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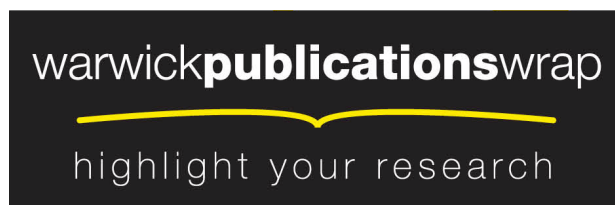
Flexibility within the middle ears of vertebrates

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Abstract

Introduction and aims: Tympanic middle ears have evolved multiple times independently among vertebrates, and share common features. We review flexibility within tympanic middle ears and consider its physiological and clinical implications.

Comparative anatomy: The chain of conducting elements is flexible: even the 'single ossicle' ears of most non-mammalian tetrapods are functionally 'double ossicle' ears due to mobile articulations between the stapes and extrastapes; there may also be bending within individual elements.

Simple models: Simple models suggest that flexibility will generally reduce the transmission of sound energy through the middle ear, although in certain theoretical situations flexibility within or between conducting elements might improve transmission. The most obvious role of middle-ear flexibility is to protect the inner ear from high-amplitude displacements.

Clinical implications: Inter-ossicular joint dysfunction is associated with a number of pathologies in humans. We examine attempts to improve prosthesis design by incorporating flexible components.

Key words: Middle Ear; Flexibility; Ear Ossicles; Malleus; Incus; Stapes; Vertebrates

Introduction: vertebrate middle ears

Sound transduction in vertebrates is performed by the hair cells of the inner ear, which are surrounded by fluid. This presents a problem for the detection of air-borne sound because the acoustic input impedance of the inner ear is much higher than that of air, which would tend to result in the reflection of acoustic energy at the interface. A tympanic middle ear, found in amphibians, reptiles, birds and mammals, consists of a tympanic membrane overlying an air-filled middle-ear cavity, vibrations of the membrane being somehow coupled to the oval window, the entrance to the inner ear. The tympanic middle ear represents an impedance-matching device, allowing a far greater proportion of incident sound energy to be transmitted through to the inner ear than would be the case in its absence. It has been theoretically and clinically demonstrated in humans that ossicular interruption in the presence of an intact drum results in a conductive hearing loss of around 60 dB.[1]

Among vertebrates in general, the tympanic membrane is coupled to the oval window by means of a chain of bony or cartilaginous structures, generically referred to here as 'conducting elements'. In mammals, the conducting elements are the three auditory ossicles: the malleus, incus and stapes. Non-mammalian tetrapods lack a malleus and incus:

their stapes (sometimes referred to as the columella) is coupled to the tympanic membrane via a cartilaginous extrastapes (also known as the extracolumella).

The tympanic middle ear is believed to have evolved several times independently in different vertebrate groups.[2–6] Although details are debated among palaeontologists, it is generally agreed that a tympanic ear evolved once in the ancestors of living amphibians,[7,8] and probably several times within amniotes, including independent origins within the turtle, diapsid (a group including lizards, crocodiles and birds) and mammalian lineages.[2] The mammalian three-ossicle ear is thought to have evolved from ancestors which used their malleus (equating to the articular and prearticular bones) and incus (equating to the quadrate) as part of the jaw joint; it is still unclear if and where a tympanic membrane was present in these ancestors, and to what extent they used their stapes to conduct sound vibrations.[6,9–11] Whether or not a three-ossicle ear actually evolved more than once among mammals remains controversial.[12–14]

Given that a tympanic ear appears to have evolved multiple times within vertebrates, it is instructive to look for convergently derived features which might represent necessary design constraints. Flexibility within the chain of conducting elements, manifested either as relative movement at an articulation between

two components or as bending of one particular component, appears to be one such feature. This paper will review the existence and anatomical basis of flexibility within the ears of living vertebrate groups, with a view to gaining insights into its functional and clinical implications for humans.

Amphibian middle ears

Among amphibians, there is a wide diversity of pathways by which vibrations, travelling initially in air, through a solid substrate or through water, can get to the inner ear.[15] Frogs are the only living amphibian group to possess tympanic ears, but many frog species show reduction or loss of various components. Of those frogs with 'complete' tympanic ears, the best-studied examples are found within the family Ranidae.

The tympanic membrane of ranid frogs is located on the side of the head. The air-filled middle-ear cavity beneath the membrane communicates with the mouth cavity through a wide and typically patent eustachian tube. Tympanic membrane vibrations are communicated to the inner ear via a cartilaginous extrastapes and a largely bony stapes (Figure 1a). Two recent studies on ranid frogs have shown that the stapes is hinged where it articulates with the skull along the ventral rim of the oval window, such that an inwards movement of the tympanic membrane results in an outwards movement of the stapes footplate.[16,17] The conducting elements therefore work as a first-order lever

(like a see-saw or crowbar). Furthermore, given that the ratio of lengths from the tip of the extrastapes to the fulcrum and from the fulcrum to the centre of the stapes footplate exceeds one, force amplification is expected at the oval window relative to the tympanic membrane, at the cost of velocity reduction. This is presumably part of the impedance-matching function of the middle ear. However, in both cited studies the anatomical lever ratios were found to be much lower than the velocity ratios obtained using laser vibrometry, over the measured frequency range of up to 2–3 kHz which largely encompasses the hearing range of these animals. Although velocity ratios were approximately flat over these frequencies, a phase lag was observed between tympanic membrane and footplate which increased with frequency. These observations imply some kind of flexibility within the chain of conducting elements.

