A REVIEW OF SOME CURRENT CONCEPTS OF THE FUNCTIONAL EVOLUTION OF THE EAR IN TERRESTRIAL VERTEBRATES

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The evolution of the middle ear, including the origin of the mammalian ossicles, has been a major concern of palaeontologists over the last 30 years. A general consensus has been reached, which needs no elaboration here, that the malleus and incus are mostly derived from bones in the ancestral reptile made redundant by the selection of a more efficient jaw articulation system (Hopson, 1966; Hotton, 1959; Parrington, 1967, 1971; Tumarkin, 1955; Watson, 1953). As emphasized by Hopson (1966) the selective pressures which gave rise to the middle ear mechanism of mammals acted primarily on the masticatory apparatus of therapsids. Because of the nature of the fossil record however, little can be learned from it concerning the evolution of the soft parts of the middle ear and the membranous labyrinth of the inner ear. Recent comparative anatomical and physiological studies now make it possible to bring together data on the functional significance of differences in the ears of modern vertebrates. The data also give some indication why certain structural and functional arrangements were selected for in the evolution of the mammals. In this paper I will discuss the functional significance of changes in the middle ear transmission system, particularly in connection with the origin of the mammalian middle ear, the development of large inner ear potentials and dimensional changes in the inner ear.

THE MIDDLE EAR TRANSMISSION SYSTEM

The origin of the middle ear of early amphibians has been traced (Thomson, 1966) and the basic pattern persists in modern non-mammalian terrestrial vertebrates. The mechanisms which gave rise to an imped-ance-matching middle ear during the aquatic-terrestrial transition have been adequately discussed by van Bergeijk (1967) and Thomson (1966). Of course, there has been much convergent and parallel evolution (Olson, 1966) and the structures in the middle ear may have diverse origins in the various groups (Tumarkin, 1955). Also, there is uncertainty in many fossil forms as to whether the columella, or extracolumella, was actually attached to a tympanic membrane or derived its energy from other tissues (Hotton, 1959; Olson, 1966; Smith, 1938; Toerien, 1955; Watson, 1953). If the quadrate and articular ceased functioning as a jaw joint during the Late Triassic (Barghusen and Hopson, 1970) the three-ossicle middle ear probably arose sometime in the Jurassic. This is approximately the time suggested by Fernandez and Schmidt (1963) for the appearance of the truly coiled cochlea.

Modern mammals show a great variety of adaptation of middle ear structure to varied modes of life. Large differences exist with respect to the type and shape of the middle ear cavity (Hinchcliffe and Pye, 1969a; Pye and Hinchcliffe, 1968; Simkin, 1965; Webster, 1966); the shape and size of the eardrum and the structure of the ossicles (Fraser and Purves, 1960; Hensen, 1961; Hinchcliffe and Pye, 1969a; Reysenbach de Haan, 1960).

Implicit in many discussions on the origin of the mammalian ossicles is the idea that the new middle ear is a "better" system than the columella middle ear (e.g., Taylor, 1969). This is no doubt a safe assumption in the context of the therapsid descendents which gained some functional advantage from the 'new' middle ear, but is not safe to use with respect to modern
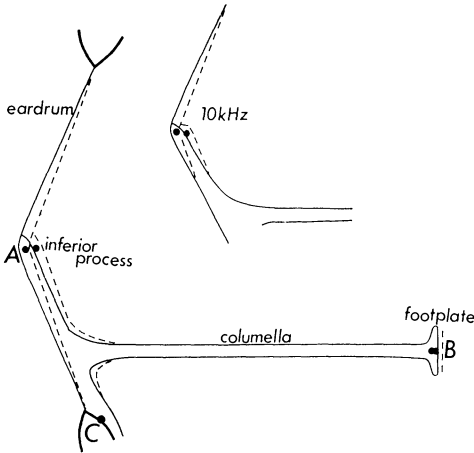
FIG. 1. Simplified diagram of a non-mammalian middle ear to illustrate lever system. At low frequencies, the inferior process moves like a bar hinged at C. The amplitude of the tip of the inferior process at A is larger than the footplate amplitude (B). The inset shows the bending of the middle of the inferior process at high frequencies (e.g., 10 kHz).

vertebrates unless the advantages are defined. Masterton et al. (1969) correctly state that high frequency hearing is a distinctively mammalian characteristic and then claim that this special ability of mammals depends on the ossicular linkage in the middle ear. This claim was made on the basis that the ossicular linkage was the most obvious anatomical difference between the ears of mammals and non-mammals. Leaving aside the debate the latter statement could prompt, it is clear that Masterton et al. believe that in modern mammals the leverage in the impedance-matching system of the middle ear explains

"... the radical difference between mammals and non-mammals in the upper limit of hearing. . ."

