the hairline, the observer could determine when the spot was at an extreme position in one direction or the other. In our standard procedure, the observer made five settings for the most lateral position and five settings for the most medial position. The averages obtained from these settings usually differed by 180°±5°. For very small displacements (at high frequencies), the error was sometimes as much as 20°. The delay for subsequent measurements was set at a value determined from an average of these readings.

The phase difference between the stapes displacement and the sound pressure at the drum membrane was calculated from: (1) the phase of the strobe trigger pulses relative to the microphone amplifier output (read from an oscilloscope), (2) a correction for phase shift in the probe tube, (3) a correction for the phase shift in the microphone and microphone amplifier, and (4) a correction for the delay between the strobe trigger pulse and the light flash. The corrections were determined experimentally and have been included in the results presented here.

E. Procedure for Measuring Displacement Magnitude

After the phase measurement was made, the variable delay was set so that the middle ear was illuminated at the two times during the cycle when the silver particles (and the ossicles) were at their extreme positions. The eyepiece was rotated so that the hairline was perpendicular to the displacement. One of the pulse-generator outputs was then turned off. The observer aligned the hairline over the chosen spot and read its position from the drum and vernier. The second experimenter then reversed the switches, thereby illuminating the particle at the other extreme, and the observer aligned the hairline over the spot again. The difference between these two readings gave the peak-to-peak amplitude of the displacement. Usually we repeated each of these readings five times and computed the average difference. When the motion was very small, 10 pairs of position readings were taken. The experimenter who operated the switches attempted to randomize the order of presentation, so that the observer would not know which position he was measuring.

It was found that under the best conditions (i.e., a silver particle of the proper size with good illumination and focus), the observer could position the hairline over a spot with an accuracy that was equivalent to a small fraction of a micron in the focal plane of the microscope. Since the judgment involved the location of a spot with a diameter of a few microns relative to a line of nearly the same thickness (in the eye of the observer), the setting did not involve *resolution* of objects as small as the wavelength of light.

The accuracy of the measurements varied considerably from preparation to preparation and with time on the same preparation, depending on: (1) illumination, (2) size of silver particles, (3) the visual acuity and aligning ability of the observer, and (4) the amount of movement of the cat's head. (Motion of the head resulting from breathing was considerably reduced by ear bars and a snout clamp that held the skull firmly. Motion of the ossicles resulting from building vibrations were reduced by performing the experiments with the animal and microscope on a heavy shock-mounted table in a vibration-isolated chamber.)

When the stroboscope flashed, it produced a rather loud "ping" at approximately 7000 Hz. Measurements of the cochlear potentials in response to this "ping" indicated that, at most, it was equivalent to a 80-dB 7000-Hz tone pip in the external meatus. The ossicular motion in response to this sound is very small compared with the motions we measured.

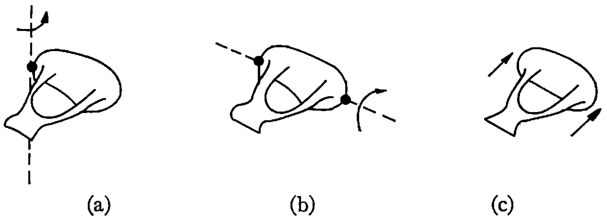

Fig. 4. Modes of vibration of the stapes; the dashed lines represent axes of rotation. (a) Rotation about an axis through the posterior end of the footplate. This mode was observed by von Békésy in cadavers with very-low-frequency stimulation and SPL's below the threshol d of feeling. (b) Rotation about the long axis of the footplate as observed by von Békésy at SPL's above the threshold of feeling. (c) "Pistonlike" motion such as we have observed in cats for stimuli below 140 dB. (a) and (b) after von Békésy (1960, p. 113).

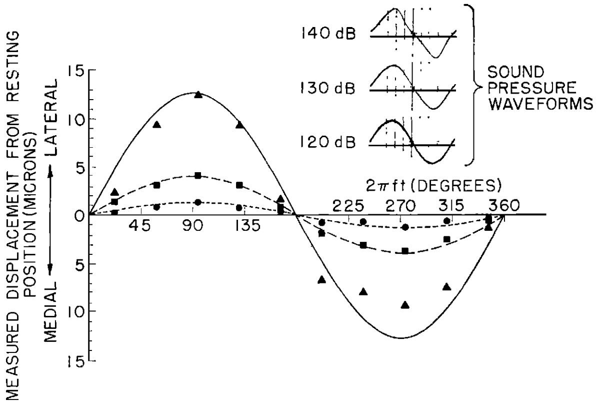

Fig. 5. Stapes displacement and sound-pressure waveforms for Cat 31. Triangles, squares, and circles represent optical measurements of stapes displacement: 140, 130, and 120 dB, respectively. Superimposed on these points are three sinusoids whose amplitudes differ in 10-dB steps. The amplitude and the time origin were chosen so that the dashed curves would fit the 120- and 130-dB data points. Upper right photographs represent the output of the probe-tube microphone. $f=300$ Hz.

Since our method of measuring displacement was quite time consuming, the experimental measurements often lasted a long time (up to 36 h). Although repeated displacement measurements for a given stimulus condition often showed a gradual decrease (see Fig. 12), the net decrease was seldom more than 3 dB over the whole experiment.

II. RESULTS

A. Gross Observations

In preliminary observations, we viewed the ossicles through a binocular operating microscope (Zeiss "Otoscope" 302393) with a relatively low magnification (40× or less). The stroboscope was adjusted to flash at a frequency of a few Hertz above or below the stimulus frequency so that the motion appeared to be at the difference frequency. Under these conditions, the motions of the tympanic membrane and the ossicles were large enough to be seen when the SPL was over 130 dB and the frequency below 5000 Hz.

Below 140–150 dB, the three bones appeared to rotate as a single rigid body with an axis of rotation oriented in an anterior–posterior direction. The position of the axis could not be judged accurately, but our observations were consistent with observations on cadavers that the axis runs from the anterior ligament of the malleus through the short process and the posterior ligament of the incus.[9] The stapes appeared to move in and out of the cochlea as a piston with little

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[9] Dahmann (1929); von Békésy (1960), p. 102; Kobrak (1959), p. 41; Kirikae (1960), p. 98.

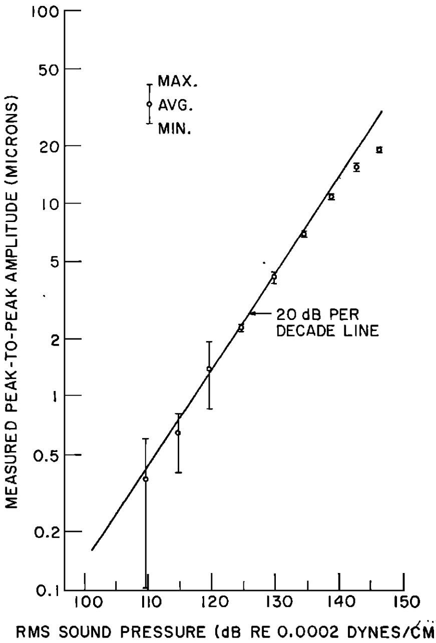

FIG. 6. Stapes displacement versus SPL for Cat 10. Each point represents the average of 5–10 measurements. Range of measurements is indicated by a vertical line. Stimulus frequency: 315 Hz.

if any rocking. Detailed measurements (see Sec. II-C) were made to verify this latter observation since, as illustrated in Fig. 4, it disagrees with results on cadavers.[10]

We found three exceptions to the otherwise "rigid-body" motion of the ossicles: (1) At SPL's of above 150 dB, the incudo-stapedial joint stretches during rarefaction and compresses while slipping sideways during condensation, and the stapes shows appreciable rocking in addition to its pistonlike movement. (2) At frequencies of above 3000 Hz, the movement of the drum membrane becomes quite complicated.[11] (3) Also at high frequencies, relative motion was detected between the incus and the malleus which was not apparent in the gross observations (described in detail in Sec. II-F).

B. Linearity

Our first objective was to determine the ranges of stimulus frequency and SPL in which middle-ear displacement is linearly related to sound pressure. In one experiment, we measured the displacement of a point on the stapes as a function of the timing of the strobe flash. In the resulting plot (Fig. 5), the stapes movement is a sinusoidal function of time for sinusoidal sound pressure.

Figure 5 also indicates that the stapes displacement changes in amplitude by 10 dB when the sound pressure is raised from 120 to 130 dB. At 140 dB, both the stapes displacement and the sound-pressure waveforms deviate appreciably from sinusoidal. During the rarefaction phase, the stapes moves laterally (out of the cochlea) farther than it moves medially (into the cochlea) during the condensation phase. This asymmetry of ossicular displacement at high input pressures and low frequencies is similar to observations made on cadavers (Dahmann, 1929; Kobrak, 1948).

We usually measured only the peak-to-peak amplitude of the stapes displacement without verifying that its waveform was sinusoidal. In several cases we measured amplitude over as wide a range of SPL as possible. These measurements indicate that for frequencies below 1500 Hz the system is linear at least up to 130 dB SPL. For higher frequencies, the linear range often extended up to 140 or 150 dB. Figure 6 is an example of these data.

C. Mode of Stapes Motion

To evaluate in detail our impression that the stapes motion is pistonlike, we made a series of measurements with the monocular microscope. These measurements were intended to answer the questions: (1) is the motion purely translational, and (2) if the motion is purely translational, what is the direction of the displacement?

To answer the first question, we measured the motion of three or more noncolinear points on the stapes. We assumed that the motion of a single point is sinusoidal and approximately along a straight line. The motion of a point can therefore be characterized by its direction, amplitude, and phase. We found that the phase did not vary from point to point, so in general, it was measured at only one point. Let us define $\mathbf{i}_s$ as a unit vector pointing in the direction of the displacement of a point on the stapes, $\mathbf{s}=|\mathbf{s}|\mathbf{i}_s$ as the peak-to-peak displacement vector of a point on the stapes, $\mathbf{i}_p$ as a unit vector pointing in the direction of the projection of $\mathbf{s}$ onto the focal plane of the microscope, and $\mathbf{p}=|\mathbf{p}|\mathbf{i}_p$ as the projection of $\mathbf{s}$ onto the focal plane.

We wish to determine $\mathbf{s}$; we are restricted to measuring angles and amplitudes in the focal plane of the microscope, therefore we can only measure $\mathbf{p}$. If we measure $\mathbf{p}$ for two orientations of the microscope, however, we can combine these data to determine $\mathbf{s}$. The method of combining data is given in Appendix *A*. Briefly, the two measured $\mathbf{i}_p$ (from two microscope orientations) were combined to give $\mathbf{i}_s$. Each $|\mathbf{p}|$ was then used to calculate a displacement amplitude $|\mathbf{s}|$ in the previously determined direction $\mathbf{i}_s$. This was done for several points on the stapes so that, for each point, we obtained one direction $\mathbf{i}_s$ and two amplitude determinations $|\mathbf{s}|$.

Figure 7 illustates the results of one such calculation. Part A of this figure gives the displacement directions $\mathbf{i}_s$ of the four points on the stapes. Part B gives $|\mathbf{s}|$ and

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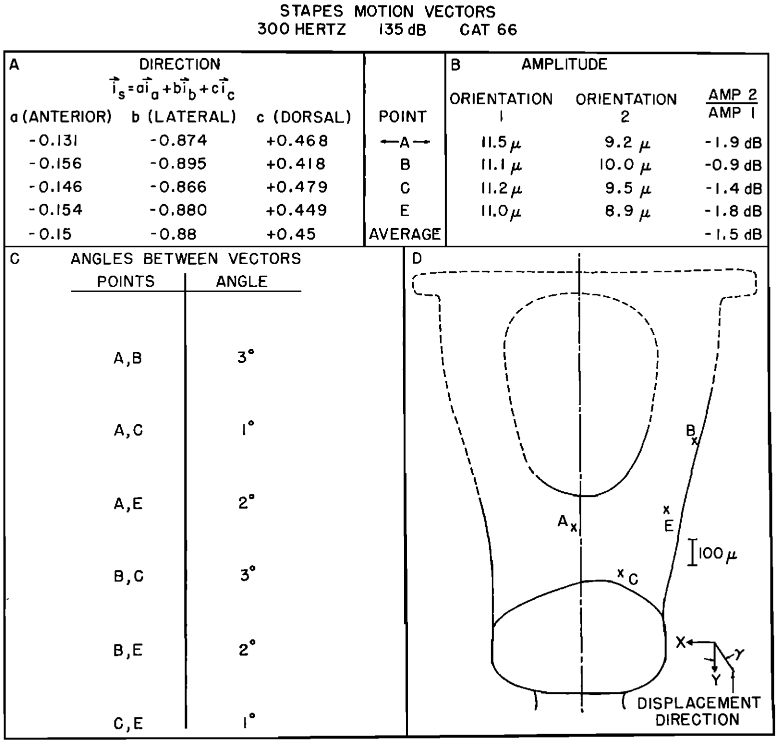
[10] See von Békésy (1960), p. 113.

