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THE EVOLUTION AND FUNCTION OF THE MIDDLE EAR IN MAN*

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INTRODUCTION

In the animal kingdom there is a great variety of middle and inner ears. This suggests that these variations in structure are either due to the hearing requirements of the animal, or alternatively they are not essential to the problem of hearing. For example, why do we need three bones in the middle ear when a bird only has one? To answer these questions it is helpful to examine the evolution of the auditory system.

Evolution of the Auditory System

The inner ear of man has developed from the lateral line system of fish. This lateral line system detects movement and vibration in water, and probably gave rise to the labyrinth when a portion became buried beneath the surface of the skin.

The middle ear, on the other hand, has developed along entirely different lines. At first it was a simple structure like an otolith and its density allowed it to vibrate in a watery medium. It has further evolved in fish, and in many consists of an air bladder and three Weberian ossicles. Sound causes the air bladder to vibrate because air is more compressible than water. These vibrations are then transferred to the inner ear by three modified vertebrae called the Weberian ossicles (Fig. 1). So it would appear that the three-ossicle pattern of the mallus, incus and stapes bas been established in fish. However, this did not occur, because the Weberian ossicles have a different origin, and Nature dispensed with them in favour of a single columella.

A further stage in evolution occurred when fish left the water for dry land, and their descendants, the amphibia, show interesting changes. The chief problem in hearing then became how to match the impedances of sound in air and water. This was solved by amplifying sound and transmitting it by a single columella to an opening in the cochlea. At first the outer end of the columella was attached to the quadrate bone of the skull and in others to a cartilage or jaw muscle. A further advance was made by the Tuatera Lizard from New Zealand where the outer end of the columella became attached to a membrane. Finally, a tympanic membrane developed which was in direct contact with the external environment, and this can be seen in the frog.

Reptiles, birds and mammals have all evolved from the amphibia and various parts of their auditory apparatus show this development. In reptiles and birds, a major evolutionary advance occurred when the lagena of the primitive saccule enlarged to produce a cochlea similar to that of man, although it is straight and not coiled. This great development of the cochlea has not been accompanied by corresponding changes in the middle ear, and, although variations in detail occur, the plan is the same as the amphibian. However, despite a single columella in the middle ear, a bird can hear within the same range as man. In some ways birds can surpass humans, and can hear and respond to fluctuations in a song that are ten times faster than can be perceived by our own ears.

Insects evolved on dry land alone, and were therefore free to develop hearing along lines which were unrelated to the system of balance. They have dispensed with ossicles, and only have an ear drum and sensory nerves that pick up sound vibrations directly (Fig. 2). This very simple design is highly efficient and insects often hear sounds beyond the range of man's hearing. They are also different in other ways, and have ears located in many different parts of the body, for example the base of the wings, midsections and antennae.

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The Katydid is particularly interesting, as the ears are slits below the knees. This enables it to control directional hearing by moving the legs apart, and makes it easier for the female to locate the male from its mating call.

This summary of hearing evolution in different orders or phyla indicates that hearing in man is not the most efficient, and the three ossicles do not seem to offer an advantage over the single columella of birds. The malleus and incus or articular and quadrate bones were originally jaw bones which lost their function. They became connected with middle ear sound transmission in man, but there does not appear to be any obvious reason why this occurred.

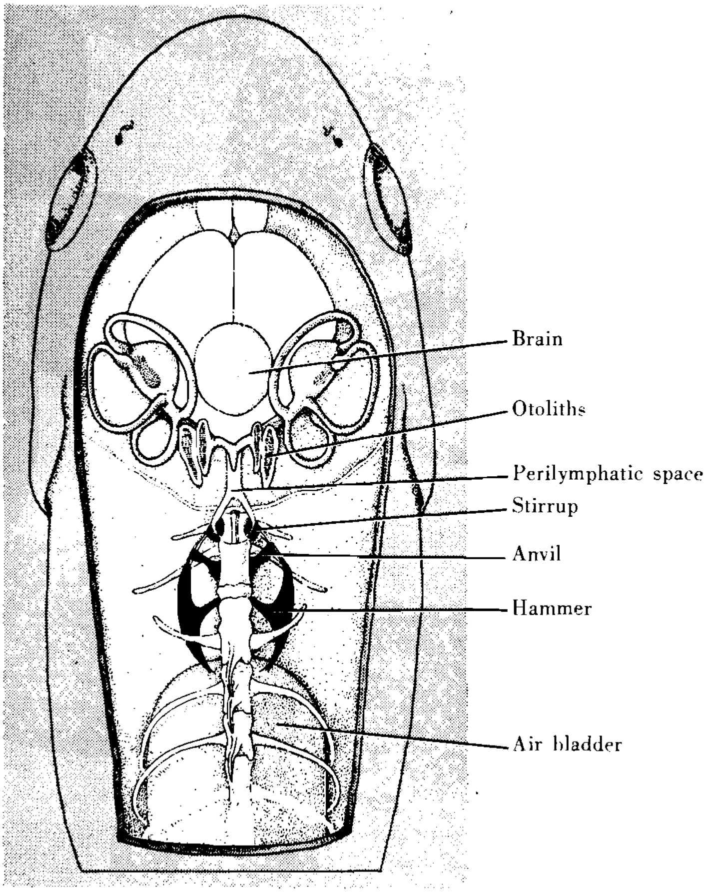

FIGURE 1.
A diagram of the middle and inner ears of a fish (Von Frisch, 1936).