The cartilaginous extrastapes in the American bullfrog (*Lithobates catesbeianus*, formerly *Rana catesbeiana*) is tethered to the skull via its thin ascending process, which bends to generate a rocking movement of the extrastapes when the tympanic membrane is pushed inwards.[17] This requires some movement of the distal extrastapes relative to the tympanic membrane, to which it is only loosely attached. The resulting motion of the extrastapes is then coupled to the bony stapes shaft, to which it is fused. Although there is some relative movement at the stapes–extrastapes articulation, which acts as a hinge-joint, researchers
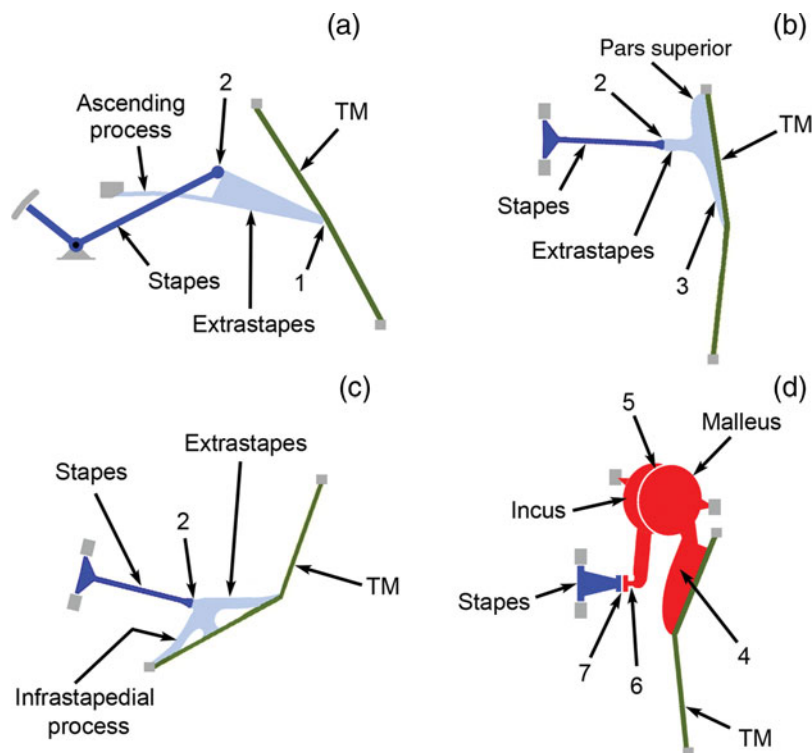
FIG. 1

Diagrammatic representations of the middle-ear structures of vertebrates (not to scale): (a) frog; (b) lizard; (c) bird; and (d) mammal (freely mobile morphology). Some key elements of the conducting apparatus, referred to in the text, are labelled. Numbers indicate regions believed to represent points of flexibility in each group: 1 = attachment of frog extrastapes to tympanic membrane; 2 = articulation between extrastapes and stapes; 3 = reptile extrastapes pars inferior; 4 = manubrium of malleus; 5 = malleo-incudal articulation; 6 = pedicle of lenticular apophysis; 7 = incudo-stapedial articulation. TM = tympanic membrane

have found no evidence of bending of the shaft of the extrastapes itself, up to at least 2 kHz. Although unossified, the extrastapes in the bullfrog therefore works in effect as a second 'ossicle' coupled via a flexible articulation to the stapes proper, a conclusion reached independently by Werner.[18]

The stapes footplate of frogs typically shares the oval window with a cartilaginous operculum; vibrations of the footplate in response to airborne sound are conveyed to the operculum in bullfrogs.[19] The articulation between these two coupled elements represents another source of flexibility within the amphibian middle ear.

Reptile middle ears

Living reptiles are commonly divided into four groups: Testudines (turtles and tortoises), Squamata (lizards, snakes and amphisbaenians), Rhynchocephalia (the tuatara) and Crocodylia (crocodilians). Of these, snakes, amphisbaenians, tuatara and some lizards (e.g. chameleons) lack tympanic ears as defined above, and will not be considered here.

The middle-ear structures of lizards (Figure 1b) have been reviewed by Baird,[20] Wever[21] and Saunders et al.[22] Lizard tympanic membranes are convex externally, unlike those of mammals, and are found at the bottom of short external ear canals. As in frogs, the middle-ear cavities are in free communication with the pharynx by means of short, wide, patent eustachian tubes, and vibration transmission from tympanic membrane to oval window involves a cartilaginous extrastapes and bony stapes. The extrastapes terminates in a number of radiating processes which attain different degrees of prominence in different species. Of these processes, the pars superior and pars inferior together form a bar which inserts along a radius of the tympanic membrane. The ligamentous attachment of the pars superior to the bony frame surrounding the tympanic membrane forms a fulcrum. In some lizards, the articulation between extrastapes and stapes has some degree of mobility and thus is considered a flexible joint, while in others the joint appears to be stiff and is supported by a dense connective tissue sheath.