The problem is, however, not that simple. Although it has long been thought that the leverage present in the mammalian middle ear was unique, it has now been shown conclusively in all non-mammalian middle ears which have been studied that these, too, possess leverage (Manley, 1972; Saunders

and Johnstone, 1971; Wever and Werner, 1970). This leverage arises from the configuration of the columella and extracolumella. The fulcrum of the columella–extracolumella system is dorsal to the axis of the columella, and the point of maximum amplitude of the system is the tip of the inferior process of the extracolumella which is in intimate contact with the tympanic membrane (Fig. 1). The extracolumella can be regarded as a bar with a hinge at one end and the columella inserted about half way down. Because the extracolumella consists of cartilage the hinge and insertion flex and the main movements of the columella are piston-like. The lever ratios so obtained are as high as or higher than those found in mammals. Thus the existence of a lever ratio in modern mammalian middle ears cannot explain superior high-frequency hearing. In addition, it has been shown that, although the sensitivity of the ear of, for example, the Tokay gecko (Gekko gecko) is poor above approximately 6–8 kHz., the absolute amplitude of the tympanic membrane as measured at the tip of the inferior process is (at frequencies up to 15 kHz., the entire range of measurement) not inferior to that of the guinea pig tympanic membrane as measured at the tip of the manubrium of the malleus (Manley, 1972). This is in spite of the fact that the sensitivity of the guinea pig ear exceeds 30 kHz. Also, the area ratios between the eardrum and the columella footplate in modern reptiles and birds are similar to area ratios found in mammals. At least in this case, the characteristics of the eardrum also are not responsible for poor high frequency sensitivity.

It has been shown that in this species there are two main factors which limit the frequency response. One of these factors is that the inner ear is incapable of analysing frequencies higher than about 5 kHz. It has been shown that there is a clear relationship between inner ear structure and frequency response, as discussed below. When corrected for the middle ear characteristics the sensitivity of the inner ear it-
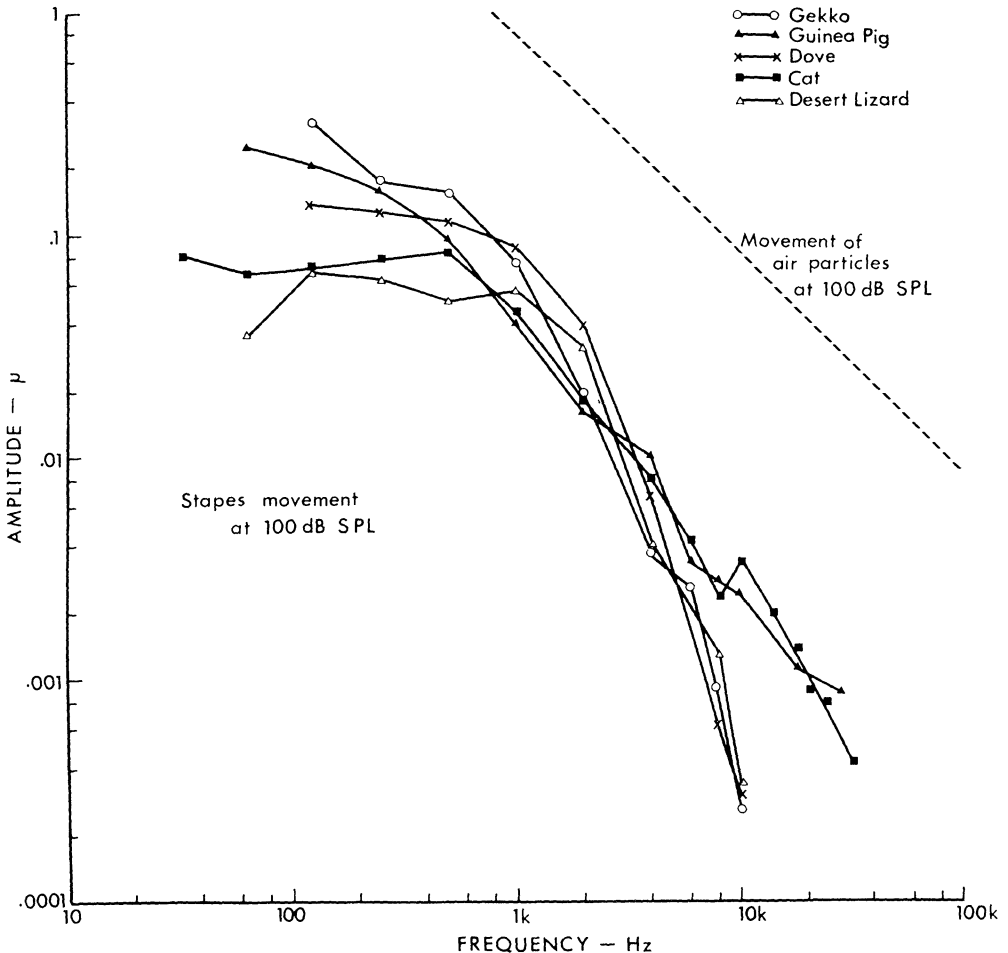
FIG. 2. Amplitude of the columella or stapes in representative reptiles, bird and mammals at various frequencies and for a constant sound intensity of 100 dB re. 0.0002 dynes/cm². Note that above 8–10 kHz the mammalian stapes has a greater amplitude for the same sound levels. After Johnstone, B. M. and K. J. Taylor (1971), J. Oto-Laryngol. Soc. Australia 3: 226–228, Fig. 3.