[11] As has been observed by von Békésy (1960), pp. 101–102.



STAPES MOTION VECTORS
300 HERTZ 135 dB CAT 66

A DIRECTION $\vec{i}_s = a\vec{i}_a + b\vec{i}_b + c\vec{i}_c$

B AMPLITUDE

a (ANTERIOR)	b (LATERAL)	c (DORSAL)	POINT	ORIENTATION 1	ORIENTATION 2	$\frac{\text{AMP 2}}{\text{AMP 1}}$
-0.131	-0.874	+0.468	←A→	11.5 μ	9.2 μ	-1.9 dB
-0.156	-0.895	+0.418	B	11.1 μ	10.0 μ	-0.9 dB
-0.146	-0.866	+0.479	C	11.2 μ	9.5 μ	-1.4 dB
-0.154	-0.880	+0.449	E	11.0 μ	8.9 μ	-1.8 dB
-0.15	-0.88	+0.45	AVERAGE			-1.5 dB

C ANGLES BETWEEN VECTORS

POINTS	ANGLE
A,B	3°
A,C	1°
A,E	2°
B,C	3°
B,E	2°
C,E	1°

FIG. 7. Three-dimensional displacement of four points on the stapes. Locations of the points are indicated by x's in D. The solid outline represents the portion of stapes visible from the first microscope orientation; the dashed outline represents the rest of the stapes and was derived from pictures of excised stapes. The dot–dashed line is the projection of the center line determined by visual inspection. In A, the direction of motion of each point is represented by a unit vector $\mathbf{i}_s$. The angles between these vectors, e.g., $\cos^{-1}(\mathbf{i}_{sA}\cdot\mathbf{i}_{sB})=3°$, are shown in C. Peak-to-peak displacement amplitudes $|\mathbf{s}|$ (each in the direction of the unit vector listed in A) are given in B as determined from amplitude measurements $|\mathbf{p}_1|$ and $|\mathbf{p}_2|$, made from each microscope orientation. The ratios of the amplitudes are shown in the right-hand column of B. The vectors, the differences in amplitude from one point to another, and the location of the points on the stapes are typical of all of our data. The ratio AMP 2/AMP 1 is greater than usual (see Col. 6 of Table I). Part of this amplitude difference may be attributed to the slow decrease in middle-ear mobility mentioned previously. Approximately 5 h elapsed between the measurements in Orientation 1 and those in Orientation 2.

TABLE I. The direction of the stapes motion relative to its center line.[a]

1	2	3	4	5	6	7	8	9	10	11	12	13
Cat	Frequency (Hz)	SPL (dB)	No. of points	$\cos^{-1}$ $\times(\mathbf{i}_{Z1}\cdot\mathbf{i}_{Z2})$	$\frac{\text{AMP 2}}{\text{AMP 1}}$ (dB)	$\mathbf{i}_s=a\mathbf{i}_a+b\mathbf{i}_b+c\mathbf{i}_c$ a	b	c	θ	$\theta+\phi$	ϕ	γ
32	300	130	1	37°	−2	−0.19	−0.80	+0.56	27°	41°	+14°	−8°
37	300	140	1	39°	0	−0.04	−0.92	+0.39	26°	38°	+12°	+0°
57	30	129	4	57°	0	−0.09	−0.98	+0.12	38°	30°	−8°	−4°
57	3000	136	4	57°	+2	−0.11	−0.98	+0.12	38°	29°	−9°	−3°
66	30	134	4	45°	−2	−0.16	−0.89	+0.43	47°	49°	+2°	−1°
66	300	134	4	45°	−2	−0.15	−0.88	+0.45	47°	50°	+3°	+0°
66	3000	138	4	45°	−1	−0.13	−0.89	+0.44	47°	50°	+3°	−1°
Av.											+2°	−2°

[a] Columns 1, 2, 3, and 4 give cat number, frequency, SPL's, and number of points on the stapes that were used for the direction determinations. Measurements were made from two microscope orientations; Column 5 gives the angle between the two optical axes. Column 6 gives the ratio of the amplitude $|\mathbf{s}|$ derived from measurements in the second orientation to the amplitude derived from the first orientation. Columns 7, 8, and 9 are the components of the stapes displacement vector in the anterior, lateral, and dorsal directions, respectively. Columns 6–9 are averaged across the number of points indicated in Column 4 (see Fig. 7 for an example of the averaging procedure). Column 10 gives the angle θ between the centerline and the Y axis of the microscope (see Fig. 8). Column 11 gives the angle $(\theta+\phi)=\cos^{-1}(\mathbf{i}_s\cdot\mathbf{i}_y)$ between the motion and Y axis. Column 12 gives the angle ϕ between the motion and the center line in the (approximately) transverse plane. Column 13 gives the angle γ, the projection of the angle between the motion and the center line into the focal plane of the first microscope orientation.

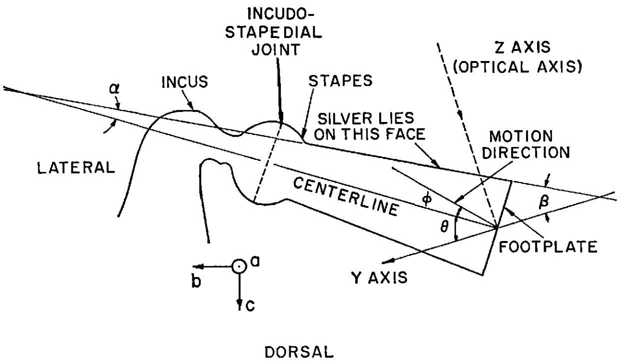


FIG. 8. Side-view sketch (in an approximately transverse plane) of the stapes, indicating the geometric relations involved in the calculations of stapes motion.

the ratio of the second value to the first. Part C gives the angle between each pair of displacement directions indicated in Part A. From these results, we conclude that, within the accuracy of our measurements, all the points move in the same direction (Part C) with the same amplitude (Part B). Similar measurements made on four cats (as listed in Table I) support this conclusion.

Since the footplate of the stapes was not normally visible when we made our measurements, it might have been possible for the displacement of the footplate to differ from the displacement of points on the head of the stapes. For this to occur, the crura would have to deform in some way, and the stapes would not be moving as a rigid body. Two observations indicated that the stapes *is* rigid under the conditions of our experiments. (1) In two cats, part of the ventral wall of the vestibule was removed to expose the stapes footplate. Even with sound pressure levels that produced visible flexing of the incudo-stapedial joint, points on the footplate and head of the stapes moved in phase, in the same direction, and with essentially equal amplitudes. There was no evidence of lack of rigidity. Since removal of the fluid behind the footplate undoubtedly changes the distribution of mechanical loading, these observations cannot be considered to be a conclusive test of rigidity. (2) In one cat in which the view of the stapes was relatively unobstructed, we were able to make measurements on a point located on the footplate with the cochlea intact. The displacement of this point was equal in amplitude and direction to that of points on the head and body. Hence, this observation confirmed that the stapes moves as a single rigid body.

To a first approximation, then, *the stapes moves as a rigid body in pure translation.*

Next, we consider the direction of the stapes motion relative to its center line. Let us define the center line as running through the center of the head to the center of the footplate, approximately perpendicular to the footplate. It is convenient to define a coordinate system Z, Y, X, with directions given by $\mathbf{i}_Z$, a unit vector along the optical axis of the microscope pointing approximately dorsally; $\mathbf{i}_Y$, a unit vector along the projection of the stapes center line in the focal plane of the microscope pointing approximately laterally (left), and $\mathbf{i}_X=\mathbf{i}_Y\times\mathbf{i}_Z$ (vector product).

The usual orientation of the microscope (Orientation No. 1 whenever we used two microscope orientations) was such that $\mathbf{i}_Z$ was almost perpendicular to the long axis of the footplate (i.e., approximately in a transverse plane pointing dorsomedially). We visually determined the Y axis ($\mathbf{i}_Y$) by picking a line that appeared to be in the center of as much of the stapes as could be seen (e.g., as in Fig. 7D). The Y axis is $\theta°$ from the actual center line as is shown in the "side view" of Fig. 8. θ was determined by adding the angles α and β shown in Fig. 8. The angle α, between the vertical face of the stapes and its center line, was obtained by taking half the angle between the dorsal and ventral faces measured on three excised stapes. The values were 3°, 4.5°, and 7°. We used the average value $\alpha_{\text{av}}=5°$ in our determination of θ. The angle β, between the ventral face of the stapes and the Y axis, was determined by measuring the X, Y, and Z positions of the silver particles on the ventral face of the stapes. A graph of one set of these measurements is shown in Fig. 9, together with a sketch showing the position of the silver particles on the stapes. Some representative values of $\theta=\alpha_{\text{av}}+\beta$, are given in Table I. Since by definition, the center line is in the YZ plane, its position is completely specified by the angle θ.

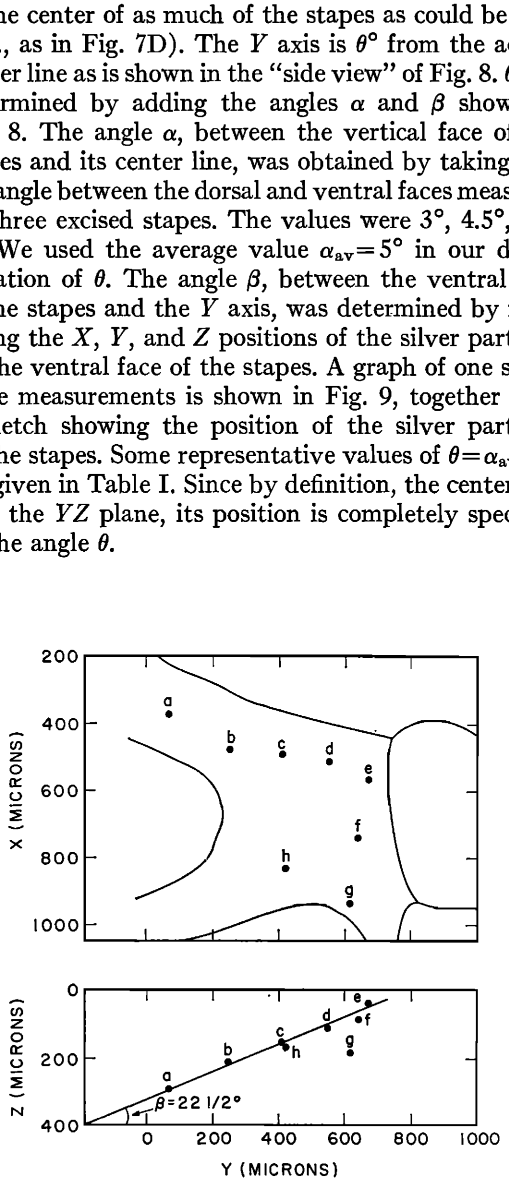


FIG. 9. Method of determining β. Potitions of eight points on the stapes were measured in three dimensions. Distances along X and Y were measured with the filar eyepiece micrometer and along Z with the calibrated fine-focus control. The angle β is determined from the line drawn through the points. The fact that the points in the lower graph lie approximately on a straight line indicates that the face of the stapes is approximately planar and, in this case, parallel to the X axis.