The extrastapes in lizards is considered to act as a second-order lever (like a wheelbarrow), one lever-arm being the distance between the tip of the pars inferior to the fulcrum at the tip of the pars superior, the other the distance from the point of origin of the extrastapes shaft to the same fulcrum, which equates to the length of the pars superior only.[23] Experimental studies suggest that this kind of lever motion prevails at least up to around 1 kHz in the alligator lizard Gerrhonotus multicarinatus.[24] Studies on the tokay gecko (Gekko gecko), using the Mössbauer technique,[25] have enabled a comparison of the vibrations of the tip of the pars inferior with those of the point of origin of the extrastapes shaft. It was found that the amplitude ratio varied between 6 and 14 dB at low frequencies but increased at frequencies greater than 4 kHz, and exceeded 20 dB at 10 kHz. This increase was attributed

to flexion of the pars inferior at higher frequencies, which would increase the relative velocity of its tip.[26] Using laser vibrometry, Werner et al.[27] found an increase in velocity ratio between the same two points at frequencies over 4 kHz in the gekkonoid Oedura marmorata; however, results from another study, in which the Mössbauer technique was used to compare eardrum and stapes footplate movement in two other species of lizards, were less consistent with this general picture.[28]

The middle ear of crocodiles has not been extensively investigated, but it appears to resemble that of birds (see below). The cartilaginous extrastapes has a number of processes radiating from its distal end.[20,21] The connection between extrastapes and stapes is described as 'a more or less flexible joint'.[29]

Although considered to possess a tympanic ear,[6] testudines lack the thin tympanic membrane usually found in vertebrates specialised for hearing in air. The extrastapes of the terrestrial box turtle Terrapene carolina is expanded distally into a cartilaginous plate, lying underneath largely undifferentiated skin and separated from it by 'a loose network of fibrous and fatty tissue'.[30] The extrastapedial plate is hinged through a stiff ligamentous connection to the skull at its posterior edge, resulting in a lever action which increases force (slightly) at the stapes footplate.[21] No flexibility has been described in the turtle ear, and the structure of the extrastapes appears simpler than that of other non-mammalian vertebrates. However, the connective tissue layer between the skin and the extrastapedial plate would be expected to show some compliant behaviour, and one might expect some kind of bending between the conducting elements if a rocking movement of the extrastapedial plate was to be translated into a piston-like motion of the stapes within the oval window, as Wever and Vernon observed. Marine turtle middle ears are essentially similar to what is described above, except that more fat is present between extrastapes and skin.[31,32] The ear morphology of testudines in general has been regarded as a compromise between aquatic and terrestrial hearing.[33]

Bird middle ears

Birds emerged from within the reptile group. They are most closely related to crocodiles, among living reptiles, which explains the similarities in their auditory structures. Like reptiles, birds have a long, bony stapes which is attached to the externally convex tympanic membrane via a cartilaginous extrastapes (Figure 1c), although the extrastapes may show partial ossification in some adult birds.[34,35] The extrastapes possesses a number of radiating processes which vary in morphology and orientation according to species. Of these, the infrastapedial process extends towards the edge of the tympanic membrane and in some species articulates with its supporting bony rim.[22,36]

Based on a consideration of the anatomy and micromanipulation of the structures involved, the extrastapes

of birds is generally believed to undergo a rocking movement. The exact location of the axis or fulcrum about which the extrastapes rocks differs according to different studies on different species, but the tip of the infrastapedial process is commonly implicated, either as the position of a fulcrum[37] or as one point on a rotatory axis.[36,38] The rotation of the extrastapes would then work as a second-order lever, increasing force at the footplate. Vibration velocities recorded using the Mössbauer technique suggest that simple, rigid-body rotation of the extrastapes occurs at low frequencies up to approximately 1 kHz.[38] At higher frequencies, a rise in the velocity ratio and an increasing phase-lag was observed between the extrastapes and the stapes footplate, thought to indicate a change in vibratory mode which might, at some frequencies at least, involve flexion somewhere within the chain of conducting elements.[38] In anatomical studies and those employing static pressure changes to displace the tympanic membrane, the flattened extrastapes–stapes junction region has been identified as a point of flexibility within the avian middle ear.[36,37,39–41]

Mammalian middle ears

Anatomy of the mammalian ossicular chain

Ossicular morphology in mammals varies considerably, the most extreme adaptations being found, as would be expected, in those species which inhabit atypical acoustic environments, e.g. cetaceans (which are modified to hear underwater)[42] and golden moles (which appear to hear ground vibrations through inertial bone conduction).[43] As Fleischer[44] observed, however, the majority of living mammals fall somewhere on a spectrum ranging between the 'freely mobile' ossicular morphology seen in humans and guinea pigs (Figures 1d and 2a) and the 'microtype' morphology characteristic of bats, shrews and mice (Figure 2b). Anatomical observations suggest that the malleus–incus complex should rotate about an axis extending between the main points of its attachment to the surrounding tympanic cavity walls, i.e. from the anterior process of the malleus to the short process of the incus.[45] The tip of the manubrium of the malleus, which inserts into the tympanic membrane pars tensa, is typically further from this 'anatomical axis' than is the articulation of the stapes at the end of the long process of the incus (Figure 1d), resulting in a second-order lever action which is widely believed to contribute to middle-ear impedance matching. However, the ligamentous attachments of ossicles to the walls of the tympanic cavity tend to allow more than one degree of freedom of movement: rotation about the 'anatomical axis' may be a reasonable approximation only at low frequencies.[46,47]

The human malleo-incudal articulation has been described in detail.[48,49] Among mammals in general, this articulation is typically synovial,[50] the joint surface usually being described as saddle-shaped.[44]
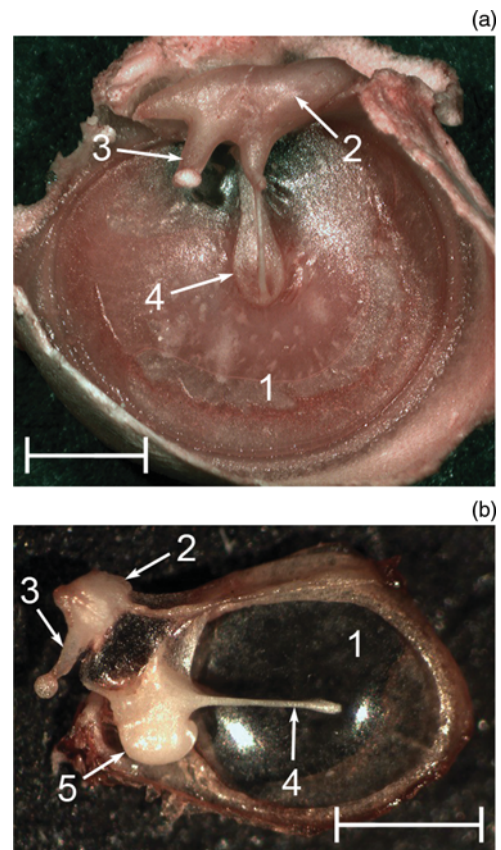
FIG. 2

