

How Do Contractions of the Stapedius Muscle Alter the Acoustic Properties of the Ear?

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Abstract

We describe our investigations of the *mechanisms* through which contractions of the stapedius muscle in the cat cause alterations in acoustic transmission through the middle ear. We have observed that stapedius contractions displace the stapes head along the direction of the stapedius tendon, which is perpendicular to the direction of stapes motion in response to sound. This stapes-head displacement (SHD) occurs *without* detectable displacement of the incus or malleus. This result suggests that the changes in transmission are solely caused by changes in the stapes impedance due to the SHD. Measurements of SHD were made together with the associated transmission changes. For SHDs up to 40 μm , the transmission was reduced up to 10 dB in the frequency range below 1.5 kHz with little change for higher frequencies. For SHDs larger than 40 μm , reductions in transmission up to 30 dB were observed in the low frequency range and up to 15 dB for high frequencies. We explore the possibility that changes in the configuration of the annular ligament at the stapes footplate are the source of the acoustic changes by comparing our results with other measurements of changes of stapes impedance. We conclude that this hypothesis is tenable.

I. Introduction

The effects of the stapedius-muscle contractions on the acoustic transmission through the middle ear have been studied in human, cat and other species (e.g., see Møller, 1984). However, the mechanisms by which the stapedius contractions alter properties of specific middle-ear structures are not clear. From the anatomy of the middle ear (Fig. 1) one can suggest several possibilities for changes in the configuration of the ossicular chain that might result from contraction of the stapedius muscle. The simplest possibility is that the stapes alone is displaced without moving the incus and malleus. On the other hand, all three ossicles and the tympanic membrane could be displaced. The primary goal of our study has been to understand the mechanism through which the stapedius muscle modulates the acoustic properties of the middle-ear. Our approach was first to observe and quantify the displacements of the ossicular chain in response to stapedius contractions. Our second step was to relate the ossicular displacements to changes in acoustic transmission of the middle ear. The third step was to analyse the mechanical consequences of the ossicular displacements so as to identify the middle-ear structures that alter the transmission.

Because of differences among published measurements of stapedius-muscle effects (e.g., see reviews by Rabinowitz, 1977, 1981), we also wished to determine how large an effect the stapedius-muscle contraction can have on the middle-ear transmission (in cat). In previous studies in the cat, the muscle

contractions elicited by an intense sound (acoustic reflex) had rather small effects (e.g., Møller, 1965), whereas electric stimulation near the muscle motoneurons in the brainstem produced larger effects (Teig, 1973). In neither case is it clear whether all muscle fibers contracted. Even larger effects have been demonstrated when stapedius contractions were simulated by an external force applied on the stapedius tendon (Wever & Bray, 1942), but it is not clear whether the muscle by itself is able to generate those forces. We have used electric stimulation of the stapedius muscle (as did Nedzelnitsky, 1979) with the goal of producing maximum possible contraction of the muscle.

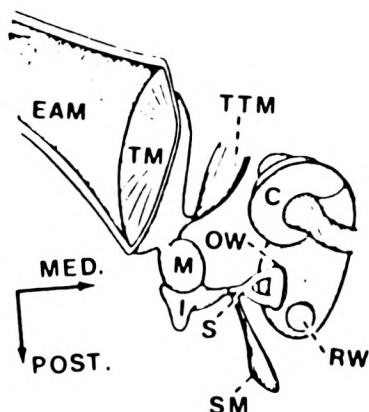


Fig. 1. A somewhat schematic view of the cat middle ear. In response to sound the stapes vibrates in the medial-lateral direction. The stapedius tendon pulls in a posterior direction. The symbols are: C: Cochlea; EAM: External Auditory Meatus; I: Incus; M: Malleus; OW: Oval Window; RW: Round Window; S: Stapes; SM: Stapedius Muscle; TM: Tympanic Membrane; TTM: Tensor Tympani Muscle. MED. and POST. stand for the medial and posterior directions, respectively.