Experimental Stapedectomies

Experiments have been performed on cats to study some of the problems of middle ear sound transmission. These experiments have also been biased towards solving problems associated with middle ear surgery. Two questions in particular have been studied: firstly, does it matter how loose the linkage is between the prosthesis and the long process of the incus, and secondly, is the wire gelfoam strut any more efficient than the stainless steel piston in sound transmission?

Nine experimental procedures were performed to determine how tight the connection between the strut and long process of the incus must be for optimum sound transmission. In each ear, the wire gelfoam strut was first inserted and very loosely crimped to the incus before a 20 microvolt cochlear microphonic threshold was obtained. The strut was then firmly crimped to the incus and a further threshold measurement recorded. All thresholds before and after crimping were averaged and can be seen in Fig. 3. Twenty frequencies were tested and the thresholds measured in decibels. The interrupted line is the threshold obtained with a loose strut, and the continuous line is the threshold after it had been tightened. The vertical lines indicate one standard deviation on either side of the mean, and are a measure of the scatter of results among the nine cats. There is a lot of scatter, and although the difference in means suggests a difference between loose and tight crimping for low frequencies, a statistical test is needed to show whether this difference would be likely to occur by chance.

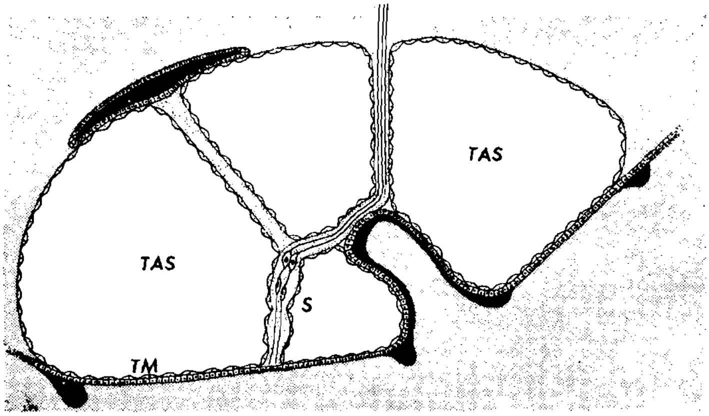

FIGURE 2.
A diagram of the auditory apparatus of an insect (Roeder and Treat, 1957).

This can be done with a two-way analysis of variance, but as this involves a lengthy calculation, the results were programmed in Fortran IV and the calculations performed by an IBM 7040 computer. The results can be seen in Table I. In an analysis of variance, the result is expressed as an F value, and if this value is greater than a certain amount, the experiment is said to be significant at the 1% or 5% level. In this particular experiment, when the F value was greater than 11.26, the result was significant at the 1% probability level, and is marked with two asterisks. When the F value was greater than 5.32 but less than 11.26, the result was significant at the 5% probability level, and is marked with one asterisk. Any results not marked with an asterisk occurred by chance.

TABLE 1

A. Loose and Tight Struts.

B. Wire-gelfoam Struts vs Stainless Steel Pistons.

Frequency (KC)	*A. F value*	*B. F value*
0.20	36.43**	2.18
0.30	46.85**	0.17
0.40	81.56**	0.40
0.50	227.76**	0.11
0.75	31.27**	0.18
1.00	10.88*	1.09
1.25	5.84*	1.50
1.50	13.87**	0.88
1.75	7.08*	0.00
2.00	0.66	0.00
2.20	2.79	0.13
2.40	3.56	0.01
2.60	6.42*	0.23
2.80	0.63*	0.10
3.00	1.01	0.63
4.00	2.48	0.05
5.00	7.31*	0.25
6.00	16.33**	1.00
7.00	2.78	1.00
8.00	1.73	1.00