Light micrographs showing internal views of the tympanic membrane, malleus and incus of two mammalian species. In both, the malleus and incus are fused and the line of articulation between the two ossicles is barely visible. (a) Guinea pig (*Cavia porcellus*), left structures of a stillborn neonate from a laboratory colony (scale bar = 2 mm); the ossicles are 'freely mobile' in this species. (b) Common shrew (*Sorex araneus*), structures in an adult found dead in Cambridgeshire, UK. This species has 'microtype' ossicles (the original image of right structures has been laterally inverted to facilitate comparison) (scale bar = 1 mm). 1 = tympanic membrane pars tensa; 2 = head of malleus; 3 = long process of incus; 4 = manubrium of malleus; 5 = orbicular apophysis

The articular surfaces can be flattened and the inter-ossicular connection very loose in some mammals, notably subterranean species,[51–54] but in certain other mammals the malleus and incus may actually be fused. This seems to be the normal condition among most rodents of the Ctenohystrica clade,[53,55–58] a group including guinea pigs and chinchillas. In the guinea pig, the malleo-incudal articulation starts to form in the embryo but never cavitates.[59]

Contrary to the belief that only 'freely mobile' species such as guinea-pigs have fused ossicles,[44,59] the malleo-incudal articulation also appears to be fused in shrews of the genus *Sorex* (as noted by Burda[60] and M.J. Mason, unpublished observations), which have a 'microtype' ossicular morphology (Figure 2b). The malleus and incus are said to be fused in the echidna and adult platypus too,[56,61] although in the case of the latter this is disputed.[62] There are contradictory reports of malleo-incudal fusion in various other species of mammals, which remain to be confirmed; some of these claims

may arise from stiffened capsular ligaments in dried or preserved specimens.

The anatomy of the incudo-stapedial articulation, formed between the lenticular apophysis of the incus and the head of the stapes, has been best described in humans and cats.[63–65] This articulation is synovial in mammals, with the possible exception of some bat species[50] and the platypus.[61] A fibrocartilaginous disc (meniscus) has been described in humans, separating the joint cavity into two compartments.[63,65] The lenticular apophysis is usually attached to the long process of the incus by means of a thin, bony pedicle, which in many species appears to be flexible.[51,63,66] A finite-element model of the cat incudo-stapedial articulation prompted the conclusion that the pedicle may in fact be more flexible than the articulation between the lenticular apophysis and the stapes itself.[64]

Experimental evidence for flexibility within the mammalian middle ear

From experiments using a capacitive probe, Møller[67] concluded that the malleus and incus of the cat are rigidly coupled at frequencies up to 2.5 kHz, at 'reasonably low' sound pressure levels. Examining ossicular motion visually using stroboscopic illumination, Guinan and Peake[68] found that the cat incus lagged in phase relative to the malleus at sound frequencies over approximately 3 kHz, which they interpreted as evidence of movement at the malleo-incudal articulation. Decraemer and Khanna[69] also reported slippage, increasing with frequency, at the feline malleo-incudal joint. Using the Mössbauer technique in guinea pigs, Manley and Johnstone[70] found an increase in the malleus–incus lever ratio together with an increasing incudal phase lag at frequencies over 25 kHz; it was suggested that this might arise from energy loss at the malleo-incudal articulation, despite this being fused. The source of flexibility within the guinea pig ear merits further investigation.

Guinan and Peake[68] found no significant differences in amplitude or phase between the end of the incudal long process and the stapes in cats at the tested frequencies up to 15.5 kHz at moderate sound pressure levels; however, they did observe movement at the incudo-stapedial joint at sound pressure levels of more than 150 dB.

However, movement at the ossicular articulations is not the only possible source of flexibility within the mammalian middle ear. Experimental evidence from mouse, bat (*Rhinolophus ferrumequinum*), cat and gerbil suggests manubrial bending at high frequencies, the frequencies in question being species-specific but exceeding a few kilohertz.[46,47,71–73] However, significant manubrial bending was not observed in the guinea pig ear, over the measured range of up to 45 kHz.[70]

Flexibility within the human middle-ear apparatus

Although movement at the human malleo-incudal joint at 'physiological' sound pressure levels has long been regarded as negligible,[74–77] recent results obtained using more sophisticated measurement systems show that this is not the case.[69,78–80] Using scanning laser Doppler vibrometry of human temporal bone preparations, Willi et al.[79] demonstrated movement at this joint even at moderate sound pressure levels (i.e. 75–90 dB SPL). A 90 dB SPL stimulus results in a transmission loss of approximately −10 to −15 dB at frequencies greater than 2 kHz.[80] This malleo-incudal flexibility appears to be sufficient to explain the fact that tympanic membrane (umbo) velocity changes little with stapes fixation in humans, such that stapes fixation cannot be reliably diagnosed using tympanometry.[81]

Flexibility elsewhere in the human ear in response to acoustic stimulation has been less extensively examined. Elpern et al.[77] found that experimental fixation of the incudo-stapedial articulation made essentially no difference to the transmission of sound through the middle ear, as measured via vibrations of the round window, but these experiments have been criticised.[79] By introducing experimental fixations of the ossicles within a human temporal bone preparation exposed to a chirp stimulus (containing frequencies from 0.025 to 20 kHz, at 105–114 dB SPL), Nakajima et al.[82] demonstrated that flexibility of the human ossicular chain over the measured frequency range (0.1 to 4–6 kHz) includes a significant incudo-stapedial component. Of the total compliance of the system seen at the umbo, Nakajima et al. estimated that 55 per cent arises from the annular ligament around the footplate of the stapes, 27 per cent from the incudo-stapedial joint, 13 per cent from the malleo-incudal joint and 4 per cent from manubrial bending, although certain simplifying assumptions were made in obtaining these values.