II. Methods

Experiments were conducted on seventeen adult cats whose tensor tympani tendons were cut and whose acoustic reflex was blocked by anesthesia. The stapedius muscle was stimulated with a sinusoidal electric current (67 Hz) through a pair of electrodes placed either on or near the muscle. When the electric stimulation was turned on it produced a steady contraction of the muscle that was maintained for 30 seconds or longer. The resultant ossicular chain displacement was observed and measured during this interval through a dissecting microscope with an eyepiece micrometer. With tonal stimuli ranging from 0.1 to 10 kHz, the input and output of the middle ear were monitored through measurements of sound pressure at the tympanic membrane and cochlear potential (CP) from the round-window (through a narrow-band filter). Moderate sound pressure levels were used (e.g., 70 dB SPL) so as to avoid the noise floor and saturation of CP. Control experiments showed that the transmission-change measurements were not particularly sensitive to the sound levels for the range 65-85 dB SPL. Transmission changes during electric stimulation were eliminated after the stapedius tendon was cut. This demonstrates that the observed transmission changes were caused by the stapedius-muscle contractions.

III. Results

A. Ossicular displacement

When the stapedius muscle contracted, the stapes head was pulled posteriorly by the stapedius tendon in a direction perpendicular to that of stapes' motion in response to sound (see Fig. 1). No

displacement of the incus or malleus (detection threshold $1 \mu\text{m}$) was observed for stapes-head displacements up to $65 \mu\text{m}$. Thus the incudo-stapedial joint appeared to be perfectly flexible in allowing the posterior sliding motion of the stapes head with respect to the incus. This is a sharp contrast with the rigidity of this joint in coupling the incus and stapes motion (in the medial-lateral direction) in response to sound (Guinan & Peake, 1967). The restriction of the ossicular displacement to the stapes allows us to characterize the ossicular displacement in response to stapedius contractions with one variable, the stapes-head displacement (SHD) in the direction of the stapedius tendon (Fig. 2).

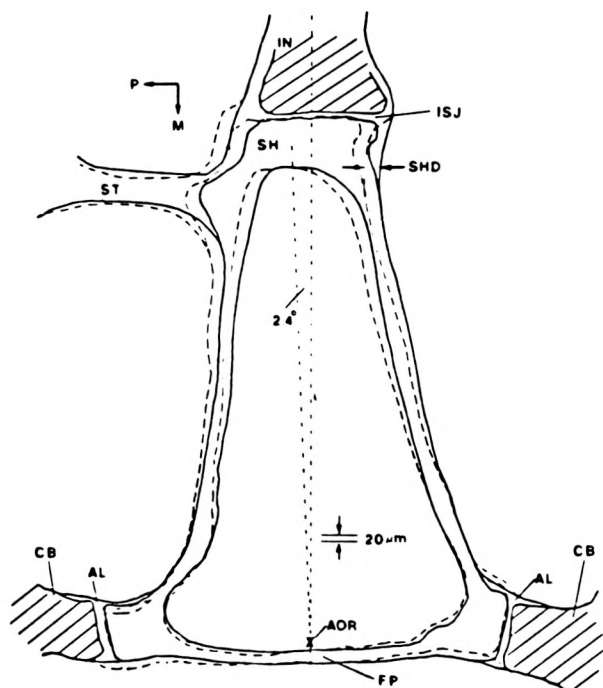


Fig. 2. Representation of stapes displacement in response to contraction of the stapedius muscle. The undisplaced configuration (solid lines) was obtained by tracing a histological section of the cat middle ear. In the experiments the region of the incudo-stapedial joint and the tendon was viewed from a direction perpendicular to this plane. We have assumed that the stapes rotated as a rigid body about an axis at the footplate (AOR) that is perpendicular to this plane. This notion is consistent with our observation that there was no stapes-head displacement in the medial-lateral direction in response to stapedius contractions. The "displaced" tracing (dashed contour) was designed to mimic a stapes-head displacement (SHD) of $60 \mu\text{m}$, with a 2.4° angle of rotation. No displacement of the lenticular process of the incus is shown, which is consistent with our observations. For comparison of displacement amplitudes, the peak-to-peak displacement of the stapes for a sound input of 140 dB SPL at the tympanic membrane ($20 \mu\text{m}$) is shown. Symbols: AL: Annular Ligament; AOR: Axis Of Rotation; CB: Cochlear Bone; FP: Foot-Plate; IN: Incus (lenticular process); ISJ: Incudo-Stapedial Joint; M: Medial; P: Posterior; SH: Stapes Head; SHD: Stapes-Head Displacement; and ST: Stapedius Tendon.