Let us now consider the direction of the stapes displacement relative to the center line. The angle ϕ between the center line and the motion direction in the "side view" of Fig. 8 was obtained from

$$\phi\approx\cos^{-1}(\mathbf{i}_s\cdot\mathbf{i}_y)-\theta=(\phi+\theta)-\theta. \qquad (1)$$

Table I gives $(\phi+\theta)$ and ϕ (averaged across points on the stapes) for several frequencies on several cats (each measured at a SPL that was in the linear range). The average value of ϕ (Table I) is not significantly different from zero. Hence, the displacement as observed in a transverse plane is (on the average) approximately along the center line.

Next, we would like to know the angle δ between the motion and the center line in the plane determined by the center line and the long axis of the footplate; however, the focal plane of the microscope is $\theta°$ from this plane. Since ϕ is negligibly small and θ is substantially less than 90°, it will suffice to find the angle γ (see Fig. 7, Part D), the projection of δ onto the focal plane of the microscope. If γ is small, δ must also be small. We determined γ either by direct measurements on the animal or by measurements made on photographs such as the left-hand photograph in Fig. 3. The value of γ is given in Table I for each case in which we determined ϕ. As with ϕ, the average γ is not significantly different from zero. Therefore the stapes displacement is essentially along the center line, and the *motion is not only translational, but also "pistonlike."*

Since it was possible that the motion of the stapes with the middle-ear cavities closed could have been quite different from that with the bulla and bony septum open, we made visual measurements of stapes motion through a glass window that was sealed into the bulla. The bony septum had been removed through the opening in the bulla. Measurements at frequencies from 30 to 2000 Hz on three cats indicated that the direction of the stapes displacement changed less than 2° when the bulla was closed and the displacements of of all points on the stapes were in the same direction. At low frequencies, the amplitude of the displacement was reduced approximately 5 dB with the window in; the phase of the displacement relative to sound pressure was not changed appreciably. These data agree with our measurements on the effect of closing the bulla, based on cochlear potentials and are treated in more detail in Sec. II-G. The pertinent point here is that no substantial change in the mechanical mode of vibration of the stapes was observed with the bulla closed.

Since all the published observations of stapes motion in human middle ears have been made on cadavers, we measured stapes motion after death in two cats to determine if large changes took place. In both cases, the displacement amplitude decreased after death and the size of the decrease depended on frequency. Studies of cadaver middle ears[12] emphasize the importance of keeping the ear moist in order to maintain its mobility. Our measurements also indicated large differences between displacements in wet and dry ears. However, wet or dry, the direction of the displacement changed less than 5° after death. It seems clear that the motion of the cat's stapes remains predominantly pistonlike for at least several hours after death.

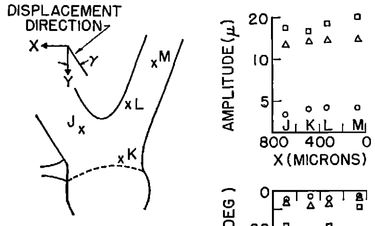


FIG. 10. Peak-to-peak amplitudes and direction angles of the displacements of four points vs position of the points on the stapes. Cat 14. □: 157 dB SPL. △: 147 dB SPL. ○: 137 dB SPL. $f=300$ Hz.

For sound pressures high enough to drive the ossicles out of the linear range, the motion of the stapes has components in addition to pistonlike translation. The measurements plotted in Fig. 10 indicate the changes in direction and amplitude of motion in one case. At 137 and 147 dB SPL, there are only small differences in the directions and amplitudes of displacement from point to point; however, at 157 dB, the angles have changed and the differences are larger, which indicates that the rotational components have increased relative to the translational component. Since we have few data of this kind, we cannot describe the motion completely. It seems clear, however, that for SPL's above the linear range, the motion of the stapes is no longer entirely pistonlike.

D. From Linear Displacement to Volume Displacement

Figure 11 shows the dimensions of the stapes footplate in histological preparations. (This figure is also intended to display the shape of the annular ligament and is referred to again in Sec. III-A.) The footplate area was measured on four excised dry stapes, one of which had also been measured before it dried. From the four "dry" areas (1.22, 1.18, 1.14, and 1.17 mm^2) and the measured shrinkage factor (0.94), we calculate an average "wet" area of 1.26 mm^2. This figure agrees quite well with the results of Wever, Lawrence, and Smith (1948).

We determined the linear displacement amplitude $|\mathbf{s}|$ by dividing the projected amplitude in the focal plane $|\mathbf{p}|$ by the cosine of the average angle $(\theta+\phi)_{\text{av}}$ between the displacement direction and the measurement axis (see Fig. 8). For $(\theta+\phi)_{\text{av}}$, we used the sum of the average θ and the average ϕ (averaged across all cases in which

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[12] von Békésy (1960), pp. 91–102; Onchi (1961); Rubinstein, Feldman, Fischler, Frei, and Spira (1967).

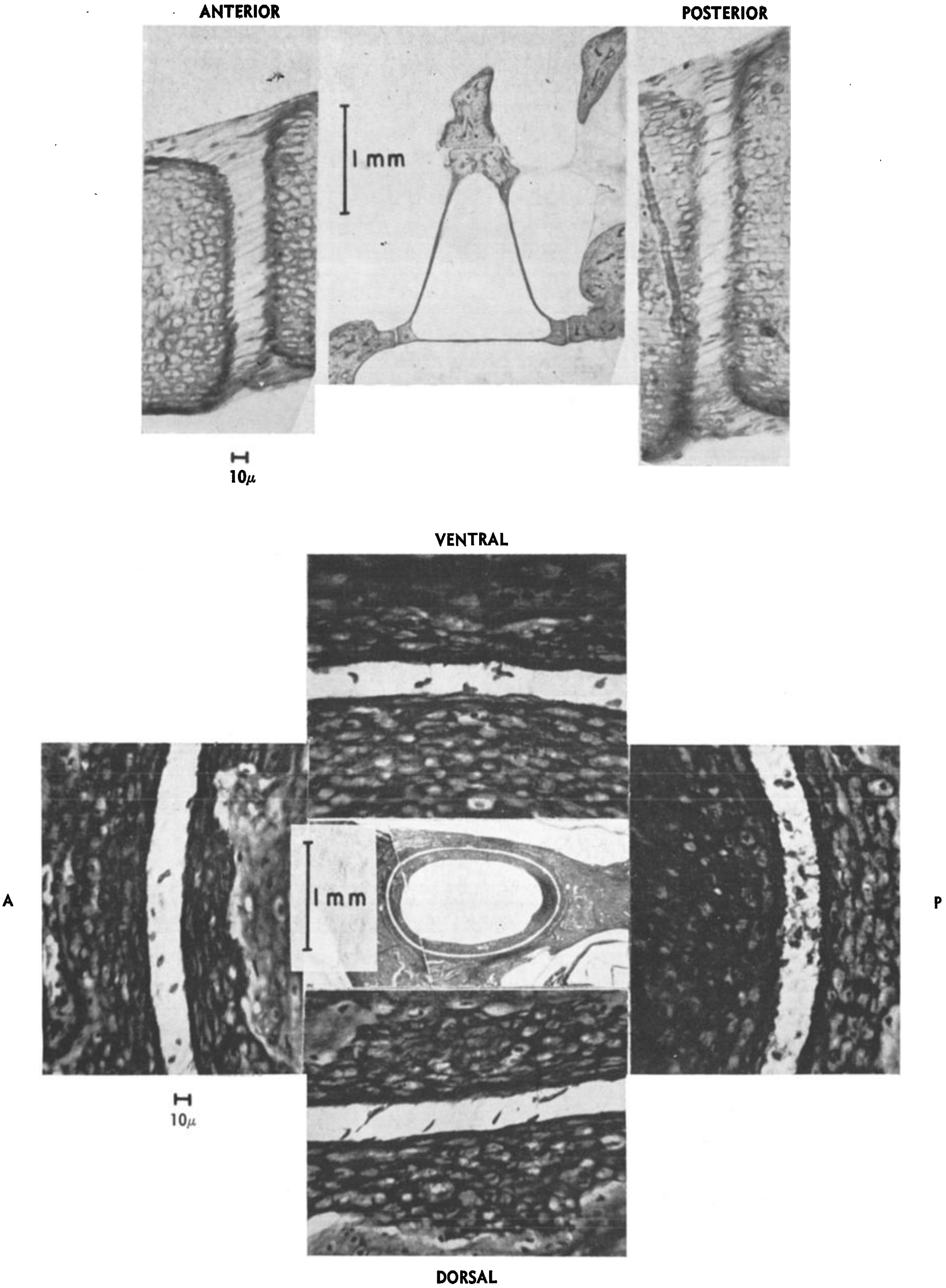

FIG. 11. Photomicrographs of sections through the stapes in two perpendicular planes. *Upper:* The center photograph was made from a section in a roughly horizontal plane showing the stapes from the footplate (bottom) to the incudo-stapedial joint. Photographs at right and left were made from the same section at higher magnification to show the annular ligament in detail at the anterior and

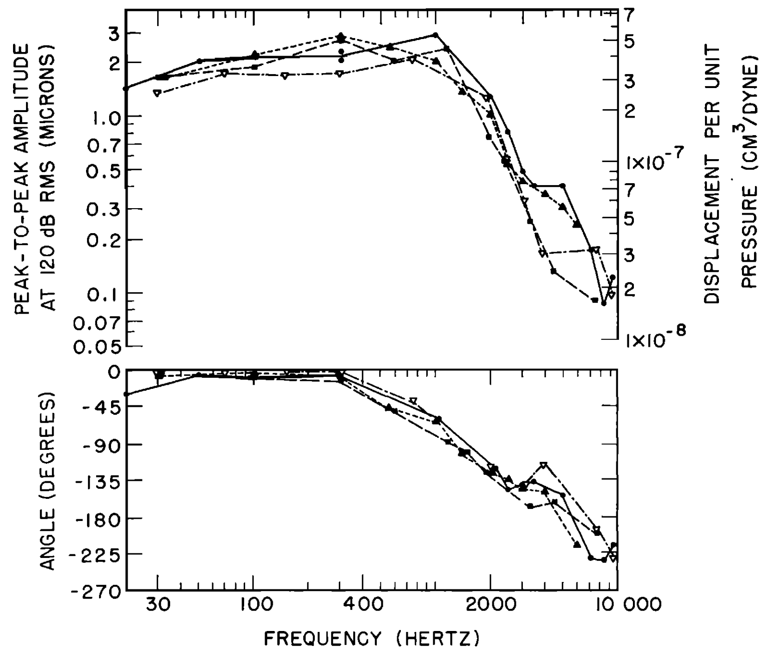

FIG. 12. Middle-ear transfer characteristics for the four cats on which measurements were made at the largest number of frequencies. It took between 12 and 32 h to take the data for each cat. For Cat 30, the decrease in amplitude from the beginning to the end of the experiment is indicated by the two dots at 300 Hz. In this case, the readings were taken 16 h apart. ▽- — -▽: Cat 19. ■- -■: Cat 20. ▲- - - -▲: Cat 28. ●——●: Cat 30.

we have measured them). θ was measured on 11 cats; it varied from 19° to 47° with an average of 31°. ϕ was measured in seven cases (four cats); it varied from $-9°$ to $+14°$ and averaged $+2°$ (see Table I). The "projection angle" correction is therefore

$$1/\cos(\theta+\phi)_{\mathrm{av}}=1/\cos 33°=1.2.$$

If we consider the extremes of the measured values for both θ and ϕ, we obtain extreme values of 10° and 61° for $(\theta+\phi)$. These give projection-angle corrections of 1.0 and 2.1, respectively. Hence the use of the same correction for all cats may contribute an apparent intercat difference to our results ranging over approximately 6 dB.

Since the motion of the stapes is pistonlike, the volume displacement is the product of its linear displacement and the area of the footplate. We have used the average footplate area of 1.26 mm² and the average projection-angle correction of 1.2 to get the volume displacement for *all* transfer characteristics plotted subsequently.