A. $P = 0.05$ F1, 8 $>$ (5.32)*;
$P = 0.01$ F1, 8 $>$ (11.26)**.

B. $P = 0.05$ F1, 6 $>$ (5.99)*;
$P = 0.01$ F1, 6 $>$ (13.75)**.

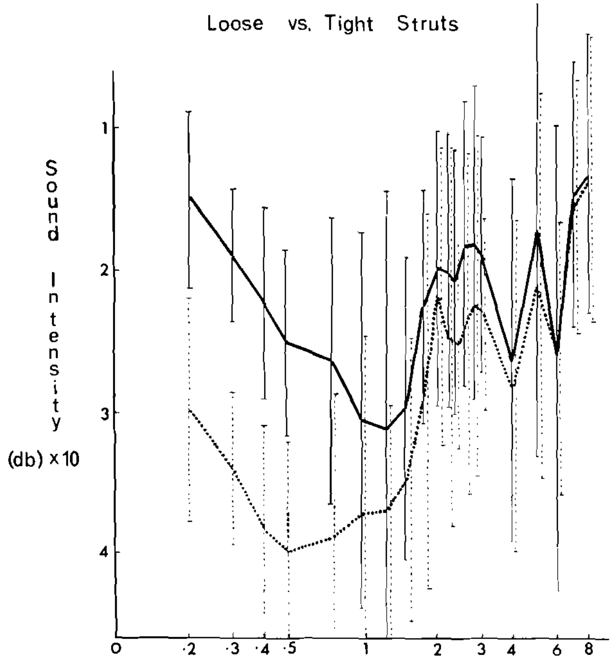

FIGURE 3. (CLARK & DUNLOP, 1968).

Cochlear microphonic threshold levels for struts with loose (interrupted line) and tight (continuous line) connections to the long process of the incus. Vertical lines are one standard deviation on either side of the arithmetic mean.

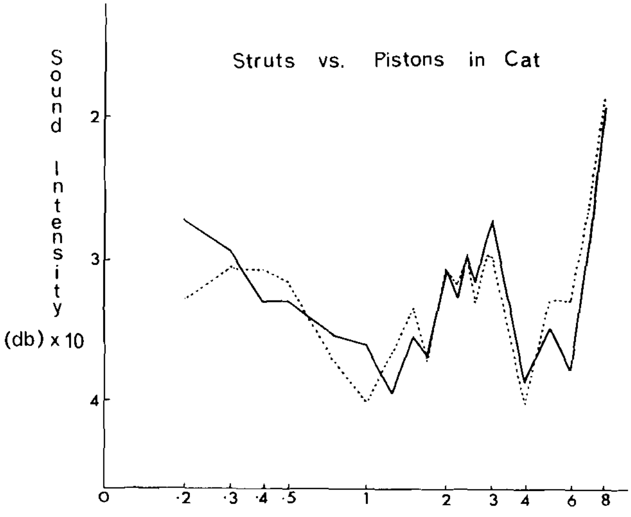

FIGURE 4. (CLARK & DUNLOP, 1968).

Cochlear microphonic threshold levels after stapedectomies with wire-gelfoam prostheses (continuous line) and stainless steel pistons (discontinuous line).

From this table it can be seen that the difference between loose and tight struts is highly significant for the frequencies 0.2, 0.3, 0.4, 0.5, 0.75, 1.5 and 6.0 Kc. It is difficult to explain the result at 6.0 Kc, but it would appear that a tight connection between the strut and long process of the incus is important for the efficient transmission of low frequencies. This selective loss for low frequencies is interesting and difficult to explain in terms of alterations in stiffness, mass or friction. It seems more likely that there are two different mechanisms for transmission of sound: one which operates more efficiently for high frequencies, and the other more efficiently for low frequencies. More research is required, however, to confirm this hypothesis.

The other question of interest is whether the greater mass of the stainless steel piston makes it less efficient than the wire gelfoam strut for transmitting high frequencies. Seven ears were operated on to determine whether any differences exist, and threshold measurements were obtained after stapedectomies had been performed using a wire-gelfoam strut and stainless steel piston. In alternate experiments, the order of prostheses was reversed to reduce bias in favour of the first operation, and the results are seen in Fig. 4. The thresholds after wire-gelfoam stapedectomies are shown by the continuous line, and the thresholds after stapedectomies with stainless steel pistons, by the discontinuous line. These results show that there is very little difference between the two methods. A two-way analysis of variance indicates that any difference between the two methods would have occurred by chance as the F values are all below the value required for a 5% probability level. Therefore, the greater mass of the stainless steel piston does not affect high frequency sound transmission.