Although the idea of significant malleo-incudal flexibility in humans at normal sound pressure levels has only recently gained general acceptance, it has long been recognised that greater pressures applied to the ear result in joint movement. Such pressures include 'non-physiological' sound pressures[83] and the results of physical probing.[84] Hüttenbrink[85] found that static air pressures of up to ±400 mmH$_2$O in the external ear canal resulted in a gliding movement at both inter-ossicular joints, the result of which was a reduction of stapes displacement relative to the displacement of the tympanic membrane. Hüttenbrink found that stapes displacement was 21 times less than manubrium displacement in the normal ear, but only 4.2 times less following experimental fixation of the malleo-incudal joint.

Effects of flexibility in vertebrate ears

Rather than working as simple pistons, the evidence reviewed above suggests that the 'columellar' conducting elements of frogs, lizards and birds actually rotate about an axis. The resulting lever arrangement is believed to increase force at the oval window, in an analogous manner to what is achieved by the three-ossicle system of mammals. Some form of flexibility,

often occurring at a joint between conducting elements, also appears to be universal within tympanic ears: the supposedly 'single ossicle' ears of non-mammalian vertebrates are functionally 'two ossicle' ears. Testudines may represent an exception, but these animals appear adapted to some extent towards aquatic sound reception, for which different rules apply.

Some level of flexibility must be inevitable given stimuli of high enough amplitude or frequency. It may in some cases be geometrically necessary, for example in order to convert rotation of the extrastapes into a piston-like motion of the stapes shaft in birds.[37,39] Whether an inevitable by-product or an adaptive feature in its own right, flexibility will have an effect on the function of the middle ear.

Predictions from a simple model

In order to assess the likely effects of flexibility within a chain of conducting elements, we shall first consider the implications of a very simple model (Figure 3a), based on that of Nakajima et al.[82] The model consists of two ossicular elements (ossicle 1 and ossicle 2, consisting of masses L_1 and L_2 moving at velocities v_1 and v_2, respectively) connected together by a spring (compliance C_1) representing a flexible inter-ossicular joint; ossicle 2 is articulated with the skull by means of a second spring, C_2. The motion of any real middle-ear apparatus is clearly far more complex than the one-dimensional vibration considered in our model, especially at high frequencies, but our purpose here is only to outline the general effects that flexibility between the ossicles might be expected to have, in the simplest case.

An electrical analogue to the mechanical model of Figure 3(a) is represented as Figure 3(b). Here, velocities are represented as currents: current I_1 (passing through inductor L_1) represents the velocity of ossicle 1, while I_2 (passing through L_2) represents the velocity of ossicle 2. We shall assume for the moment that

FIG. 3

(a) A simple mechanical model of a middle ear containing two ossicular conducting elements separated by a compliant articulation. (b) An electrical analogue of model (a). See text for details.

the system is driven by a sinusoidal pressure source (a voltage, in the electrical analogue) with no source impedance. It can be shown that:

$$\frac{I_2}{I_1} = \frac{1}{1 - \omega^2 C_1 L_2 + \frac{C_1}{C_2}} \quad (1)$$

where ω is the radian frequency of vibration. As frequency tends to zero, the denominator of equation 1 tends to $1 + (C_1/C_2)$, the result obtained by Nakajima et al.[82] This means that ossicle 2 moves with a lower velocity than ossicle 1, for all non-zero values of C_1. When frequency is very high, the relative velocity of ossicle 2 tends to zero. Without a concomitant increase in force as might be expected of a stiff lever mechanism, a reduced velocity of ossicle 2 reflects a loss of power.

It is instructive also to compare the difference in absolute velocity of each ossicle, between the conditions of inter-ossicular flexibility ($C_1 > 0$) and total ossicular fusion ($C_1 = 0$). The ratio of the two velocities of ossicle 1 can be calculated as follows:

$$\frac{I_{1(C_1>0)}}{I_{1(C_1=0)}} = \frac{[C_1 + C_2 - \omega^2 C_1 C_2 L_2][1 - \omega^2 C_2(L_1 + L_2)]}{C_2[1 - \omega^2 C_2(L_1 + L_2) - \omega^2 C_1 L_1 + \omega^4 C_1 C_2 L_1 L_2]} \quad (2)$$

As ω tends to zero, the right-hand side of equation 2 tends to $(C_1 + C_2)/C_2$, while at high frequencies it tends to $(L_1 + L_2)/L_1$. A flexible ossicular joint therefore increases the velocity of ossicle 1 at the lowest frequencies, and it does the same at the highest frequencies for all non-zero values of L_2.

Turning to ossicle 2, the equivalent ratio of velocities in the flexible and fused states is:

$$\frac{I_{2(C_1>0)}}{I_{2(C_1=0)}} = \frac{[1 - \omega^2 C_2(L_1 + L_2)]}{[1 - \omega^2 C_2(L_1 + L_2) - \omega^2 C_1 L_1 + \omega^4 C_1 C_2 L_1 L_2]} \quad (3)$$

As ω tends to zero, the right-hand side of equation 3 tends to one. At high frequencies, the ratio tends to zero, the result of the velocity of ossicle 2 tending to zero faster with a flexible inter-ossicular joint than it would if fused to ossicle 1.