self is increasingly poor above this frequency (Manley, 1972). The second factor may be partly due to the first, as it appears that the inner ear/columella system impedance as "seen" by the eardrum rises above 6 kHz, such that the columella becomes more resistive to movement. As a result of this, the cartilaginous inferior process bends between its tip and the columella axis, such that very little energy is transmitted down the columella above 8–10 kHz (Fig. 1). Rather, it is absorbed in the bending of the inferior process. When the columella is dis-

connected from the eardrum, no such bending occurs. Thus there are two factors, which may not be unrelated, which limit the frequency response of the ear in this reptile. Because of these factors, the amplitude of the stapes in this non-mammal is below that of mammals above 8–10 kHz. Similar considerations probably apply to other non-mammalian species (Fig. 2).

It should be noted that the inner ear is not capable of analyzing (that is, discriminating between) frequencies which are not normally transmitted through the middle

ear. This was simply demonstrated by Pumphrey (1950) who showed that bone-conducted sounds (which by-pass the eardrum) can be perceived at frequencies much higher than those perceived by the normal route. Above the normal limit there was, however, no perceived change in pitch (for example, a 50 kHz tone had the same pitch as a 15 kHz tone). Where no bending occurs in the middle ear linkage, that is, where the manubrium of the malleus of mammals consists of the more rigid bone, the frequency response of the eardrum itself becomes more important in determining the upper frequency limit. Thus in man, the tympanic membrane response is poor above about 15–20 kHz.

It has recently been shown (Manley et al., 1972) that the tympanic membrane response in the guinea pig is good up to about 35 kHz., and in an echolocating bat up to about 70 kHz. Hensen (1961) noted that the size of the tympanic membrane varied systematically with the hearing ranges of the bats and insectivores he studied. This is partly an effect of animal size (Khanna and Tonndorf, 1969). In the smallest bats and insectivores, an eardrum of small area is correlated with the use of high ultrasonic frequencies (Hensen, 1961). The only large mammals which are able to utilise high ultrasonic frequencies are cetaceans, and in an underwater environment a normal eardrum is useless and unnecessary. It is clear that the middle ear and inner ear characteristics are closely bound up with one another in each species.

Frequency response is only one aspect of middle ear efficiency; sensitivity is also very important. Recent studies on the middle ear in amphibians, reptiles and birds have indicated that from the point of view of energy transmission, the columella ear is very efficient up to 6–8 kHz. (Gaudin, 1968; Manley, 1972; Saunders and Johnstone, 1971; Werner and Wever, 1972). Wever and Werner (1970) in a detailed analysis of middle ear function in lizards demonstrated that the inner ear (in, for example, *Crotaphytus collaris*) suffers an average loss in sensitivity of 35dB when sound is fed directly to the oval window instead of to the tympanic membrane. The middle ear system, which includes a lever action, thus raises the pressure at the oval window about 50 times. This value is greater than equivalent measures for the cat. At some frequencies the middle ear response in some reptiles comes very close to the theoretical maximum (Saunders and Johnstone, 1971). As far as sensitivity is concerned, there is, statistically, no difference between the columella ear of birds and the ear of mammals at the best hearing frequency in each species (Manley, 1971; Masterton et al., 1969) (Fig. 3).

All the above tells us only that the modern non-mammalian terrestrial vertebrates have developed an extremely efficient middle ear, and makes the origin of the mammalian middle ear seem probable only if the Mesozoic reptiles ancestral to mammals had much less efficient systems. In view of our poor understanding of the ear mechanics and hearing abilities of those Mesozoic reptiles ancestral to mammals, do the new data help us to understand the functional changes which caused the selection of the mammalian-type middle ear?