Measures of SHD (the displacement from the normal position of the stapes head) were repeatable with a given electric stimulation level of the muscle. The SHD increased monotonically with increasing muscle stimulation level until the stimulation level was so high that jaw muscles contracted. In this range the SHD increased up to about $60 \mu\text{m}$, which is about one-tenth of the diameter of the incudo-stapedial joint (Fig. 2).

B. Dependence of transmission changes on the stapes-head displacement

We have used the fundamental component of the cochlear potential as a measure of the output of the middle ear. Thus the transmission through the middle ear is proportional to the ratio of the cochlear potential to the sound pressure at the tympanic membrane; the change in transmission (ΔT) was defined as the ratio of the transmission with SHD to the transmission without SHD and we express it in decibels.

Figure 3 shows the magnitude of the change in transmission as a function of SHD and acoustic frequency for a typical ear. Transmission was generally attenuated by the stapedius contractions. For small SHDs (i.e., $< 40 \mu\text{m}$), the transmission change occurred primarily in the low frequency range ($< 1.5 \text{ kHz}$), and the amount of attenuation was 7 dB or less. At larger SHDs, the low frequency transmission decreased by as much as 25 dB (in this case), and the high frequency transmission also decreased by as much as 14 dB at 7 kHz. In general, the attenuation increased monotonically with SHD. For frequencies above 1 kHz the attenuation was not monotonic with frequency. These general features of the data in Fig. 3 were seen in the 13 preparations in which transmission changes were measured. In several ears the attenuation at low frequencies was as much as 30 dB.

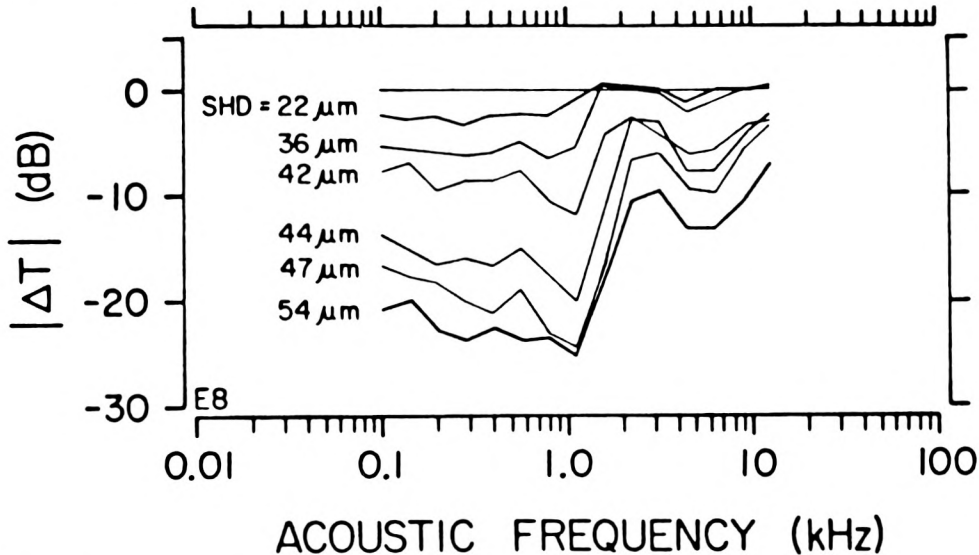


Fig. 3. Change in transmission in one middle ear as a function of acoustic frequency for six different stapes-head displacements (SHDs). Measurements at ten other SHDs are not shown to avoid congestion of the figure. Each curve is an average of six measurements. Each measurement was made during an interval (≈ 30 seconds) after the onset of the electric stimulation of the muscle. During this interval SHD, cochlear potential, and sound pressure at the tympanic membrane were constant. Measurements were made at equal intervals of $1/7$ decade in log frequency. The horizontal line marks 0 dB. The sound pressure level used for the measurements was about 70 dB SPL.