Overall, this simple model suggests that inter-ossicular joint flexibility will have the following effects. (1) The relative velocity of ossicle 1 exceeds that of ossicle 2 at both very low and very high frequencies. (2) The absolute velocity of ossicle 1 is increased at both very low frequencies (compliance-dominated; both springs flex) and very high frequencies (in which case it becomes substantially easier to move one mass than two). (3) Although unaffected at very low frequencies, at very high frequencies the absolute velocity of ossicle 2 declines to zero faster with a mobile inter-ossicular joint. (4) At certain intermediate frequencies (when the denominators of equations 2 and 3 are equal to zero), resonance will occur within the system.
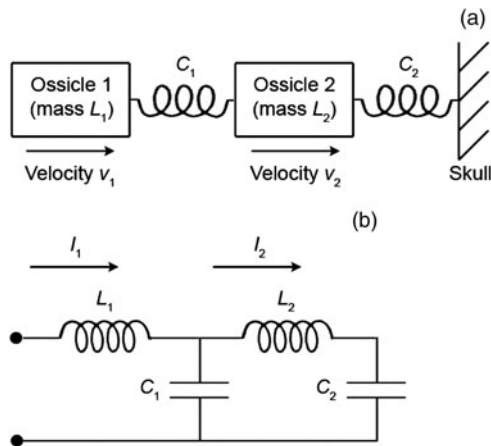
These conclusions are essentially the same if the model is extrapolated to three ossicles. In general terms, the velocity of 'upstream' ossicles at both the lowest and highest frequencies is increased by 'downstream' compliance, while the velocity of 'downstream' ossicles is reduced by 'upstream' compliance, but at high frequencies only. A reduced velocity of ossicle 2 will translate into reduced power transmission to the cochlea at these frequencies. Resonance will increase the velocity of ossicle 2 at intermediate frequencies, but high amplitudes and sharp tuning could be detrimental to hearing. Resonance can be reduced by resistance in the inter-ossicular joint(s), at the cost of reduced power transmission to the cochlea; resistive source or load impedances can also reduce resonance in the system. If we introduce a high source impedance, the limiting case being a pure velocity source driving the system (a current source, in the electrical analogue), the absolute velocity of ossicle 1 is less affected by ossicular fusion, but the above conclusions 1, 3 and 4 still hold.

In a comparison of power flow from middle to inner ears between humans, cats and guinea pigs, at frequencies from approximately 0.2 to 10 kHz, guinea pigs were calculated to have a higher power transfer efficiency than the other two species across nearly the whole frequency range.[86] Of these species, only the guinea pig has a fused malleo-incudal articulation, consistent with the above model's predictions that ossicular flexibility is generally detrimental to the transmission of sound energy.

Given that ossicular flexibility is predicted to result in reduced velocity of 'downstream' ossicular elements at high frequencies, we would expect it to be particularly detrimental to high-frequency hearing. Hearing tends to be limited to the sonic range in non-mammalian vertebrates,[22,87,88] although Feng et al.[89] report an exception. Sound localisation at low frequencies is made possible in these animals through the use of their acoustically coupled ears as pressure-difference receivers.[90] Flexibility-induced reduction of sound transmission at higher frequencies may therefore be of little consequence.

The hearing ranges of mammals extend to much higher frequencies than those of other vertebrates, exceeding 100 kHz in some echo-locating bats (for an example, see Heffner et al.).[91] It has been argued that such high-frequency hearing was made possible by the evolution of the mammalian ossicular chain, which, being ossified, has greater stiffness than the equivalent conducting elements in non-mammalian tetrapods.[5] However, only a minority of living mammals (not including bats) possess fused mallei and incudes, despite the fact that fusion would appear to benefit sound transmission still further. Why do ossicular articulations remain flexible in most species?

Could flexibility ever improve acoustic transmission?

Ossicular fusion is clearly achievable among mammals and, according to our simple model, should improve sound transmission at high frequencies at least. Most mammals, however, retain mobile ossicular articulations, which suggests that flexibility confers some kind of adaptive advantage. Three proposals from the literature suggest that flexibility could under certain circumstances improve sound transmission through mammalian middle ears.

'Transmission line' hypothesis. The controversial theory that the mammalian middle ear works as a 'transmission line'[72,92,93] requires that the conducting elements be regarded as a series of masses coupled by springs, each mass-stiffness pair being matched to the load impedance of the cochlea. The flexible joints between the ossicles then act as shunting stiffnesses which counteract the effect of the ossicular masses, the result of which is wide-band and potentially 'lossless' sound transmission at the cost of acoustic delay.[92,93] Such a mechanism would explain not just the presence of the inter-ossicular articulations but also the otherwise paradoxical capability of the mammalian middle ear to transmit acoustic energy at very high frequencies. A phase lag has indeed been measured in human middle-ear transmission from umbo to stapes, and this is reduced by experimental fixation of the ossicular joints.[94] However, the predictions of the transmission line hypothesis are only upheld in the gerbil middle ear at frequencies from 5 to 35 kHz, not at lower or higher frequencies,[95] suggesting that things are not this simple.