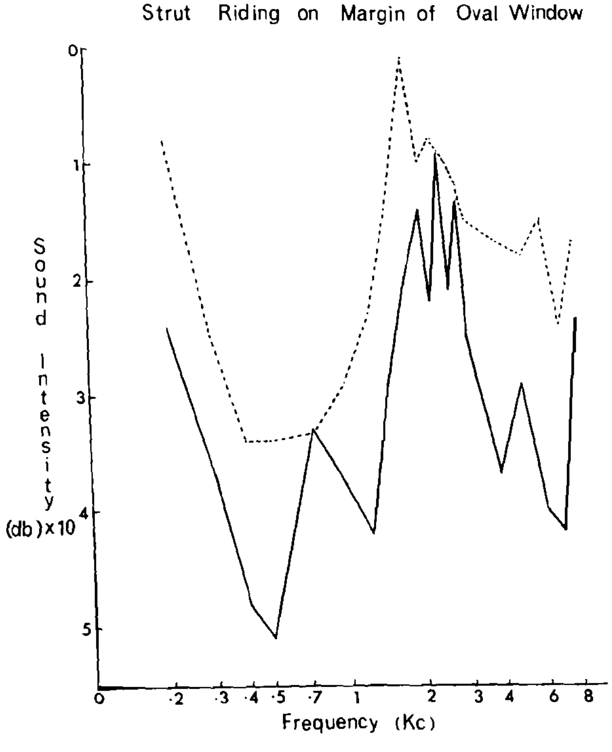

FIGURE 5. (CLARK & DUNLOP, 1968).

Cochlear microphonic threshold levels with the distal end of the strut riding on the margin of the oval window. Continuous line, before correction; discontinuous line, after correction.

During these experiments two observations were noted that also have clinical interest. Firstly, alteration in the position of the distal end of the prosthesis affected the transmission of all frequencies (Fig. 5). In the graph the continuous line represents the threshold with the distal end of the strut riding on the margin of the oval window, and the discontinuous line, the threshold after its correction. This overriding of the distal end of the prosthesis occurred during the crimping process when manipulation at the long process of the incus caused the distal end to ride forwards and contact the margin of the oval window.

Secondly, it was found that a wire strut with gelfoam attached to one end did not completely seal the oval window, and resulted in a loss of sound transmission for low frequencies (Fig. 6). In this graph the continuous line represents the threshold with the oval window incompletely sealed with gelfoam, and the discontinuous line, the threshold after this had been corrected. This finding is consistent with the flat type of audiogram seen in patients with a post-operative fistula of the oval window (Willis, 1967).

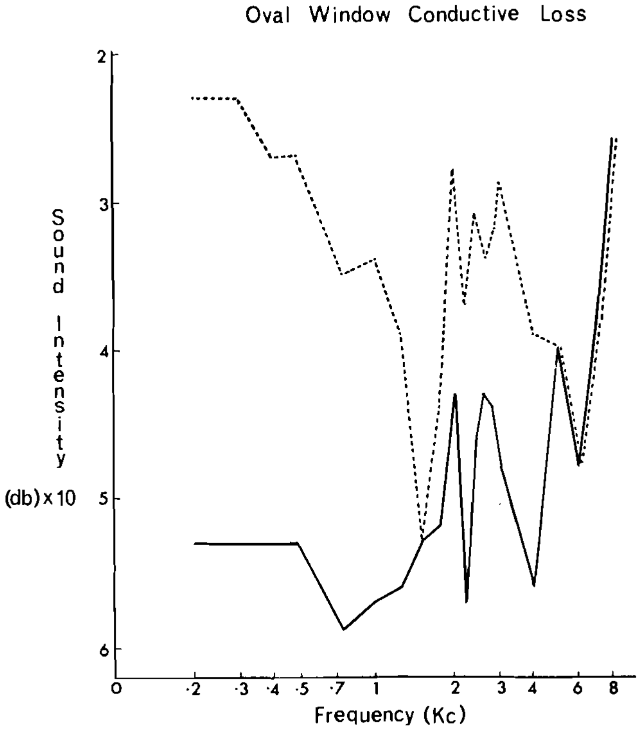

FIGURE 6. (CLARK & DUNLOP, 1968).

Cochlear microphonic threshold levels due to a poor seal of the oval window. Continuous line, before correction; discontinuous line, after correction.

SUMMARY

The survey of the evolution of hearing indicates that the complicated structure of the middle ear is probably not necessary for sound transmission. Many varied evolutionary trends may have been operating on the middle ear to produce its structure in man, and therefore its present form is not necessarily the most efficient for sound transmission. If these conclusions are correct the approach to tympanoplasties could be simplified, and efforts directed to connecting the handle of the malleus directly to the oval window.

The experimental study suggests that there are possibly two mechanisms for the transmission of sound of different frequencies across the middle ear: one which operates more efficiently for high frequencies, and the other more efficiently for low frequencies. The study also shows that a rigid connection between the incus and a stapes prosthesis is required for the transmission of low frequencies, and the greater mass of the stainless steel piston does not affect the transmission of high frequencies.

It was noted that when the distal end of the strut was overriding the margin of the oval window, a lowered threshold occurred for all frequencies. Also, failure to completely seal the oval window with the gelfoam of a wire-gelfoam strut resulted in a lowered threshold, especially for low frequencies. This result may have relevance to a post-operative fistula of the oval window.

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