E. Transfer Characteristic

If the middle ear acts as a linear system, the stapes displacement will be a sinusoidal function of time for sinusoidal sound pressures, that is,

$$x_s(t)=|X_s|\cos(2\pi ft+\lambda), \tag{2}$$

when

$$p_d(t)=|P_d|\cos 2\pi ft, \tag{3}$$

where $x_s(t)$ is stapes displacement, X_s is complex amplitude of the stapes displacement,[13] $p_d(t)$ is sound pressure at the drum membrane, P_d is complex amplitude of the sound pressure, f is frequency, t is time, and λ is phase angle by which x_s leads p_d. The relationship of x_s and p_d can be described by a complex function of frequency, the transfer characteristic

$$H(f)=X_s/P_d=(|X_s|/|P_d|)\epsilon^{j\lambda}. \tag{4}$$

Our measurements indicate that the middle ear acts as a linear system for most of SPL's that animals are likely to encounter. (Note that the action of the middle-ear muscles may modify this situation in unanesthetized animals.) Much of the middle ear's performance can therefore be summarized by a transfer characteristic. We have determined this transfer characteristic

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[13] Since we are no longer using vector quantities and we wish to use complex quantities, a different notation is used. Note that $2|X_s|=|s|$.

posterior ends of the footplate (Heidenhain-Susa fixed, hematoxylin and eosin stained, celloidin sections, Slide No. KRP 63-100) *Lower:* these figures were made from sections in a roughly parasagittal plane intended to be parallel to the stapes footplate. Center picture is a composite of photographs from two sections, 160 μ apart. The composite was made so that it represents the central region of the ligament (i.e., that part in which the edge of the footplate and the petrous bone are relatively straight and parallel). The four photographs surrounding this composite were made from the same two sections to show the annular ligament at higher magnification (10% potassium dichromate fixed, Protargol stained, paraffin sections. Slides No. BW 48L 4–1 and 4–9).

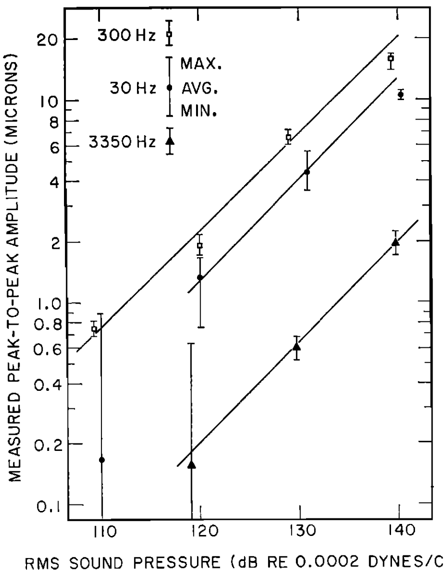


FIG. 13. Stapes displacement amplitude vs SPL for three frequencies for Cat 20. Each point represents the average of 5–10 measurements. The range of individual measurements is indicated by the vertical lines. The three sloping lines represent a linear dependence of amplitude on SPL; they were drawn to fit the three sets of points. These are projected amplitudes $|\mathbf{p}|$.

by measuring the magnitude $|H|=|X_s|/|P_d|$ and the angle λ of the complex function $H(f)$.

The transfer characteristics of four cats are shown in Fig. 12. Each point in the top half of the figure was obtained by measuring $|X_s|$ at two or more values of $|P_d|$. If the measured change in $|X_s|$ at *two* values of $|P_d|$ was within 1 dB of the change in $|P_d|$, the data were judged usable. Except where otherwise specified, all data in this paper represent measurements for which we have this indication of approximately linear behavior. Some examples of data that were judged to be usable are given in Fig. 13. This figure shows projected displacement amplitudes vs SPL with straight lines representing linear relations that were visually fitted to the points. The displacement values of these lines at 120 dB SPL (multiplied by the projection angle correction of 1.2) give the displacements that are plotted in Fig. 12.

Data were also discarded if the waveform of the sound pressure was too distorted. The criteria for "too distorted" were not precisely defined; the judgments were made by eye. Roughly, data were used if the distortion in the pressure waveform was less than 15%.

The four cats in Fig. 12 are those on which measure-

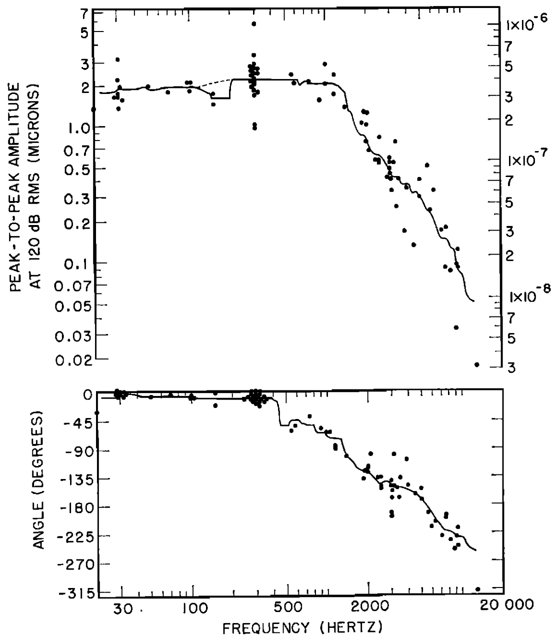


FIG. 14. Transfer characteristic based on data (●) from 25 cats. Some points (particularly at 300 and 30 Hz) have been shifted slightly to the right or left to minimize overlapping. Curves obtained by taking average of all points in a 1-oct band. The dashed line bridges an artifactual dip in the solid line (see text).

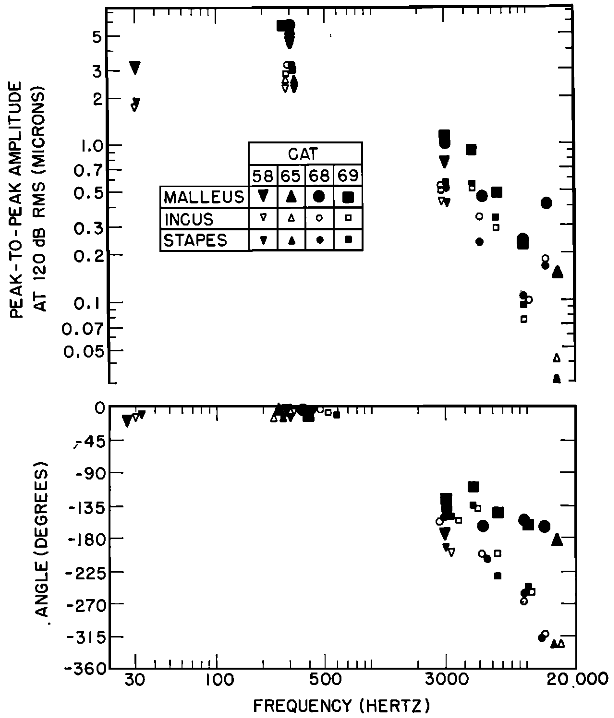


FIG. 15. Displacement amplitude and displacement phase relative to sound pressure at the tympanic membrane vs frequency for points on each ossicle. The malleus measurements were made near the umbo, the incus measurements at the end of the long process, and the stapes measurements near the center of the body. The linearity and waveform criteria described in Sec. II-E have been applied to these data, but with linearity checked only on one ossicle. All of the points pass the criteria, except those at 15 500 Hz. At this frequency, the malleus displacement increased only 3.8 dB when the SPL was changed from 145 to 150 dB. These points are included because we lack better data at high frequencies. Some symbols have been moved right or left a small amount to reduce overlapping (particularly in the lower plot at 300 Hz).

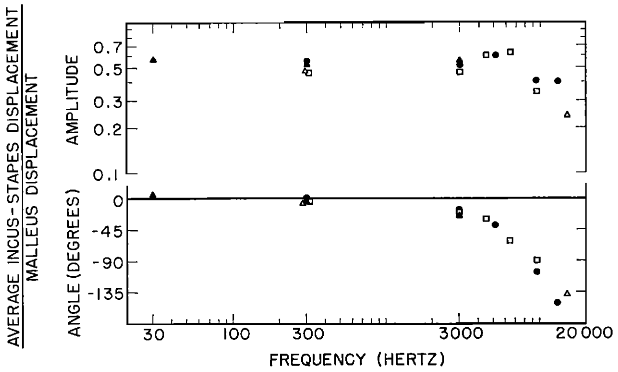


FIG. 16. Displacement of the incus and stapes relative to the malleus displacement. The averages of stapes and incus measurements (from Fig. 15) have been divided by (amplitude) or subtracted (angle) from the corresponding malleus measurements. ▲: Cat 58. △: Cat 65. ●: Cat 68. □: Cat 69.

ments were made at the largest number of frequencies. Figure 14 shows all data that met the linearity and waveform criteria given above. The continuous line was obtained by plotting the average (on a logarithmic scale) of all points in a 1-oct band. This scheme provides an average curve rather simply, but it has disadvantages. *First*, "bumps" and "dips" that are significant in the individual curves but do not occur at the same frequency in all cats will be smoothed out in the average. *Second*, the average curve is influenced by the way the data points are bunched along the frequency dimension. For instance, the only measurements taken between 100 and 300 Hz are the two at 150 Hz. These are somewhat low in amplitude and produce a dip in the curve around 150 Hz. Data from individual cats (see Fig. 12) indicate that the stapes amplitude is constant at low frequencies, and we have indicated this with a dashed line in Fig. 14. Later, we use these curves (with the dashed section) as an average middle-ear transfer characteristic with the tympanic cavities open.

F. Motion of the Stapes Relative to the Incus and the Malleus

It is clear from the phase curves in Figs. 12 and 14 that the stapes motion lags behind the sound pressure by more than 180° for frequencies above 5000 Hz. If all points on the drum membrane and ossicles move in phase (as we have observed at low frequencies), then we might expect that for high frequencies the motion would be controlled by the inertia of the system (i.e., acceleration proportional to pressure). If this were the case, the phase angle between displacement and pressure should be −180°. The occurrence of phase angles more negative than 180° implies that additional phase lag is introduced somewhere in the system.

To determine where this phase lag is introduced, we measured amplitude and phase at points on each of the three ossicles. Results from four cats are shown in Fig. 15. Although the high-frequency measurements are not as accurate as one might like, these conclusions seem clear: (1) In no case was there a significant difference in amplitude or phase between the incus and stapes displacements. (2) The malleus displacement clearly leads the other two in phase at the higher frequencies. (3) The phase of the malleus displacement does not become significantly more negative than −180°. *Apparently, the additional phase lag is introduced between the malleus and the incus.*

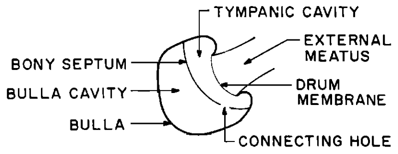
The displacement of the incus and stapes relative to the malleus is plotted in Fig. 16. Here we see that the "lever ratio," i.e., the ratio of the displacement of the manubrium to the displacement of the stapes (and long process of the incus), is approximately 2 for frequencies below 3000 Hz. Note, also that it seems to be a frequency-dependent "lever ratio" at higher frequencies.

The same microscope orientation was used on all three ossicles. This orientation was roughly perpendicular to the displacement direction of each ossicle, so that a projection-angle correction of 1 was used in all cases. If the ossicles move in slightly different directions, this will not substantially affect our calculated value of the lever ratio.

G. Corrections for Opening the Bulla and Bony Septum

To see the ossicles, we had to open two bony shells—the bulla and the bony septum—that enclose the bulla cavity and the tympanic cavity, respectively (see Fig. 17). It has been shown in several species that altering middle-ear cavities can have appreciable effects on the transmission of the middle ear.[14] We therefore made measurements to determine these effects in the cat.

FIG. 17. Schematic drawing of the cat's middle-ear cavities.



1. Methods

We recorded (a) electric responses between a wire placed on the bone near the round window and a reference lead (on the headholder or neck muscle), and (b) sound-pressure waveforms from the output of the probe-tube microphone. An average-response computer (Clark *et al.*, 1961) was used to improve the signal-to-

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[14] Møller (1963); Onchi (1961); Mundie (1963); Webster (1962); Møller (1965); Tonndorf *et al.* (1966); Benson and Eldredge (1955).