Change in ossicular rotatory modes. Based on calculations of ossicular rotatory moments of inertia, Puria and Steele[96] have argued that the mallei of humans and cats adopt different rotatory axes in response to high-frequency sound, which would reduce their moments of inertia and so improve sound transmission. The new mode of malleus vibration could be communicated through to the incus by means of the flexible malleo-incudal articulation, working as a type of gear. Puria and Steele have suggested that this change in rotatory mode is not necessary in small mammals such as guinea pigs and chinchillas because their ossicular moments of inertia are already small, hence their fused malleo-incudal articulations. Given that ossicular fusion is actually very unusual among small mammals, fusion of the malleo-incudal joint in guinea pigs and chinchillas is more likely to relate to something specific to these animals rather than just to size,[97] perhaps their unusual malleus morphology.[98]

Reduction in tympanic membrane constraint. The simple model described above predicts that inter-ossicular flexibility will increase the absolute velocity of motion of ossicle 1, at both the lowest and the highest frequencies. Could this make it easier for the tympanic membrane, to which this ossicle is attached, to vibrate? A related idea has been proposed by Funnell et al.,[99] considering just the manubrial process of the malleus. Although a completely flexible manubrium will fail to couple vibrations through to the

malleus body, a rigid manubrium might significantly constrain membrane movement and add mass loading if rigidity is conferred through making it more robust. This being the case, a light manubrium with some limited flexibility might, at least in principle, represent the optimal design.

Any or all of these three proposals might help to explain the prevalence of ossicular flexibility in mammals. However, it should be noted that there is as yet only limited evidence supporting the transmission line hypothesis, and that the other two proposals (i.e. altered ossicular rotatory modes and reduced tympanic membrane constraint) await experimental verification.

Flexibility and pressure-buffering

The high pressures found within the middle-ear cavities of frogs, associated both with 'force-pump' ventilation and vocalisation, result in sometimes visible bulging of the tympanic membranes outwards.[100–103] The externally located membranes are also vulnerable to external insult. Flexibility within the frog middle ear must confer some protection against such 'quasi-static' pressure changes, which would otherwise result in damagingly high-amplitude movements of the stapes footplate within the oval window.[17,19] Contraction of the opercularis muscle might contribute to this protection,[19] as might pressure-release features of the inner ear.[100,104]

In other terrestrial vertebrates, ventilation does not involve the high pressures expected of a force-pump mechanism, and the tympanic membrane is protected by an external meatus. However, a slow decrease in middle-ear pressure has been recorded in birds, reset probably by opening of the eustachian tubes and pressure changes during vocalisation.[105] The avian middle ear might also be subject to significant pressure changes when flying or (in some species) diving.[41] Middle-ear pressure changes in birds affect the frequency response of the tympanic membrane through their effects on membrane displacement.[105] Flexibility within the chain of conducting elements is believed to protect the avian inner ear against the effects of such pressure changes.[39,41] Contraction of the stapedius muscle might contribute to this protective mechanism by increasing the amount of flexion that is possible between stapes and extrastapes.[41]

Flexibility within the mammalian ossicular chain is also thought to protect the annular ligament and inner ear against excessive stapes displacement caused by high static pressures.[75,85,106] Middle-ear pressure changes exceeding 1 kPa are said to occur with events such as gushes of wind, sneezing and diving in humans,[85] and pressures of up to 5 kPa can occur during the Valsalva manoeuvre.[107] When middle-ear pressure was increased by 1.6 kPa in a human temporal bone preparation, the umbo was found to be displaced by over 300 μm, a value three orders of magnitude greater than the umbo displacement measured by Tonndorf and Khanna[108] in response to a 121 dB SPL acoustic stimulus at 525 Hz.[109] Positive pressures inside the middle-ear cavity give rise to a greater umbo displacement than negative pressures,[110] which may relate to the amount of flexion possible at the inter-ossicular joints in each direction.[111] Given that mammalian middle-ear pressure fluctuates slowly throughout the day,[112] the flexibility of the articulations might also contribute to accommodation of the middle-ear apparatus, allowing efficient transmission at all times.

It is unknown to what extent static pressure changes represent a problem for reptiles, and whether they too use flexibility as a protective mechanism.

Middle-ear muscles and ossicular joints

Middle-ear muscles have been described in all tympanic middle ears except, apparently, the unusual testudine ear. The literature on middle-ear muscle function in mammals is very extensive, and there are significant differences between species. We shall restrict our discussion here to the possible relationships between the muscles and ossicular chain flexibility in mammals.

Although the most familiar role of the mammalian middle-ear muscles is in the acoustic reflex in response to loud sounds, muscle activity in humans has been found to occur in many circumstances which might involve changes in middle-ear pressure relative to atmospheric pressure, including vocalising, laughing, coughing, eructation, swallowing, yawning, voluntary contractions of the soft palate or base of the tongue, and a general startle arising from an air-jet to the eye.[113–116] When middle-ear pressure is high, the tensor tympani could be used to restrain outwards movement of the malleus.[85] This circumstance might also arise in acute otitis media. It has been proposed that hearing thresholds are affected by intracochlear static pressures,[117] in which case restraining the movement of the ossicular chain could be useful in maintaining optimal pressure within the inner ear. Conversely, if tensor contraction indirectly pushes the stapes footplate further into the oval window and thereby increases inner-ear pressure, this could form part of a protective reflex.[117] However, it is currently unclear what effect the tensor tympani actually has on ossicular movement; while some have suggested that contraction of this muscle tightens the ossicular joints among mammals in general,[44] others have found that traction applied to the tensor in humans appears to decouple malleus from incus.[83]

The effects of stapedius contraction are better understood. In both cats and humans, this results in a sliding motion of the incudo-stapedial joint, such that the stapes head moves caudally relative to the lenticular apophysis.[75,118,119] This is thought to pull the footplate outwards from the oval window, stiffening the annular ligament and reducing transmission of vibrations.[118] Pulling the lenticular apophysis backwards in human temporal bone preparations also results in lateral