In view of the fact that the mammalian middle ear is not unique in possessing a lever system, it is unlikely that any supposed improvement in high frequency response was the important factor in selection. Also the trends discernable in the evolution of the inner ear, as discussed below make it appear unlikely that mammalian ancestors had the highly elongated basilar membranes necessary for the analysis of high frequencies (i.e., above 6–8 kHz). The cochlear canals of early mammals, which probably also contained a lagena macula, were very short e.g., 3–4 mm in *Triconodon mordax* (Kermack, 1963). It seems probable then that an improvement in sensitivity as a result of the introduction of a lever system where none existed before was the main selective pressure. Hotton (1959) noted that the middle ear of most early reptiles does not show the highly refined adaptation
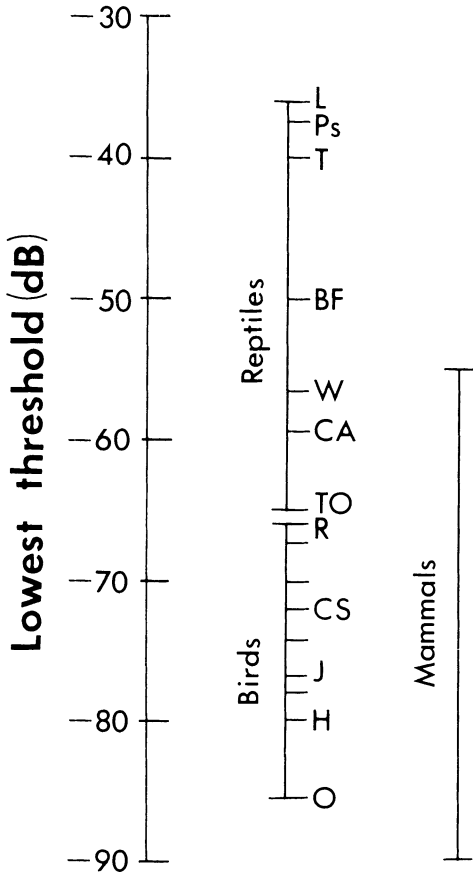
FIG. 3. Distribution of lowest threshold of hearing sensitivity among reptiles, birds and mammals. The dB scale is with reference to 1 dyne/cm². on this scale –74 dB is equivalent to 0.0002 dynes/cm². The mammalian range is from Masterton et al., 1969. Abbreviations: L = Leopard lizard, *Crotaphytus wislizenii* (Iguanidae); Ps = Pond-slider turtle, *Pseudemys scripta* (Chelonia); T = Gulf-coast box turtle, *Terrapene carolina major* (Chelonia); BF = Blue fence lizard, *Sceloporus cyanogenys* (Iguanidae); W = Western banded gecko, *Coleonyx variegatus* (Eublepharidae); CA = spectacled caiman, *Caiman crocodilus* (Crocodilia); To = Tokay gecko, *Gekko gecko* (Gekkonidae); R = American robin, *Turdus migratorius* (Passeriformes); CS = Chipping sparrow, *Spizella passerina* (Passeriformes); J = Slate-coloured Junco, *Junco hyemalis* (Passeriformes); H = House sparrow, *Passer domesticus* (Passeriformes); O = Barn owl, *Tyto alba* (Tytonidae). Reproduced from Nature with permission.

for the reception of air-borne sound as in modern vertebrates. Although in many cases (notably Pelycosaurs and Captorhinomorphs) the stapes or columella was massive, in others it was large but lightly built (Hopson, 1966), was inserted in a relatively large oval window and had a functionally obscure connection with the quadrate. Most authors assume a small cartilaginous extrastapedial process which attached to the tympanic membrane. As noted by Hopson (1966) the mechanics of these middle ears is poorly understood, especially perhaps with regard to the mode of vibration of the various parts in response to air-borne sound. Because of the connection of the stapes with the quadrate it seems unlikely that the relative motion could have been as in modern reptiles, with a lever ratio to assist with impedance matching. Certainly if the configurations were similar to those suggested by Hotton (1959) the middle ear would have had very poor sensitivity to air-borne sound. In Hotton's model, the motion of the medial end of the stapes would have been *greater* than the part in contact with the tympanic membrane, thus amplifying the movement amplitude. Under these conditions, the mass of the stapes and inner ear as "seen" by the eardrum would be much greater than if an amplitude reduction occurred. With an already large stapes and relatively small eardrum it is doubtful whether the eardrum could activate this system, particularly since it was not entirely supported by bone. Hotton's poorly calibrated experiments provide no useful evidence in this regard.

Of course a massive stapes, having high inertia, would be ideal to detect tissue conducted sounds from the substrate. If Hotton's model is correct, perhaps the tympanic membrane served as a release for motions of the stapes induced by tissue conducted sounds in those reptiles with that configuration of middle ear structures. In other cases, where the stapes was more lightly built, as in late therapsids (Hopson, 1966) the situation is different. However, the system would be fairly insensitive to air-

borne sound because the area ratio of tympanic membrane to oval window was small, and it seems unlikely that a lever action existed as described above in modern reptiles.

In spite of this insensitivity, there seems little doubt that in cases where groups of reptiles developed a less massive stapes and a bony support for the eardrum (Romer, 1967) that low frequency air-borne sounds would have activated the system. It is likely that the early reptile inner ear was only able to respond to such low frequency sounds. With regard to the impetus which lead to selection of a middle ear sensitive to air-borne sound, one can only speculate. It certainly seems possible that during the reptile/mammal transition and perhaps other periods, vocal communication became important. A more sensitive middle ear would be necessary in these cases, and greater development of the inner ear would enable more elaborate vocal patterns to be analyzed. In modern reptiles, a well-developed inner ear is associated with vocal behaviour in e.g., crocodiles, alligators and geckos. Where vocality is non-existent or limited and the inner ear basilar membrane is short and poorly elaborated (the latter generally indicating a sensitivity only at low frequencies) it would seem that an air-sensitive middle ear is often lost in favor of a more efficient feeding or chewing mechanism (Berman and Regal, 1967; Olson, 1966; Smith, 1938).