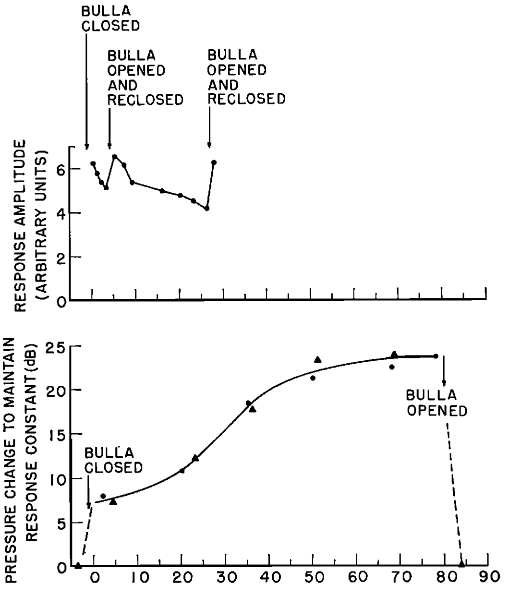

FIG. 18. Two examples of slow changes following closure of the bulla. Horizontal scales are identical for both graphs. *Upper* (Cat 70): amplitude of the round-window response (linear scale) vs time. 800-Hz tone, Stimulus level is approximately 90 dB SPL. *Lower* (Cat 62): SPL changes necessary to maintain a constant round-window response amplitude. 100-Hz tone. Stimulus levels are approximately 100 dB SPL ▲ and 90 dB SPL ●.

noise (S/N) ratio of both signals (Goldstein and Peake, 1959). Our procedure was, first, to obtain averaged responses at a given sound pressure and a number of frequencies with the bulla (and- or septum) closed. After opening the bulla (or septum), the SPL was adjusted at each frequency until the averaged electric response was the same amplitude that it had been before opening. The averaged electric responses and sound-pressure waveforms were then recorded for this condition. The effect of opening was obtained from the ratios of the sound-pressure amplitudes and from the phase shifts in the electric responses and sound-pressure waveforms.

We assume that constancy of the electric (round-window) response implies that the stapes displacement is constant (at each frequency). If there are appreciable components in the round-window response which do not involve stapes displacement (e.g., bone conduction through cochlear deformation) this assumption would be incorrect. To test this assumption, we measured the round-window response in two cats before and after interrupting the incudo-stapedial joint. In both cases the response decreased at least 20 dB throughout the frequency range of our measurements, thereby indicating that the assumption was reasonable.[15]

Theoretically, measurements of changes in the middle-ear transmission made by this "method of constant response" are insensitive to the relation between the round-window response amplitude and the stapes displacement amplitude, provided the relation is single valued and constant with time. All of our "matchings" were done at SPL's for which the amplitude of the response increased if the stimulus level was increased to ensure that we avoided the high levels at which cochlear-microphonic potential decreases with increasing level.[16] When we "matched" responses for two or more different response amplitudes, the difference in sound pressure was, in fact, independent (within 1 dB) of the value of the round-window response. In order to check the time invariance of the response, we repeated measurements at one frequency (1) at the start of the "closed" series, (2) just before opening, (3) just after opening, and (4) at the end of the "open" series. The differences between (1) and (2) and between (3) and (4) were always less than 4 dB over the few hours required to make the measurements.

Normally, access to the round window is obtained by opening the bulla. Hence, in using the "method of constant response" to measure the effect of opening the bulla, either we had (1) to record an electric response with a wire placed outside the bulla (Rosenblith and Rosenzweig, 1951) or (2) to close the bulla after placing the wire near the round window. Both techniques were used. When both were used on the same cat the results agreed.

In preliminary experiments, we discovered that after the bulla was closed slow changes occurred in the middle-ear sensitivity, particularly at low frequencies. Consider the case illustrated in the lower portion of Fig. 18. Soon after closing, the SPL had to be increased 7 dB in order to produce a response amplitude equal to the amplitude that had been produced with the bulla open. As time passed, the stimulus had to be increased more and more to maintain a constant response amplitude. After an hour, the SPL had to be 23 dB higher. When the bulla was opened after being closed for 80 min, the original amplitude was produced at the original stimulus level. The upper part of Fig. 18 illustrates (in another preparation) that, although the response amplitude sometimes decreased quite rapidly after the bulla was closed, the initial bulla-closed response amplitude was restored simply by opening and reclosing the bulla. Apparently, the slow change was not a result of a decrease in sensitivity of the "generator" of the round-window response, but was rather an alteration of the middle-ear transmission resulting from prolonged closure of the bulla.

One technique that we used for closing the bulla was to fit a glass window into the hole. If the window was removed slowly after it had been sealed for some time, we observed that air bubbled into the bulla cavity

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[15] Detailed measurements of transmission loss resulting from interruption of the ossicular chain in cats have been reported by Wever, Lawrence, and Smith (1948).

[16] As illustrated in Stevens and Davis (1938), Chap. 13, and in Wever and Lawrence (1954), Chaps. 8 and 9.

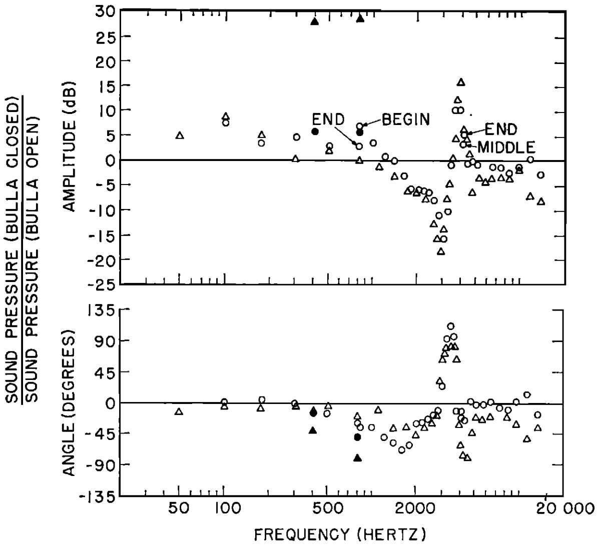

FIG. 19. Effect of opening the bulla for Cats 71 (circles) and 72 (triangles). The SPL was adjusted until the amplitude of the averaged response with the bulla open was equal to the amplitude recorded when the bulla was closed. Open symbols (reclosed to open) were obtained with an electrode near the round window; filled symbols (unopened to open) were obtained with an electrode on the ventral side of the nuchal ridge. The points labeled END, BEGIN, and MIDDLE for Cat 71 have been included to indicate the stability of this preparation during the 5 h that elapsed while the data were being collected.

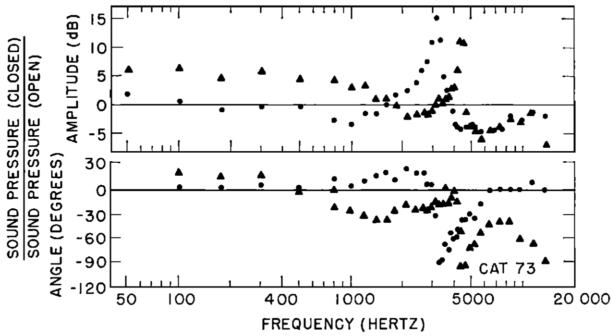

FIG. 20. Effects of opening the bulla and bony septum. The SPL was adjusted until the amplitude of the averaged round-window response after opening was equal to the amplitude recorded before opening. (The electrode was near the round window.) ▲: Opening bulla and septum. ●: Opening septum (bulla open).

through the moisture between the window and the bulla. Apparently, there was a negative air pressure in the bulla cavity. Our results suggest that a gradual buildup of negative pressure after the bulla is closed probably accounts for the slow decrease in sensitivity.

In most cats, the sensitivity increased 20–30 dB when the bulla was opened after prolonged closure. This large change was not a result of *re*sealing the bulla, since we found changes of the same magnitude (using an electrode outside the bulla) when the bulla was first opened (see solid triangles for Cat 72 in Fig. 19). In a few animals, large changes were not found when the bulla was opened initially; in these cases the size of the change (≈ 5 dB) was approximately the same as that obtained immediately after reclosing (see solid circles for Cat 71 in Fig. 19). Apparently, a negative pressure did not build up in some cats (e.g., Cat 71) but but did in others (e.g., Cat 72).

In order to avoid the effect of negative pressure in the middle-ear cavities, measurements with the bulla closed were taken according to the following procedure: Two small (1–2-mm diameter) holes were drilled in the bulla. An insulated wire was inserted through one hole and observed through the other. The bare tip of the wire was placed on the bone near the round window, and the wire was sealed into the bulla with dental cement. Petrolatum was smeared on the bone around the second hole, and a small piece of glass was slid over the hole to seal the bulla. An averaged round-window response and probe-tube microphone output for a given frequency and sound pressure were recorded within 30 sec after closing. Before the responses were recorded for another frequency, the bulla was vented by sliding the glass cover off and on again. This procedure prevented the buildup of a negative pressure, so that we measured only the immediate effect of closing the bulla.

2. *Correction for Opening the Bulla*

Figure 19 shows the effect of opening the bulla in two cats. The behavior in the frequency range above 1000 Hz (where the effect was quite frequency-sensitive) was measured in detail in four preparations. The frequency of the dip in the amplitude ranged from 2650 to 3100 Hz, and the frequency of the peak ranged from 3150 to 4300 Hz. The amplitude values ranged from -15 to -18 dB for the dip, and $+10$ to $+16$ dB for the peak.

For frequencies under 800 Hz, the effect of opening the bulla appeared to be relatively constant. Its average value was 5 dB, with a range of ± 2 dB for measurements on eight cats. Amplitude measurements at these frequencies were less reliable than those at intermediate frequencies (800–8000 Hz), partly because of the lower amplitude of the round-window response at low frequencies. As a result of the relatively low S/N ratio, the individual phase measurements were also inaccurate at the very low frequencies; on the average, the phase angle was not significantly different from zero under 400 Hz.

3. *Correction for Opening the Septum*

The effect of opening the bony septum was measured in six animals. A typical result is shown in Fig. 20, which illustrates both the change from opening the septum with the bulla already open and the net change from the opening the bulla and septum. It represents the one case in which we did both on the same cat.

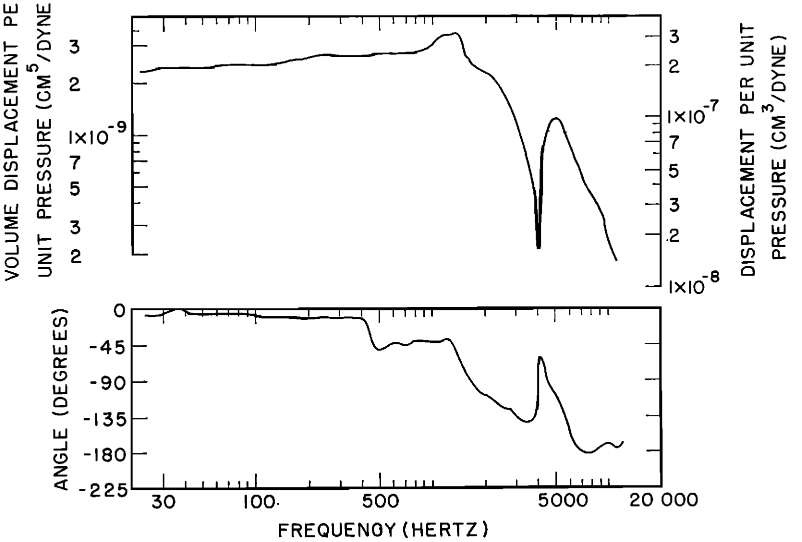

Fig. 21. Transfer characteristic of intact middle ear. The right-hand scale gives the linear displacement amplitude of the stapes per unit pressure and the upper left-hand scale gives its volume displacement per unit pressure.

In every case, opening the septum had a large effect in a rather narrow frequency range from 2000 to 4000 Hz (see dots, Fig. 20). The amplitude peak was at 3300±400 Hz with a value of 14±4 dB (± indicates the range over six preparations). A quality factor Q was calculated for these data by the following procedure: The bandwidth (BW) was measured at 3, 4.8, and 7 dB below the peak (BW_3, $BW_{4.8}$, and BW_7). These measurements showed good agreement with the theoretical relations for a system with a simple high Q resonance, i.e.,

$$BW_3 = (1/\sqrt{2})BW_{4.8} = \tfrac{1}{2}BW_7. \qquad (5)$$

Hence, for each case, the Q was calculated by averaging over the results of each of the calculations:

$$Q = \frac{\text{PEAK FREQUENCY}}{BW_3} = \frac{\sqrt{2}\times \text{PEAK FREQUENCY}}{BW_{4.7}} = \frac{2\times \text{PEAK FREQUENCY}}{BW_7}. \qquad (6)$$

For the six animals, $Q = 11 \pm 4$.