C. Mechanical consequences of the stapes-head displacement

Because the stapedius contractions apparently did not displace the incus or malleus, the change in transmission appears to be caused by a change in the stapes impedance, that is, the impedance of the stapes and its attachments. The circuit model in Fig. 4 illustrates this idea, which has been previously developed by Rabinowitz (1977, 1981). Thus, the hypothesis is that the stapes impedance, Z_S , is a variable that modulates the acoustic transmission from the tympanic membrane to the cochlea.

This hypothesis is attractive because it is generally consistent with a previous demonstration that the acoustic impedance of the stapes is substantially altered by changes in the static pressure-difference across the stapes footplate (Lynch, Nedzelnitsky & Peake, 1982, Fig. 10). We will compare these published measurements of changes in Z_S with our measurements of transmission change as a function of SHD (Fig. 3) to see whether they can be jointly consistent with the hypothesis.

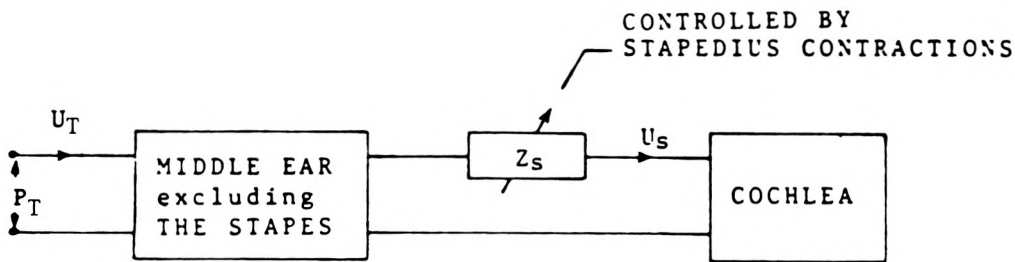


Fig. 4. Circuit model illustrating the stapedius modulation of the middle-ear transmission. The impedance of the stapes, Z_S , is shown in series with the cochlear input impedance, Z_C . Middle-ear transmission = U_S/P_T , where P_T = sound pressure at the tympanic membrane, and U_S = volume velocity of the stapes.

Lynch, et al. (1982, Fig. 10) measured the acoustic impedance of the stapes at a low acoustic frequency as a function of a static pressure on the stapes. The impedance was measured by delivering sound directly to the stapes with the other parts of the middle ear removed. Lynch, et al. had concluded that the stapes impedance was primarily determined by the annular ligament and they hypothesized that the static pressure caused a static displacement of the stapes footplate and therefore a deformation of the annular ligament. The low frequency acoustic admittance can be considered as proportional to the slope (derivative) of the displacement-pressure curve and therefore integration of the admittance measurement with a proper offset provides a relation between the pressure and the displacement (Lynch, 1978). From this displacement-pressure relation we have constructed Fig. 5A, in which the change in stapes admittance (ΔY_S) is plotted as a function of the static displacement of the annular ligament (The annular ligament was presumably displaced equally at all locations around the footplate.). The curve shows that the admittance is reduced to 1/10 of its maximum magnitude by a static displacement of 9.5 μm .