There is evidence that the mammalian three-ossicle middle ear arose at least twice (Hopson, 1966; Parrington, 1967). In therian mammals the eardrum lies above the digastric mandibular depressor, whereas in monotremes it lies below the non-homologous detrahens mandiblae muscle. The mammalian middle ear seems thus to have independent origins in these groups, after their ancestors diverged in the Triassic. The coiled cochlea also probably arose in therian ancestors after they diverged from the monotreme ancestors, as it is unlikely that the monotreme cochlea is secondarily uncoiled.

Had the mammalian ancestors had a middle ear as sensitive as modern reptiles or birds, the redundant bones of the otic region would probably have disappeared altogether. Although modern reptiles tend to be less sensitive to air-borne sound than either birds or mammals, it is probable that little of this difference is attributable to the middle ear (although within-group differences in reptiles are probably partly due to differences in middle ear structure). A poorly differentiated inner ear and low inner ear potentials probably account for most of this difference. In fact, sensitivity in reptile ears is greatest in those with well elaborated inner ears (Manley, 1970b).

INNER EAR POTENTIALS

During the evolution of more sensitive hearing systems, there has been selection for the development of high inner ear potentials. A number of these potentials have been described and measured (Bekesy, 1960; Davis, 1968; Fernandez and Schmidt, 1963; Griffiths, 1968; Schmidt and Fernandez, 1962).

One potential which is important in the transduction process has been called the endocochlear potential. This is a resting dc polarisation across the basilar membrane and the hair cells in the organ of Corti, (endolymph positive relative to perilymph), and reaches +90 mV or more in mammals. On Davis' variable-resistance theory of transduction in the inner ear, this potential and the hair cell internal resting potential of about –70 mV combine to produce a polarisation of 150–160 mV, and a substantial standing current through the depolarised top of the hair cell membrane (Davis, 1968). The effect of sound moving the basilar membrane is to change the resistance of the hair cell membrane, increasing the current flow. The ensuing depolarisation of the cell causes release of a neurotransmitter which stimulates afferent nerve terminals (Fig. 4). If this theory accurately describes at least part of the transduction process, the endocochlear potential is obviously very important in sound trans-
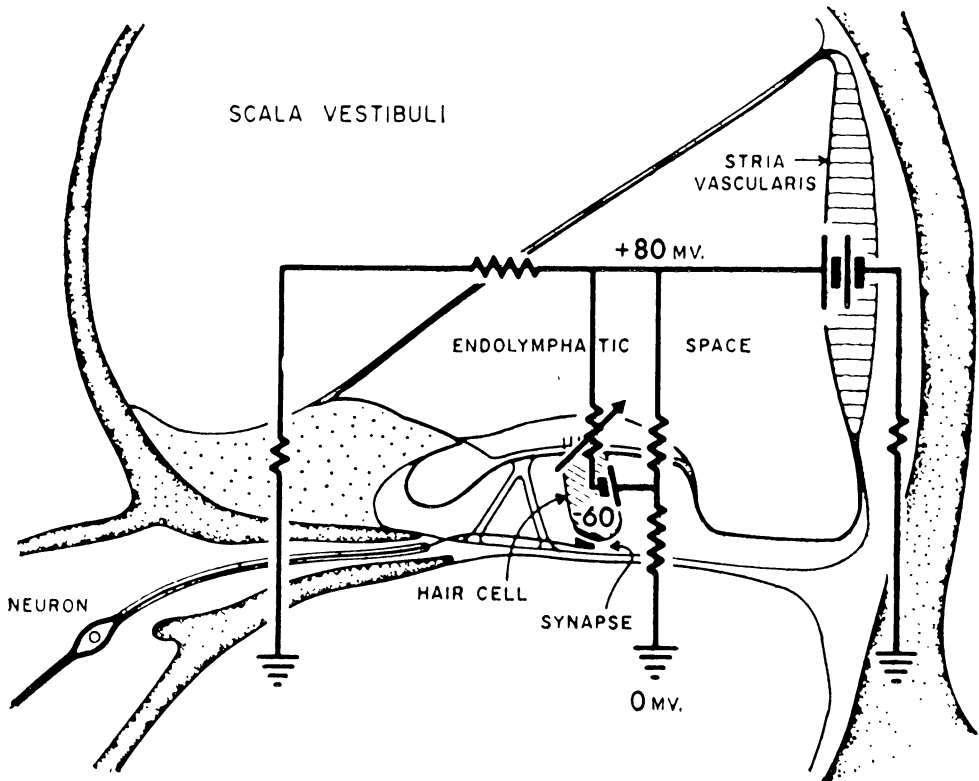
FIG. 4. Diagram of the cochlear partition of mammals illustrating Davis' variable resistance theory of sound transduction. The endolymphatic space or scala media is about +80 to +90 mV relative to the perilymph of the other scalae and, combined with the -60 to -70 mV inside the hair cells, produces a polarization of about 140–160 mV across the ciliated part of the hair cell membrane. The current through the hair cell membrane is assumed to be modulated by shearing forces in the partition produced by sound, which vary the resistance of the hair cell membrane. The stria vascularis generates the positive potential of scala media. Modified after Davis, 1968.

duction, and increases the sensitivity of the ear to sound.