4. *Acoustic Interaction of the Microscope*

Since the working distance of the highest-power microscope objective (which was used in most cases) was only 5 mm, the open middle-ear cavities were partially closed when this objective was in place. On seven cats we used the "method of constant response" to measure the effect that this had on the middle ear. With the microscope focused on the stapes, we found a reduction in the amplitude of the middle-ear transmission which had a single maximum (4±3 dB) at 3400±400 Hz. The effect was appreciable over a band approximately 1000 Hz wide. The phase angle change was as much as 40° in some cases. These measurements were not carried out on the animals on which we measured stapes displacement, and we have not included any correction for this effect. Therefore, in the average curves of Fig. 14, the amplitude curve is probably a little too low (perhaps a few decibels) and the phase curve a little too high (perhaps 25°) in the 3000–4000-Hz region.

H. Net Transfer Characteristics

The data obtained in our visual measurements of stapes motion with the bulla and bony septum open (Fig. 14) can be combined with the measurements of the effect of opening the bulla and bony septum (Fig. 20) to obtain a middle-ear transfer characteristic for the intact animal (Fig. 21). This represents our best estimate of a transfer characteristic for an intact "average" middle ear.

The following procedure was used to obtain the curves of Fig. 21. In only one case do we have measurements of the effects of opening both the bulla and the and the septum in the same cat. The data obtained were typical, except that the frequency of the amplitude maximum in the bulla-closed/bulla-open data is an extreme (i.e., 4300 Hz, the range over four cats was 3150–4300). Therefore, in choosing our "average" correction, we have shifted the triangles of Fig. 20 down on the log-frequency scale so that the peak occurs at 4000 Hz. (The average frequency of the peak was 4000 Hz in our data.) We have assumed that from 20–500 Hz the amplitude and phase of the net correction are constant at 5 dB and 0°, respectively. These figures are

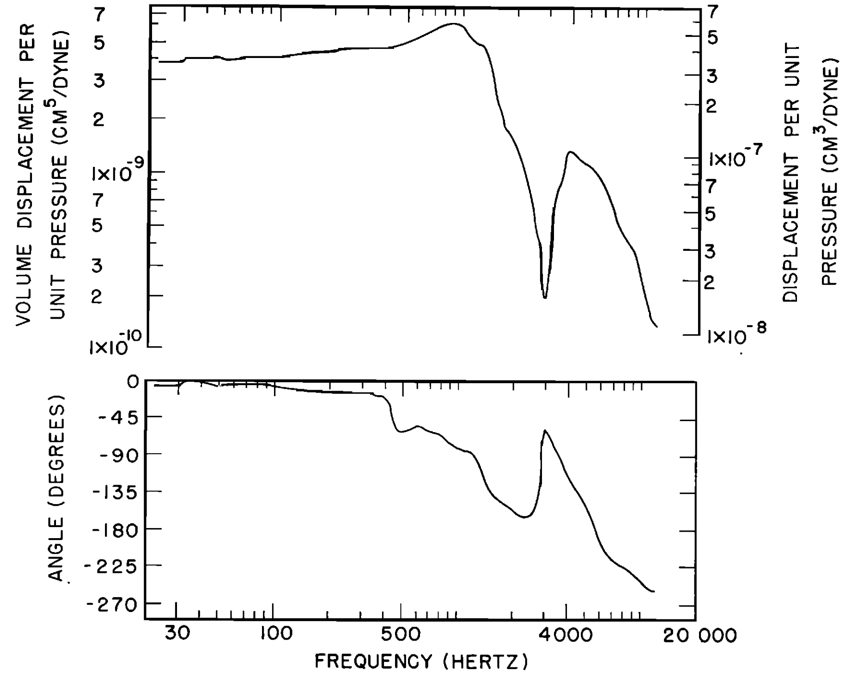

FIG. 22. Middle-ear transfer characteristic with the bulla open and the bony septum intact. (Scales the same as in Fig. 21.)

roughly the values obtained by averaging the low-frequency data over all cats and all frequencies in this range. The net curves obtained after the modified data in Fig. 20 were subtracted from the curves of Fig. 14 are shown in Fig. 21.

Since a considerable number of data on the behavior of the cat's auditory system have been obtained with the bulla opened and septum closed, it is useful to have the transfer characteristic for this condition also. This can be obtained by subtracting a typical correction for opening the septum from the average characteristic of Fig. 14. We have used the dots from Fig. 20 with a horizontal shift (of 4000/4300 for consistency) so that the peak falls at 2900 Hz rather than 3100 Hz. We have assumed that the correction from 20 to 500 Hz is 0 dB and 0°. The resulting transfer characteristic for the condition of the bulla open, septum closed is shown in Fig. 22.

The correction for opening the bulla depends on the size of the opening. The results we have presented were obtained with a large opening. Other data indicate that these measurements may not be appropriate for openings smaller than 50 mm^2.

III. DISCUSSION

A. Mode of Stapes Motion

"The stapes does not move directly in and out like a piston, but rocks like a bell-crank lever. · · · The lower posterior pole of the footplate acts as a fulcrum about which the stapes rotates."[17] This view of stapes motion, which has appeared in many publications over the last 30 years, originated from observations on human cadavers. Our measurements, on the other hand, show that in live cats the stapes move predominately "in and out like a piston." Let us examine the evidence to see if it justifies concluding that there is really a difference in stapes motion between cat and man.

Asymmetry of the annular ligament has often been cited as the cause of the rocking component of stapes motion. In our histological preparations of temporal bones from cats (Fig. 11), the dimensions of the annular ligament are relatively uniform from the anterior to the posterior pole. Eysell's (1870) measurements indicate that the human annular ligament is much wider (100 μ) at the anterior pole than at the posterior pole (15 μ). It has been assumed that the short section of the ligament holds the posterior pole of the footplate relatively immobile. More recent (but less detailed) descriptions[18] of the dimensions of human annular ligaments indicate that the width of the anterior pole of the ligament is only twice that of the posterior pole. Moreover, anatomical observations with "elastic tissue stains" (Davies, 1948) indicate that the ligament is not homogeneous, hence "depth" and "width" may not be good measures of the ligament's mechanical properties. Although Fumigalli took the position that "The structure of the ring-like ligament

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[17] From Stevens and Davis (1938), p. 256.

[18] Fumigalli (1949); Wolff and Belluci (1959); and Brunner (1954).

allows us to exclude that it might direct and determinate the characteristic movements of the stapes" (Fumigalli, 1949, p. 309), it seems clear that this issue cannot be resolved by anatomical observations alone.

Descriptions of stapes motion in response to sound in cadavers have appeared in four reports. Mach and Kessel (1874), von Békésy (1960, p. 113), and Kobrak (1948) all state that the posterior end of the footplate is essentially stationary. On the other hand, the measurements of Kirikae (1960, pp. 104–106) show that the displacement of the anterior edge of the footplate is only 50% larger than the displacement of the posterior edge. In this case, the rocking motion is accompanied by a large pistonlike component.

These observations indicate that the rotational component of stapes motion is more prominent in cadavers than in cats. It would be helpful, however, to have observations on live human ears to remove equivocation raised by the finding that the mechanical properties of of fresh cadaver ears can be substantially different from those of living ears (Zwislocki and Feldman, 1963).

B. Transfer Properties

1. Limits of Linear Operation

Our measurements indicate that stapes displacement is an approximately linear function of sound pressure up to 130 dB for frequencies below 2000 Hz and to higher SPL's for frequencies above 2000 Hz (see Fig. 13). At levels above these limits, the growth of stapes displacement with increasing sound pressure usually became clearly nonlinear (Figs. 5, 6, and 13).

Wever and Lawrence (1954, p. 89) found that the volume displacement of the cat's drum membrane resulting from a static displacement of the malleus handle is linear up to a displacement of approximately $100\,\mu$. This is appreciably larger than our limit (about $20\,\mu$ at the stapes) even when we allow for the ossicular lever ratio. It is possible, of course, that different elastic structures limit the displacements in the two experiments.

In cadavers, Rubenstein and co-workers (1967) concluded that "linear increase of vibration amplitude with sound level was found to exist up to around 104 dB; above this sound level there is a gradual limiting of the stapedial excursions." Also in cadavers, Kobrak (1948) measured malleus displacement with static pressure on the drum membrane and found a displacement–pressure relation that was linear at a pressure of 1 cm of water and nonlinear at a pressure of 2 cm of water (these correspond to the peak pressures of pure tones of 131 and 137 dB, respectively). The pressure at the limit of linearity obtained by Kobrak (on cadavers) agrees very well with our measurements on cats, whereas Rubenstein *et al.* found nonlinearities at SPL's approximately 25 dB lower. The differences in experimental procedure, and again, the problem of *post mortem* changes, make it difficult to pinpoint the reasons for this apparent discrepancy.

Our data support the conclusion (Stevens and Davis, 1938, Chap. 14; Wever and Lawrence, 1954, Chap. 9) that the deviations from linear growth of the cochlear-microphonic (CM) potential (which occur well below 130 dB) are the result of cochlear processes. Our data are not adequate, however, to determine the SPL's at which the middle ear might contribute to the production of harmonic components in cochlear potentials, since our measurement technique is not sensitive to small $<$(10%–20%) harmonic components in the motion. In fact, our measurements would not detect even harmonics at all, since we measure the differences in ossicular displacement at instants that are an integer number of half-cycles apart.

2. Shape of the Transfer Characteristic

The shape of the transfer characteristic for cats *with the middle-ear cavities open* (Fig. 14) can be described as "low pass" (i.e., the magnitude is approximately flat up to a "break frequency," above which it decreases monotonically; the phase is zero at low frequencies and monotonically becomes more negative at higher frequencies). For the most part, Møller's (1963) measurements on cats agree with this characterization. For the human middle ear the circuit models of Møller (1961) and Zwislocki (1965) (based mainly on measurements of acoustic impedance at the drum membrane in living subjects) yield low-pass transfer characteristics. On the other hand, rather flat amplitude characteristics have been obtained from measurements of round-window volume displacement in cadavers (von Békésy, 1960, p. 432; Anderson, Hansen, and Neergaard, 1963) and stapes displacement in cadavers without cochlear fluid (Rubinstein *et al.*, 1967). [von Békésy (1960, p. 436), however, shows one case which clearly has a low-pass characteristic.] The discrepancy among the shapes of published characteristics for the human middle ear has been pointed out by Flanagan (1965, p. 80).

For purposes of making quantitative comparisons, let us assume that the transfer characteristic can be represented (over the low- and middle-frequency ranges) by a second-order system,

$$H(f)=\frac{K}{1-(f/f_0)^2+j2\xi f/f_0}. \tag{7}$$

Hence the shape of the characteristic is determined by two parameters, the undamped natural frequency f_0, and the damping factor ξ. With this representation the frequency at which the phase angle is $-90°$ is the undamped natural frequency f_0.