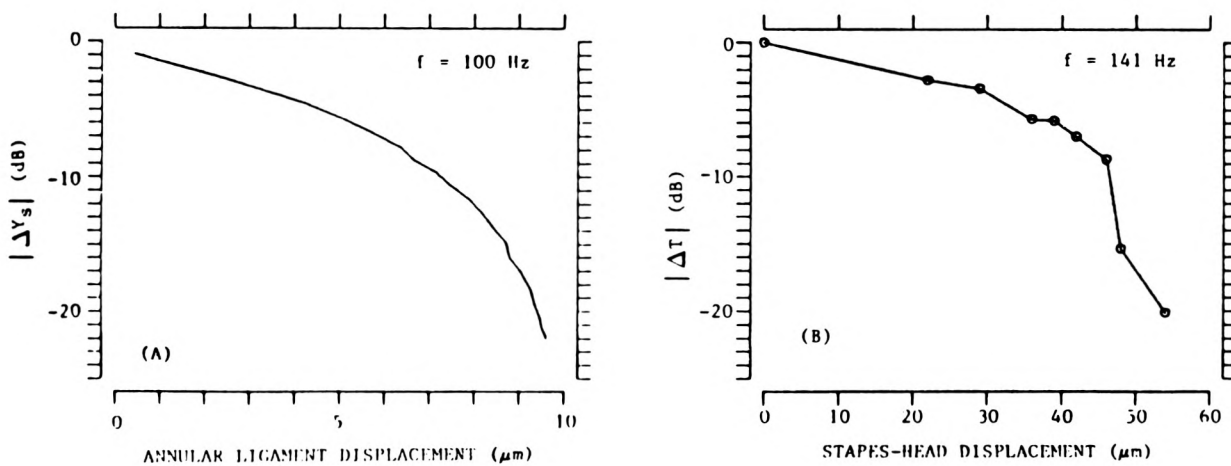


Fig. 5. (A) Magnitude of the change in acoustic admittance of the stapes ($Y_S = 1/Z_S$) vs. calculated static annular-ligament displacement. The measurements of $|Y_S|$ vs. pressure were approximately symmetrical about the maximum value of $|Y_S|$, thus this curve applies to displacements in either direction. The change in admittance is defined as the ratio of the admittance (Y_S) with static displacement to the admittance without displacement. (B) Magnitude of change in middle-ear transmission vs. stapes-head displacement (SHD) from data similar to those shown in Fig. 3. These data are typical of those in the low frequency region.

For comparison with Fig. 5A we have juxtaposed (in Fig. 5B) some of our results of the effects of the stapes-head displacement caused by stapedius contractions on middle-ear transmission (at a low frequency). In this case we see that a transmission reduction of 20 dB occurred with an SHD of 54 μm . Our working hypothesis is that both of these results (Fig. 5A and 5B) are caused by the change in the configuration (mechanical strain) of the annular ligament.

Are the available data consistent with the hypothesis? In exploring this question we first deal with a qualitative issue which may appear to invalidate the hypothesis. Lynch, et al. (1982, p.115) reported that, although static pressure variations produced large alterations in admittance magnitude at 0.1 kHz, they produced small alterations (3 dB) at 1.0 kHz. A possible explanation for this is that at 1 kHz the effects of the displacements produced by their static pressure differences were acoustically "equivalent" to those of the smaller SHDs that have effects only at low frequencies (Fig. 3). If we adopt this possibility as a part of our working hypothesis, we then expect that larger displacement than those of Fig. 5A would produce changes in Z_S at high frequencies.

We now take a closer look at the low frequency measurements. The change in middle-ear transmission can be related to the change in stapes admittance from the model:

$$\frac{T'}{T} = \frac{1 + B}{1 + \frac{B}{Y_S'/Y_S}} \quad (1)$$

where T = middle-ear transmission, Y_S = stapes admittance, the primed variables apply to the stapedius contracted situation, $B = Z_S/(Z_O + Z_C)$, Z_O is the output impedance of the middle ear block, and Z_C is the input impedance of the cochlea. At low frequencies both Y_S' and Y_S are compliance-like (Lynch, et al., 1982) and their ratio is real. From a low-frequency model by Lynch (1981), we conclude that B is also real and is approximately equal to one for low frequencies. Thus, Eq.(1) allows one to determine T'/T as a function of Y_S'/Y_S and each $[T'/T, Y_S'/Y_S]$ pair can be transformed into a [stapes-head displacement (SHD), annular-ligament displacement] pair through Fig. 5A and 5B. The result of this transformation is shown in Fig. 6. In so far as the resulting curve is a straight line through the origin, each SHD is "equivalent" to a uniform annular ligament displacement of SHD/5.4 at low acoustic frequencies.

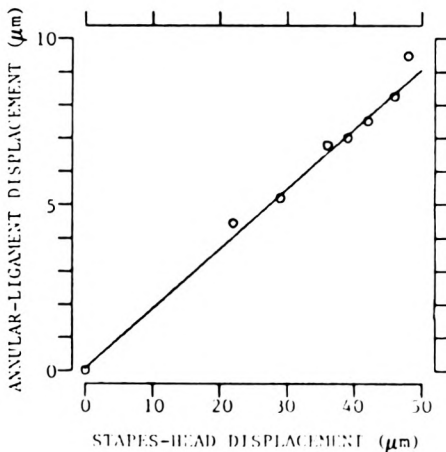


Fig. 6. Relationship between "equivalent" stapes-head displacements and the uniform annular-ligament displacements for low acoustic frequencies. Equation (1) with $B = 1$ was used along with Fig. 5A and 5B to determine "equivalent" displacements. The points were determined at the stapes-head displacements for which ΔT measurements were made (Fig. 5B). The straight line is a regression line with slope = 0.18; the correlation coefficient of the data = 0.99.