In non-mammals, the endocochlear potential is much lower than in mammals, being about +20 mV in birds and only a few millivolts in reptiles. The cochlear microphonic and summating potentials are also correspondingly smaller. The reptilian endocochlear potential also differs in that it is anoxia insensitive (Schmidt, 1963; Schmidt and Fernandez, 1962). This low endocochlear potential in reptiles means that the current through the hair cells is due mainly to the hair cell internal resting potential, and is therefore about half the current flow found in mammals. Because the current flow is correspondingly weaker, all other factors being equal, it would need a greater change in resistance (i.e., more sound energy) to produce an equal increase in current flow during stimulation of the inner ear. Although the effect on ear sensitivity would be small (about 6 dB), it is probable that part of the average 20 dB inferiority of reptile sensitivity over both birds and mammals is due to this difference. Another part of this difference is undoubtedly due to the investigation of hearing systems of reptiles at temperatures which do not exactly correspond to their

thermal optima. Temperature effects can be quite large (Campbell, 1969; Werner, 1968).

In birds, although the endocochlear potential is significantly smaller than in mammals, it is probably compensated for by introducing a larger summating effect of hair cells on nerve endings. In birds, there are about 30 hair cells in a given cross section of the basilar papilla, in contrast to 4 or 5 in mammals (Pumphrey, 1961).

Thus one of the factors selected for during evolution was high endocochlear potentials, increasing the overall sensitivity of the avian and especially the mammalian ear.

DIMENSIONAL CHANGES IN THE INNER EAR

It has long been known that there are wide variations in the structure of the inner ears of vertebrates (Evans, 1935; Gray, 1908; Pritchard, 1881; Retzius, 1884; Weston, 1939). Variations range from gross changes in the structure of the bony labyrinth and perilymphatic and endolymphatic ducts, to the fine structure of the basilar membrane and sensory cells (Baird, 1969; Pye, 1966a, b; Smith and Takasaka, 1971; Webster, 1966) and tectorial membrane (Wever, 1967a, b), distribution of hair cells (Smith and Takasaka, 1971; Wever, 1965) and hair cell orientation (Baird, 1969, 1970; Mulroy, 1968). The significance of most of these differences is not understood.

The inner ear of amphibians represents a special case, in that in many species it contains two auditory papillae, one of which, the amphibian papilla, has no homologue outside this group. The anatomy and physiology of the anuran system has been fairly well investigated. The basilar papilla is in many ways structured quite differently from that of other groups (Geisler et al., 1964). Physiologically, it has been shown that the sound receptors, the amphibian and basilar papillae, respond to restricted bands of low and higher frequency sound, respectively (Capranica and Frishkopf, 1966; Frishkopf and Geisler, 1966;

Frishkopf and Goldstein, 1963; Frishkopf et al., 1968; Sachs, 1964). The actual frequency bands and sound intensities perceived vary between species (Loftus-Hills and Johnstone, 1970). The two receptors seem to function partly to separate different frequency components in the vocalizations of different species or between the different calls within one species (Capranica, 1966; Loftus-Hills and Johnstone, 1970). This auditory system is obviously a highly specialized offshoot from the mainstream of vertebrate inner ear evolution and is associated with the obvious vocality of many anurans.

In the reptiles, the structure and morphology of the basilar papilla differs in a marked way between groups (Baird, 1960; Hamilton, 1960, 1964; Manley, 1970b, 1971; Miller, 1966; Schmidt, 1964; Wever, 1965). Schmidt (1964) is of the opinion that short, elliptical basilar membranes are the primitive type, and are most similar in morphology to the basilar papilla of modern amphibians. Such elliptical membranes are found in all turtles and snakes, in *Sphenodon* and in some lizards. In all cases, there seems to be a correlation between the width of the membrane and the adult size of the animal. All gradations exist between the ellipse and the quite elongated membranes of alligators and crocodiles, geckos, and many other lizards (Fig. 5). As shown by Bekesy (1960) in birds and mammals, tapering of the basilar membrane is associated with an increase in stiffness and presumably a higher frequency response of the transverse fibres which largely make up the basilar membrane. Although the relationship between the width of the basilar membrane and its stiffness probably varies between groups of animals, there would seem little justification for assuming that where little tapering is found in an elongated membrane no mechanical frequency analysis is possible (Schwartzkopff, 1958). Width is only one of several parameters which show gradients along the basilar membrane and would affect mechanical tuning (Wever, 1965).
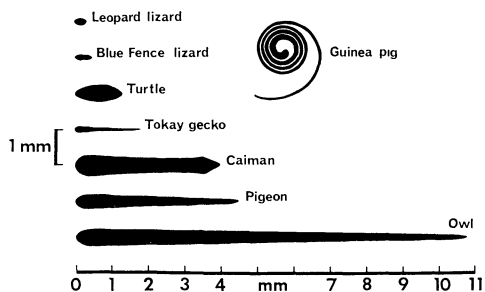
FIG. 5. Diagram of basilar membrane dimensions in some reptiles, birds and a mammal. Slight curves in non-mammalian membranes have been drawn as straight and bilateral symmetry has been assumed. All membranes are drawn to the same length and width scales. The guinea pig membrane is 18.5 mm long. Modified after Manley, 1971, and reproduced with permission.