In Møller's (1963 and 1965) measurements, the phase angle of the input impedance in six cats goes through $-90°$ at frequencies ranging from 700 to 1500 Hz with

TABLE II. The low-frequency transfer ratio of the middle ear as determined from measurements of various investigators.[a]

Source	$\lvert X_s/P_d \rvert$	Preparation	Quantity measured	Stimulus
Mach and Kessel (1874)	$1\ \times10^{-6}$ cm^3/dyn	Cadaver	Stapes displacement	256-Hz "tone"
Wilska (1935); threshold pressures from Sivian and White (1933)	$3\ \times10^{-6}$	Normal humans	Attenuation of stimulus at psychophysical threshold	Vibrating rod cemented to drum membrane
Békésy, 1936 (see von Békésy 1960, p. 72)	$1\ \times10^{-6}$	Normal humans	Acoustic-input impedance	Tones 20-40 Hz, 134 dB
Békésy, 1942 (see von Békésy 1960, p. 432)	0.02×10^{-6}	Cadavers	Round-window volume displacement	Tones
Kobrak (1948, p. 38)	$0.9\ \times10^{-6}$	Cadaver	Malleus rotation	Static pressure (1 cm H_2O) external ear
Kirikae (1960)	$4\ \times10^{-6}$	3 cadavers	Stapes displacement	Tone (400 Hz, 134 dB)
Onchi (1961)	$0.4\ \times10^{-6}$	5 cadavers	Acoustic impedance	Tones
Zwislocki (1962), summary of data from Aspinall, Morton, Jones; Metz; Zwislocki; Møller	$0.8\ \times10^{-6}$	Normal humans	Acoustic-input impedance	Tones
Flisberg, Ingelstedt, and Örtegren (1963)	$2\ \times10^{-6}$	4 normal humans	Pressure and volume changes	Static pressure in middle ear
Anderson, Hansen, and Neergaard (1963)	0.03×10^{-6}	4 cadavers	Round-window volume displacement	Tones
Rubenstein, Feldman, Fischler, Frei, and Spira (1967)	0.06×10^{-6}	17 cadavers	Stapes displacement	Tones
Møller (1963, 1965)	$0.4\ \times10^{-6}$	6 anesthetized cats (corrected to bulla closed)	Acoustic impedance	Tones
Tonndorf (1966, p. 65)	$1\ \times10^{-6}$	2 anesthetized cats (corrected to bulla closed)	Acoustic impedance	Tones
Guinan and Peake (Fig. 21)	$0.2\ \times10^{-6}$	25 anesthetized cats (corrected to bulla closed)	Stapes displacement	Tones

[a] Column 2 gives the ratio of the stapes displacement amplitude $\lvert X_s \rvert$ to sound-pressure amplitude at the drum membrane $\lvert P_d \rvert$. For the cases in which the frequency is not indicated in the right-hand column, data at or near 300 Hz were used for the calculation of the figures in Column 2. To correct the measurements on cats to the "bulla-closed" condition, the values for the "bulla-open" condition have been divided by 2.

a median of 1300 Hz. Since our average transfer characteristic (Fig. 14) passes through −90° just above 1300 Hz, these measures of f_0 agree well.

The two transfer characteristics published by Møller (1963) have broad peaks in the amplitude-vs-frequency curves somewhat below f_0. These peaks are approximately 3 dB above the low-frequency flat portion, which suggests an underdamped system with a damping ratio ξ of approximately 0.4. Our curves (Figs. 12 and 14) are appreciably flatter in the region of the natural frequency; a damping factor $\xi=0.7$ fits the curves of Fig. 14.

Since the shape of the published transfer characteristics for the human middle ear vary considerably, quantative comparisons of the data are difficult. We may note, however, that those data that indicate a "low-pass" characteristic all suggest that the human middle ear has a natural frequency near 1000 Hz.[19]

Møller (1963) has shown that his measurements of input impedance, and of incus and round-window displacement in cat are fitted quite well by a second-order transfer characteristic. He particularly points out that the phase characteristic seems to approach an asymptotic value of −180° in the 4000–5000-Hz region. Our phase data are in good agreement with Møller's, but they extend to higher frequencies and clearly indicate that the phase becomes more negative than

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[19] Møller (1961); Zwislocki (1965); von Békésy (1960), pp. 112 and 436, see also Stevens and Davis (1938), p. 262.

$-180°$. Hence, the middle-ear system is higher than second order and cannot be described completely by a damping ratio and a natural frequency (Peake and Guinan, 1966, 1967).

3. Low-Frequency Sensitivity of the Middle Ear

In our data and in Møller's (1963), the amplitude of the transfer characteristic is approximately constant in the low-frequency range. Møller's displacement measurements have no absolute calibration; however, we can calculate a low-frequency transfer ratio from his acoustic impedance measurements using the equation

$$X_s/P_d = 1/j2\pi f Z_d l A_{\text{eff}}, \tag{8}$$

where Z_d is the complex acoustic impedance at the drum membrane (essentially reactive at low frequencies), l is the ratio of umbo displacement to stapes displacement (the lever ratio), and A_{eff} is the effective area of the drum membrane. This equation is easily obtained from (1) the definition of acoustic impedance, (2) the fact that the malleus-to-stapes "lever ratio" is constant at low frequencies (Fig. 16 and Wever and Lawrence, 1954, p. 107), and (3) the gross observation (Sec. II-A and von Békésy, 1960, p. 101) that the whole drum membrane vibrates in phase throughout the low-frequency range. The last observation implies that the ratio of the effective drum membrane area to the actual drum membrane area is a constant at low frequencies. We have somewhat arbitrarily chosen this constant to be $\frac{2}{3}$ and used 0.27 cm^2 as A_{eff} [actual area$=0.41$ cm^2 (Wever and Lawrence, 1954, p. 416)]. The lever ratio that we find at low frequencies is $l=2$ (Fig. 16). According to the data from six cats given by Møller (1963, 1965), the average impedance at 300 Hz (with the relatively small resistive component neglected) with the bulla open is $Z_d = -j1100$ cgs acoustic ohms. Putting these numbers into Eq. (8), we obtain a transfer ratio of 9×10^{-7} cm^3/dyn from Møller's data. The average low-frequency transfer ratio from our data is 4×10^{-7} cm^3/dyn. The difference between these two figures may not be significant, since the range from cat to cat is approximately four to one both in the six cases taken from Møller and in our 20 cases. (There could also be an appreciable error in the constant we have chosen for A_{eff}/actual area.) From the recently published impedance data of Tonndorf (1966) (on two cats), we calculate an average low-frequency transfer ratio of 2×10^{-6} cm^3/dyn, which is near the maximum of the six cases published by Møller.

A variety of data for human middle ears have been published from which we have calculated low-frequency transfer ratios. In order to express all measurements in terms of the same quantity, we have based our calculations on the assumption that (1) Eq. (8) is applicable with $l=1.3$, $A_{\text{eff}}=0.55$ cm^2 (von Békésy, 1960, p. 102) and (2) the round-window volume displacement is equal to the stapes volume displacement with stapes footplate area$=3.2$ mm^2 (von Békésy, 1960, p. 102). These results are summarized in Table II, along with the results from cats.

By including static measurements with those made at low audio frequencies, we are implicitly assuming that the amplitude of the transfer function is constant down to $f=0$. von Békésy's (1960, p. 72) impedance measurements give rough support for this down to 5 Hz.

One might hypothesize that the low values found by von Békésy (1960), Anderson (1963), and Rubenstein *et al.* (1967) result from on unusually small compliance in their cadaver preparations. Since a reduced compliance produces an increased natural frequency (assuming that no other changes occur), the relative flatness of their amplitude characteristics is consistent with the hypothesis.

In any case, the differences from one set of measurements to another are so large that is is not possible to make a very precise statement about the low-frequency transfer ratio of the human middle ear. These data do suggest that the difference in low-frequency transfer ratio between man and cat is probably less than one order of magnitude.

4. Effect of the Cavities on the Transfer Characteristic

Møller's (1965) data and ours (Fig. 20) show the same general frequency dependence for the change in transfer characteristic produced by opening the cavities of cats; there is a relatively constant increase in transmission in the low-frequency range which diminishes gradually above 500 Hz; there is a relatively large and narrow increase near 4000 Hz. Møller's data show a change in the low-frequency transmission of 10 dB but an input impedance change of only ≈ 6 dB. We found an average change of 5 dB. Both sets of results show that the frequency of the maximum was ≈ 4000 Hz; Møller found the amplitude of this maximum was 19 dB; we found that it averaged 14 dB.

Although there are no published measurements of the change of the middle-ear transfer characteristic produced by opening the cavities in humans, Kirikae (1960, Chap. 5) and Onchi (1961) both present data on the acoustic impedance of the human cavities (from cadaver temporal bones) that suggest that the cavities can be represented fairly well as two coupled volumes (Zwislocki, 1962) [although the anatomy of the mastoid cells suggests more complicated models (Onchi, 1961)]. In this respect, the effect of the cavities in humans is similar to that in cats (Møller, 1965; Peake and Guinan, 1966, 1967). The magnitude of the effect of the cavities, however, is much smaller in humans. At low frequencies (e.g., 100 Hz), the reactance of the human cavities is only 0.1 of the reactance of the drum membrane and ossicles (Onchi, 1961; Zwislocki, 1962) so that the reduction in transmission at low frequencies attributable to the cavities should be ≈ 1 dB as compared with the 5 dB we measured on cats. [In light of the large variability found in the volume of the human middle-ear (Zwislocki, 1961; Flisberg, Inglestedt, and Örtegren, 1963), it may be that the 1-dB figure is not very accurate for some ears.] The influence of the cavities on the transfer function in the region of the cavity resonance (≈ 2000 Hz) also seems to be less dramatic in man than the 4000-Hz peak produced by the cavities in the cat (Fig. 20).

C. Relative Motion of the Ossicles

1. *Lever Ratio*

Our measurements (Fig. 16) suggest that the ossicular "lever ratio" of cats is frequency-dependent but that for frequencies below 7000 Hz, it is approximately constant at $l=2$. Wever and Lawrence determined a lever ratio for cats by measuring cochlear potentials in response to mechanical driving of the manubrium and of the stapes. They concluded that "an overall average for the cat is probably about 2.5" (Wever and Lawrence, 1954, p. 107). It is possible, however, that their results were affected by the particular way in which the mechanical stimulator was coupled to the ossicles.

A lever ratio of 1.3 is often given for the human middle ear (von Békésy, 1960, p. 102). Apparently, this value was obtained by measuring the lever arms of the manubrium and the long process of the incus (Dahmann, 1929). Kirikae's (1960, p. 97) measurements in cadavers with acoustic stimulation at 400 Hz gave average displacements of 0.12 mm at the umbo and 0.11 mm at the stapes, with a resulting lever ratio of 1.1. The lever ratio measured on cadaver bones by Fischler and co-workers (1967) "undulates around the value of 1.3" for different stimulus parameters. Apparently, the lever ratio in humans is significantly smaller than in cats.

2. *Joints*

At high frequencies, the displacements of the stapes and the lenticular process of the incus clearly lag the malleus. Possibly this results from elastic coupling in the incudo-malleolar joint. We have not observed this joint during stimulation, however, and it is possible that bending or elastic coupling at some other location(s) contribute to the high-frequency lag. For instance, there may be bending of the long process of the incus. Until more measurements are available, however, the joint is the most attractive candidate.

It is commonly stated that the incudo-malleolar joint is rigid. Although some anatomical studies (Frey, 1910; Fumigalli, 1949) have concluded that in all adult mammals this joint is ankylosed, there are many published pictures of histological preparations of adult human material[20] that show a cleft between the incus and malleus with fibers connecting the surfaces of the two bones. We have observed similar "joints" in histological preparations of cats. Hence, the anatomical evidence from these two species does not contradict the idea that relative motion between the incus and the malleus is possible.

Kirikae's (1960, p. 97) measurements in human temporal bone preparations showed that the incus and malleus vibrated as one rigid body for all tones that he used (120–2400 Hz, 110–140 dB); however, he *did* observe flexion of the incudo-malleolar joint with static pressures equivalent to 154 dB. These results can be reconciled with Kobrak's (1959, p. 42) statement that "the incus lags behind the malleus" only by assuming that the sound stimulus used by Kobrak was very intense, or that the frequency was outside the range tested by Kirikae (lower perhaps), or both. In any case, these studies demonstrate that relative motion between the incus and malleus is possible in man. Although there are no available data for humans on the relative motion of the ossicles at high frequencies, it is possible that there is relative motion between the incus and malleus such as we have found in cats.

Our measurements show no appreciable flexing of the incudo-stapedial joint for displacements in the linear range. This does not contradict reported observations of "the relative flexibility of the incudo-stapedial joint" (Stevens and Davis, 1938, p. 257). We have observed stretching and compressing of this joint at high SPL's, and it clearly slides in the anterior–posterior direction during stapedius muscle contraction (Kirikae, 1960, p. 121).