Let us now consider how the above "equivalence" can come about and whether the factor of 5.4 is reasonable. From Fig. 2 we see that a stapes-head displacement causes an annular-ligament displacement. Since the long-axis of the footplate (parallel to the stapedius tendon) is approximately equal to the height of the stapes from the footplate to the tendon, the *maximum* displacement of the annular ligament is about half of the SHD. With the assumed rotation of the stapes that is shown, the resultant displacement of the annular ligament is spatially *nonuniform* with its maximum at the poles of the long-axis of the footplate and minimum (zero) along the axis of rotation. Thus, only a fraction of the ligament is strained in the SHD case as compared to the uniform displacement of the ligament in the case of static pressure. It is conceivable then that this difference in spatial uniformity can contribute the other factor of $5.4/2 = 2.7$.

From the above comparisons, we conclude that the available data are consistent with the hypothesis that the annular ligament controls the stapes impedance through some process in which its acoustic (or incremental) "stiffness" is altered by the static strain of the ligament.

IV. Discussion

On the basis of the observed motion of the stapes head caused by stapedius-muscle contraction and the *absence* of simultaneous motion of other middle-ear ossicles, we have pursued the hypothesis that the stapedius muscle produces its effects through an increase of the stapes impedance caused by mechanical strain of the annular ligament. Our test of this hypothesis could be improved (especially for high frequencies), but with a few reasonable assumptions we concluded that the hypothesis is tenable. One way to provide a good quantitative test would be to measure the impedance of the stapes, Z_s , e.g. in the manner of Lynch, et al. (1982), as a function of SHD. In addition the value of B (or Z_0) at high frequencies needs to be determined. With these quantities it would be possible to test the hypothesis by predicting the $T'(SHD)$ from Eq.(1). In the meantime we can speculate about some larger implications of the observations.

How large can the effects of physiological contractions of the middle-ear muscles be? In human and animals, stapedius contractions evoked through the acoustic reflex produce transmission attenuations of about 10 dB for acoustic frequencies below 1 kHz and little effect for higher frequencies (Møller, 1984; Rabinowitz, 1977). However, our data and those obtained by Teig (1973) suggest that at least in the cat much larger effects can occur. It may be that the measurements of acoustic reflex have not evoked the maximum attenuation, because experimenters have not used stimuli that evoke maximum activity of the motoneurons involved. Also, recent experiments (McCue and Guinan, 1983) suggest that only a fraction of the stapedius motoneurons is involved in the acoustic reflex. Thus, it is conceivable that the brain can cause much stronger stapedius muscle contractions than those evoked in the reflex measurements. It is then conceivable that the largest effects that we have observed (including those for high frequencies) with electric stimuli (Fig. 3) can also occur with physiological activation of the muscle.

The mechanical behavior of the incudo-stapedial joint and the hypothesized consequences suggest some general speculations. The role of this joint in localizing the mechanical effect of stapedius contractions to *only* the stapes suggests a general function for ossicular joints and thereby suggests an advantage for middle ears with three ossicles as found in mammals, compared to the one-ossicle model found in birds,

reptiles, and most amphibians. If, in general, a joint allows one ossicle *only* to move when a muscle contracts, this provides the ear with a system in which a muscle can have a "localized" effect through ligaments that are attached to only one ossicle. The advantage of this arrangement might be that the other muscle (the tensor tympani) can exert its force on ligaments that are unstrained by the stapedius. Thus, two muscles can have relatively independent effects on the middle ear by having them attached to separate ossicles that are effectively "uncoupled" for the motions introduced by the muscles. This is consistent with our (not extensive) observation that electric stimulation of the tensor tympani in cat causes displacement of the malleus but not the incus or stapes at the incudo-stapedial joint. This suggests the further speculation that it is possible for the stapedius and the tensor tympani *together* to produce significantly larger effects on the middle-ear transmission than those that have been observed.

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