(outward) movement of the manubrium of the malleus.[85,119] According to Hüttenbrink,[85] the malleo-incudal articulation must be mobile for this to occur. Such an effect would allow the stapedius to act as the antagonist to the tensor tympani with respect to manubrial motion in humans, but whether this applies to mammals in general is not clear. No displacement of the malleus or incus was detected with stapes head displacements of up to 65 μm in the cat.[118] Middle-ear muscles have also been suggested to 'exercise the joints', aiding the circulation of synovial fluid and thereby keeping them from stiffening.[85]

Clinical implications of ossicular joint flexibility in humans

Ossicular joint pathology in humans

The effects of otosclerosis, whereby the stapes becomes fixed within the oval window, are well-known. However, other pathological conditions are believed to affect flexibility within the ossicular chain itself. Malleo-incudal fusion has been shown to occur in Treacher Collins syndrome,[120,121] branchio-oto-renal syndrome,[122] trisomy 13–15[121] and congenital aural atresia.[123] Joint fusion usually coexists with many other abnormalities in these congenital syndromes, making interpretation of its effects difficult.

It should in principle be easier to identify effects specifically associated with ossicular joint pathology in cases of arthritis. Evidence that the synovial inter-ossicular joints develop increased stiffness and even fusion in osteoarthritis comes both from histological observation[124–126] and tympanometric and audiometric data.[127] 'Moderate' to 'severe' arthritic changes in the malleo-incudal joint were found in all 36 ears taken from individuals older than 70 years, and also in a significant proportion of younger ears, although the donors showed no clinical evidence of middle-ear disease.[126] If flexibility decreases acoustic transmission, joint fusion may increase the sound intensities to which the cochlea is exposed; it is interesting in this regard to note that elderly people are at increased risk of noise-induced hearing loss.[128]

A histological study of rheumatoid arthritis has also suggested malleo-incudal and incudo-stapedial joint involvement,[129] and the expected increase in stiffness of the middle ear has been documented.[130–133] In contrast, other studies have found a decrease in stiffness,[134,135] but this could relate to changes in other parts of the ear, such as the tympanic membrane[134] or the joint capsules and ligaments.[133] Small conductive and sensorineural hearing losses have been reported in a proportion of patients with rheumatoid arthritis.[132,136–138] It has been suggested that the sensorineural hearing impairment may be due to an increase in compressive force on the labyrinth,[131] perhaps due to a relative inability to buffer static pressure changes. However, alternative hypotheses include the effects of systemic neuritis, vasculitis or salicylate toxicity.[133] The inter-ossicular joints may also be affected in the ears of patients with juvenile idiopathic arthritis.[139]

Flexibility in ossicular replacement prostheses

An extreme example of loss of joint flexibility in the human middle ear is reconstruction with a total ossicular replacement prosthesis (TORP). In ears reconstructed with a TORP, a 10-fold increase in pressure at the oval window (the inner ear having been removed) has been measured when pressure in the ear canal is varied.[140] The potential for most severe damage arises following surgery for otosclerosis, when the restraining effect of the annular ligament is functionally eliminated.[85] Rupture of the oval window membrane due to barotrauma on landing in an aeroplane has been reported in one patient with a prosthesis.[141] In a study of patients who had undergone stapedectomy and 'standard' wire or Teflon wire prosthesis insertion 28–30 years previously, the initial gains in hearing following surgery were found later to have been lost. After Carhart correction, sensorineural function was found to be superior in non-operated, otosclerotic ears than in operated ears of the same patients,[142] consistent with a hypothesis that loss of flexibility in a reconstructed middle ear increases the chance of hearing impairment.

Mills[143] argued that efforts at human middle-ear reconstruction should be directed towards recreating something more similar to the three-ossicle arrangement. This author's incus–stapes replica achieved this to an extent, and included a flexible 'joint'.[144] This prosthesis has been demonstrated to undergo less movement in the medial to lateral plane in response to static pressure variation, theoretically reducing the risk of cochlear damage.[144]

Variation from optimal tension across the middle ear due to sub-optimal prosthesis length leads to impaired sound transmission.[145–147] Currently, selecting the correct prosthesis length is based solely on clinical experience, which places considerable demands on the surgeon and may be complicated by post-operative inwards movement of the tympanic membrane.[148] It has been suggested that a more flexible prosthesis will lessen the deleterious effect of incorrect length selection.[149] Attempts to produce such prostheses have met with varying success.[149–154] Whether the potential benefits would outweigh the loss of transmission introduced by the additional flexibility has been questioned.[155]

Comparative anatomy has informed ossicular replacement prosthesis design, although most attention to date has been focussed on birds.[143,154] A closer look at some of the universal features of tympanic ears among vertebrates in general, such as the apparent requirement for a flexible lever, may provide important insights.[156] Given the diversity of ear types both between and within major vertebrate groups, the

species chosen as experimental models for human ear pathologies must be selected with care.

Conclusion

Tympanic middle ears have evolved multiple times independently among vertebrates. The chain of conducting elements typically forms a first- or second-order, force-amplifying lever. Flexibility may represent a universal feature of the conducting element chain in vertebrate tympanic ears, although this has yet to be demonstrated in testudines.

Simple models suggest that flexibility will generally reduce the transmission of sound energy through the middle ear, especially at high frequencies. The most likely adaptive role of such flexibility is to buffer the ear against high-amplitude static pressure changes.

Loss of flexibility could result in sensorineural hearing loss, due either to increased transmission of unbuffered pressure changes to the inner ear, or to an increase in transmitted sound intensity. Flexibility may theoretically improve acoustic transmission in some circumstances; if this is the case, then reduced flexibility may result in conductive hearing loss.

Acknowledgements

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