D. Decreased Sensitivity with Prolonged Closure of the Bulla

In measuring the effect of closing the bulla, we often found that the sensitivity of the ear slowly decreased when the bulla was closed (Fig. 18). Apparently, air in the middle-ear cavities was slowly absorbed and a negative pressure developed. We hypothesize that this pressure difference displaced the tympanic membrane and ossicles from their normal equilibrium position so much that the middle ear was operating in a nonlinear region of its displacement-vs-pressure characteristic in which the incremental displacement/pressure ratio was reduced (Figs. 5 and 6).

Since we did not measure the negative pressure, we have no direct test of this hypothesis. There is evidence, however, that is consistent with this interpretation: (1) At low frequencies the middle-ear displacement-pressure relation is close to linear for SPL's under 140 dB (see Fig. 6). Since 140 dB corresponds to a peak pressure of 2 mm Hg, pressure differences of less than 2 mm Hg should have little effect on the transmission properties of the middle ear. Measurements on cats (Møller, 1963; Wever, Lawrence, and Smith, 1948) show small effects (less than 5 dB) for negative pressures less than 5

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[20] Wolff and Belluci (1956); Davies (1948); Kobrak (1959); Harty (1953).

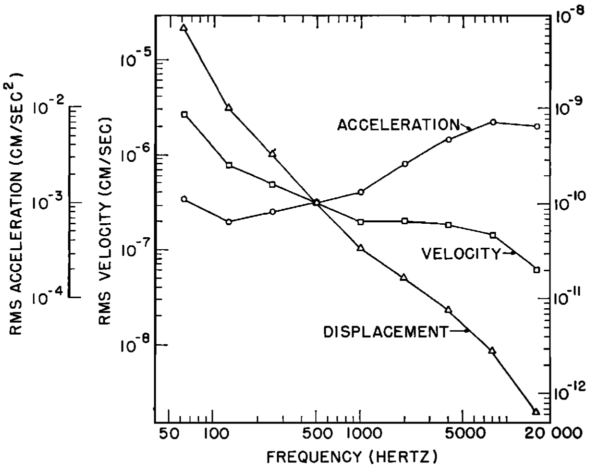

FIG. 23. Stapes motion at behavioral threshold for the cat. Free-field sound pressures at threshold were obtained from Miller, Watson, and Covell (1965, p. 22). The transformation from free-field pressure to pressure at the drum membrane was taken from the +90° azimuth curve of Fig. 7 in Wiener, Pfeiffer, and Backus (1965). These two sets of data were used, together with Fig. 21, to calculate the stapes displacement points. The velocity and acceleration at each frequency were calculated from the displacement. The vertical position of the scales was arbitrarily chosen so that the three curves intersect at 500 Hz. Since our middle-ear data and the Wiener, Pfeiffer, and Backus data are extrapolations at 16 000 Hz, the last points on the right are more uncertain than the others.

mm Hg. (2) Our measurements indicate that decreases in middle-ear transmission of 20 dB or more occur with the bulla closed in the anesthetized cat (Figs. 18 and 19). In the low-frequency range, decreases in sensitivity of 20 dB are produced by negative pressures of as little as 10 mm Hg (Møller, 1963; Wever, Lawrence, and Smith, 1948). Our hypothesis therefore requires that pressures of the order of −10 mm Hg be possible with prolonged closure of the middle-ear cavities. A variety of measurements on humans with chronically closed Eustachian tubes indicate that pressures of −10 mm Hg are not uncommon.[21]

We do not know why there were some animals that did not show a large increase in sensitivity when the bulla was first opened. Perhaps the pressure did not build up in these cats because (1) the middle-ear cavities leaked somehow (e.g., the Eustachian tube was open) or (2) the condition of the lining of the middle-ear cavities was such that air was not absorbed rapidly enough.

The most important conclusion that we derive from observation of this effect is a warning to experimenters. *Anesthetized animals with closed middle-ear cavities may have reduced middle-ear sensitivity.*

E. Absolute Threshold of Hearing

We can determine the influence of the middle-ear frequency characteristic on the threshold of hearing by combining behavioral data on the cat's minimum audible field (Miller, Watson, and Covell, 1963), the transfer characteristic from free-field pressure to pressure at the drum membrane (Wiener, Pfeiffer, and Backus, 1965), and our transfer characteristic for the middle ear (Fig. 21). From these, we obtain a curve of the stapes displacement at behavioral threshold (Fig. 23, triangles).

Wilska (1935) obtained data on the displacement of the tympanic membrane at threshold in live humans by mechanically driving a point on the drum membrane with a small stick. He was not able, however, to make a direct calibration of the displacement amplitude of his transducer above 270 Hz, and the stick may have been coupled to the drum membrane rather than to the malleus. In view of these difficulties, it does not seem useful to make comparisons between our calculations of stapes displacement at threshold and Wilska's data.

In Fig. 23 we have also plotted velocity and acceleration at threshold vs frequency. None of the three curves is horizontal over the whole frequency range. Hence, in detecting threshold tones, the cat's auditory system does not appear to work simply as a detector of the displacement, velocity, or acceleration of the stapes. This is not surprising, since the mechanical system in the inner ear may have a frequency-sensitive influence, in addition to the many possibilities for frequency-sensitive processing in the nervous system.

Note added in proof: Inasmuch as we have tried to be exhaustive in comparing our data with other data on the middle ear of the cat, we should include detailed reference to the recently published work of Tonndorf and Khanna (1967). Their technique involves either stimulation of the ear with sound, or direct mechanical driving of the ossicles with a vibrator. From measurements of the sound pressures and displacements necessary to produce a given amplitude of cochlear electric response, they have computed middle-ear characteristics that can be compared directly with ours.

Our measurements are in approximate agreement with those of Tonndorf and Khanna in the following respects. (1) For low-frequency stimuli the effect of opening the bulla is to increase the transmission by 6 dB (their Fig. 6), which is not significantly different from our average value of 5 dB. (2) They determined an ossicular lever ratio of 2.2 that is approximately constant for low frequencies. (3) The ratio of malleus displacement amplitude to sound pressure amplitude is roughly constant over the low-frequency range (up to 1,000 Hz). (4) The amplitude of the low-frequency transfer ratio obtained by averaging the data of their Figs. 6, 7, and 12, is 0.3×10^{-6} cm^3/dyn (see our Table II, Section IIIB-3).

It is difficult to make quantitative comparisons of the shapes of the transfer characteristics at high frequencies, since the two characteristics derived from the data pre-

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[21] Thomsen (1960); see also Wever and Lawrence (1954), Chap. 11 for a review.

sented by Tonndorf and Khanna (their Figs. 6 and 7) are radically different.

A significant difference between their results and ours occurs at the very low (<100 Hz) frequencies. Tonndorf and Khanna report that at low frequencies (25 and 40 Hz) the ratio of malleus displacement to stapes displacement increases and "the phase of the malleus leads that of the stapes. It is to be noted that such changes in the displacement amplitude and in phase relationships were found only in *young* animals" (Tonndorf and Khanna, p. 515). On the other hand, our measurements of stapes, incus, and malleus displacement at 30 Hz in one cat (Fig. 16) and our gross observations (III-A) indicated that all of the ossicles move in-phase at low frequencies. In addition, our measurements in eight cats at 30 Hz (Fig. 13) showed that the stapes displacement was in-phase with the sound pressure. (Our one measurement at 20 Hz with a phase angle of $-30°$ probably includes an appreciable experimental error.) If the stapes displacement is in phase with the sound pressure, as our measurements indicate, and if the malleus were to lead the stapes, then the malleus velocity would lead the sound pressure by more than 90°. This corresponds to an acoustic input impedance with a negative real part and implies that the ear can be a sound source! Hence our measurements are not compatible with the existence of a phase lead of the malleus relative to the stapes.

Tonndorf and Khanna determined the relative age of their cats by assuming that age is monotonically related to weight. Several of our cats weighed less than the lightest (1.9 kg) reported by Tonndorf and Khanna. It appears that weight differences are not the source of the discrepancy, and it is not clear what the source is. As Tonndorf and Khanna have pointed out, however, it is difficult to be certain that the motion of the ossicles when driven by a vibrator is the same as the motion in response to sound.

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Appendix A. Determination of the Vector Displacement of a Point

We use three sets of Cartesian coordinates: one set (a,b,c) coincides with anatomical directions, and the other sets (X_1, Y_1, Z_1 and X_2, Y_2, Z_2) are defined with respect to the microscope and the stapes as described in Sec. II-C. Let us use the following notation in addition to that introduced previously (the subscripts 1 and 2 are used when necessary to denote the first and second microscope orientations[A1])$\mathbf{i}_a$ is a unit vector pointing anteriorly; $\mathbf{i}_b$, a unit vector pointing toward the animal's left; $\mathbf{i}_c$, a unit vector pointing dorsally; $\psi_{py}=\cos^{-1}(\mathbf{i}_p\cdot\mathbf{i}_y)$, the angle between the projected displacement vector and the y axis ($\psi_{p_1y_1}=\gamma$); and $\mathbf{i}_q=\mathbf{i}_p\times\mathbf{i}_Z$, a unit vector in the focal plane of the microscope and perpendicular to the projection of stapes displacement in this plane.

The transformation from one coordinate system to another can be described by

$$\begin{aligned}\mathbf{i}_X&=a_X\mathbf{i}_a+b_X\mathbf{i}_b+c_X\mathbf{i}_c,\\ \mathbf{i}_Y&=a_Y\mathbf{i}_a+b_Y\mathbf{i}_b+c_Y\mathbf{i}_c,\\ \mathbf{i}_Z&=a_Z\mathbf{i}_{.}+b_Z\mathbf{i}_b+c_Z\mathbf{i}_c.\end{aligned}\qquad\text{(A1)}$$

To determine the nine coefficients of Eqs. A1, we measured (for the two microscope orientations) the angles between each of the X, Y, and Z axes and each of the a, b, and c axes. The cosines of these angles are the nine coefficients.

In the 3×3 matrix formed by these coefficients, the

[A1] The unsubscripted X, Y, and Z in the main text refer to the first microscope orientation.

sum of the squares of the coefficients in each row and column must equal unity. Hence, there are six constraining equations that apply to each set of nine angles. This is a consequence of the fact that the nine angles are a redundant measure of the three independent variables specifying a rotation of coordinates. The constraining equations were applied and the coefficients adjusted, if necessary, to produce an internally consistent set. The adjusted coefficients were used for all subsequent calculations.

In each microscope orientation, we measured ψ_{py} and $|\mathbf{p}|$ and from these measurements, calculated $\mathbf{p}$, $\mathbf{i}_p$, and $\mathbf{i}_q$ (expressed in terms of $\mathbf{i}_a$, $\mathbf{i}_b$, $\mathbf{i}_c$). Note that both $\mathbf{i}_q$ vectors are perpendicular to $\mathbf{i}_s$, and their vector product therefore defines a vector that is colinear with $\mathbf{i}_s$. (Although it is possible for the vector product to be zero, this did not occur for the microscope orientations that we used.) Therefore

$$\mathbf{i}_s = (\mathbf{i}_{q1} \times \mathbf{i}_{q2}) / |\mathbf{i}_{q1} \times \mathbf{i}_{q2}|. \qquad \text{(A2)}$$

Now, knowing the direction of the displacement, we can find its amplitude from each of its projected amplitudes:

$$|\mathbf{s}| = |\mathbf{p}_1| / (\mathbf{i}_s \cdot \mathbf{i}_{p1} = |\mathbf{p}_2| / (\mathbf{i}_s \cdot \mathbf{i}_{p2}). \qquad \text{(A3)}$$

Since we have calculated $\mathbf{p}_1$, $\mathbf{p}_2$, $\mathbf{i}_{q1}$, $\mathbf{i}_{q2}$, we can use Eqs. A2 and A3 to give $\mathbf{i}_s$ and two determinations of $|\mathbf{s}|$.[A2]

[A2] Whereas the two determinations of the amplitude are equal in theory, in practice they may differ, as indicated in Fig. 7, where

$$|\mathbf{s}| = |\mathbf{p}_1| / (\mathbf{i}_s \cdot \mathbf{i}_{p1}) = \text{AMP 1},$$
$$|\mathbf{s}| = |\mathbf{p}_2| / (\mathbf{i}_s \cdot \mathbf{i}_{p2}) = \text{AMP 2}.$$

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