Physiological studies of audition in reptiles using the cochlear microphonic technique (Wever, 1965, 1967a, b, c; Wever et al., 1965) and brain-cell recording techniques (Johnstone and Johnstone, 1969a, 1969b; G. Manley, 1970a, b; 1971, 1972; J. Manley, 1971; Suga and Campbell, 1967) have produced evidence of a strong differentiation in the ears of some reptiles.

Single auditory neurons in nuclei in the medulla each have a restricted range of frequency-intensity parameters over which they will respond. In general, each has a "characteristic frequency" to which it will respond at lower sound intensities than at other frequencies. In animals with elongated basilar membranes, these response areas all have a rather simple V-shape when graphed, in contrast to the complex shapes found in those reptiles having elliptical or short basilar membranes (Manley, 1970b, 1971, 1972; Suga and Campbell, 1967). This and other differences in response suggest that frequency analysis as carried out by these short membranes contains ambiguity, some cells giving the same response at more than one frequency. Elliptical membranes respond over narrow frequency ranges, the upper limits of which are determined by the width of the membrane. Large turtle membranes are only sensitive

to low frequencies (Gulick and Zwick, 1966; Manley, 1970b; Patterson, 1966). In addition, animals with short membranes are less sensitive to sound, a phenomenon which may be partly due to their possessing only a small number of hair cells. Elongation of the basilar membrane has obviously occurred many times in evolution, and the increase in consistency of frequency analysis which ensued must have been a powerful component of selective pressures.

The mechanical frequency analysis seen in mammals and birds (where there is a representation of different frequencies in terms of position of action on the basilar membrane) most likely occurs in some reptiles. These reptiles (for example, alligators) are those which have elongated basilar membranes and have very mammal-like neural response patterns (Manley, 1970b; Wever, 1967c). Different parts of the brain nuclei have nerve cells responding to different frequency ranges. It has been suggested that this is due to the place-principle of frequency analysis as described above, the distribution of frequencies on the basilar membranes being preserved in orderly projections of the auditory nerve fibres on the brain nuclei, as shown clearly in birds (Boord and Rasmussen, 1963; Konishi, 1970) and mammals (Kiang, 1965; Sando, 1965). This type of analysis can only occur in elongated membranes and was another powerful component of selective pressures favoring evolutionary elongation of the basilar membrane in ancestral reptiles.

Another change which favored elongation was the fact that the longer the membrane, for a given starting width, the higher the frequency to which it will respond. This relationship is a result of the physical principles which dictate the responses of fibres of various sizes to different frequencies. It was demonstrated by plotting the highest frequency analysed in each ear against a basilar membrane value which took the length of each membrane and its width gradient into account (Fig. 6). Higher basilar membrane values were accorded to long, thin membranes (Manley,
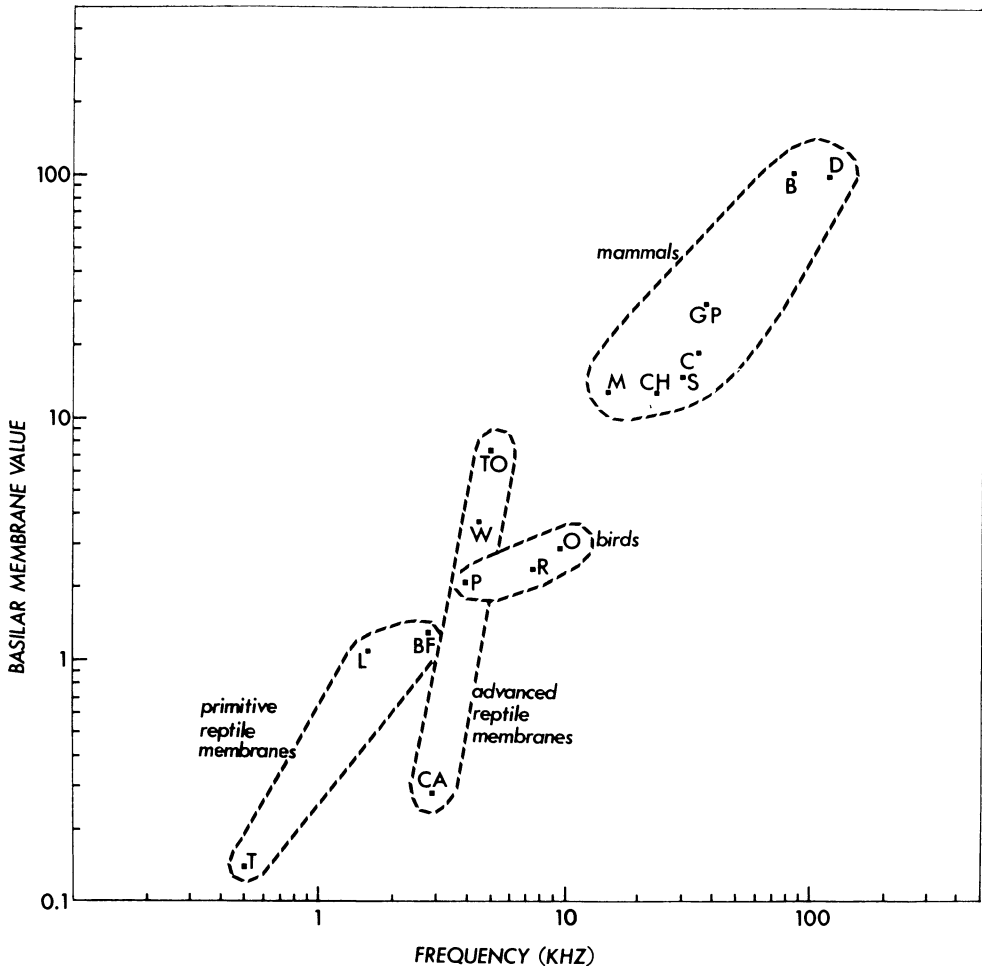
FIG. 6. Correlation between the dimensions of the basilar membrane and the highest character-istic frequencies of single neurons in various vertebrates. The membrane value is the ratio of the membrane shape (length L/widest width Ww) to its width gradient (widest width Ww × narrowest width Wn). Membrane value then = L/Ww:Ww × Wn divided by 100. High membrane values in-dicate long, thin membranes and vice versa. For non-mammal abbreviations see Fig. 3. Mammals: M = man; CH = chinchilla; S = sheep; C = cat; GP = guinea pig; B = bat (*Myotis sp*); D = dolphin. A simple linear regression analysis of these points gave a correlation coefficient of 0.973 and a students *t* test value significant at the .001 level. Modified from Manley, 1971 and reproduced with permission.

1971). Since this figure first appeared, data from the dolphin and the sheep have been added with entirely consistent values from these large mammals (Bullock et al., 1968; Keen, 1939, 1940; Kolmer, 1908; Wever et al., 1971; Wollack, 1963).

In birds, the basilar papilla resembles that of reptiles, although in general it is more elongated (Schwartzkopff, 1955, 1957; Schwartzkopff and Winter, 1960). Correlated with this are frequency response ranges higher than in reptiles (Dooling, 1969; Harrison, 1969; Heise, 1953; Konishi, 1970; Stopp and Whitfield, 1961; Trainer, 1946). In some birds (e.g., barn owl, M. Konishi, pers. comm.) the bony

canals of the cochleae meet in the midline of the head. In these species further elongation of the basilar papilla is impossible. Some birds are thus limited in their frequency response range and, of course, in the frequencies of calls and songs. Despite this limitation, two species of birds, the cave swiftlet and the oilbird have independently evolved an echolocating mechanism for cave-dwelling, using frequencies mainly below 10 kHz.

Although the monotremes have a three-ossicle middle ear, the basilar papilla is quite bird-like (Gray, 1908; Pritchard, 1881) and does not achieve even one turn of a coil. Data on hearing in these few species is scanty (Griffiths, 1968).

In the marsupials and placental mammals, the basilar papilla is, of course, enclosed in a true "cochlea." This coiling has permitted great extensions in the length of the basilar membrane (over 10 cm in some cases, see Hall, 1967) and an equivalent increase in possible frequency range. Mammals perceiving high ultrasonic frequencies have a relatively long and/or narrow basilar membrane (Fraser and Purves, 1960; Hall, 1967, 1969; Reysenbach de Haan, 1957, 1960). Within the bats, a correlation has been noted between the width of the basilar membrane and the frequency of emitted orientation sounds (Hinchcliffe and Pye, 1969b).

Conclusions and Summary

It is obvious that very diverse and very profound changes have accompanied the evolution of all structures associated with the reception and transduction of sound. This paper has presented some physiological and anatomical data which indicates some of the selective pressures which may have brought about these changes.

In the middle ear, the main selective pressure which favored the introduction of the lever ratio between ossicles in the Mesozoic reptiles ancestral to mammals was an improvement in sensitivity over the type of middle ear then extant. Modern columella-systems, for example in birds, have independently evolved to be as sensitive. An improvement noted in high frequency transmission in modern mammal middle ears is unlikely to have been a selective pressure in Mesozoic reptiles.

In the inner ear, selective pressures favoured the development and maintenance of higher endocochlear potentials for greater sensitivity at the hair cell level. With regard to the basilar membrane, elongation from the elliptical condition brought about consistent frequency analysis, and further elongation extended the range of frequencies the membrane could analyze. Physical restrictions have limited this elongation in some birds, but coiling in the mammals has permitted elongation which in some cases allows analysis of very high ultrasonic frequencies.

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