The Journal of Laryngology & Otology (2006), ***120***, *1005–1007*.

doi:10.1017/S0022215106002581
Printed in the United Kingdom
First published online 21 August 2006

Main Article

Applied comparative physiology of the avian middle ear: the effect of static pressure changes in columellar ears

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Abstract
We investigated the motion of the single ossicle found in the middle ears of four different species of birds. In the avian middle ear, the off centre attachment of the extracolumella to the tympanic membrane and the flexion of the joint between the extracolumella and columella results in rocking of the footplate rather than direct excursion in and out of the vestibule. We postulate that this is a protective mechanism to avoid excessive displacement of the footplate into the vestibule during changes in middle-ear pressure and that it is analogous to the ossicular 'decoupling' observed in the human middle ear in the same circumstances.

Key words: Ear, Middle; Hearing; Bone Conduction; Prostheses and Implants; Surgical Procedures, Operative

Introduction

The primary function of the middle ear is the transmission of sound to allow hearing. The eustachian tube is required to maintain middle-ear pressure at atmospheric pressure so that sound transmission occurs efficiently. In extreme conditions, such as during flying and diving, this mechanism may fail to equalize the pressure effectively, especially if eustachian tube function is impaired.

Huttenbrink[1] studied the motion of the ossicular chain during changes in static pressure in human temporal bones. He identified a protective mechanism in which the movements of the malleus in the lateral to medial plane are translated into motion of the incus in a predominately inferior to superior plane. This results in rocking of the stapes, rather than motion in and out of the vestibule. Our own work, also in fresh human temporal bones, has confirmed this finding and has also demonstrated that prostheses placed between the malleus and the stapes head generate a motion in which the stapes is moved in and out of the vestibule.[2] Angulation of the prosthesis, for example in specimens with a relatively anteriorly placed malleus, decreases this type of motion.

Human beings have evolved to live on land and therefore to experience relatively small changes in static pressure. It appears unlikely that any functional or structural changes have occurred to accommodate the bigger pressure changes which occur during flying and diving, given the relatively short period (in evolutionary terms) that mankind has indulged in these activities.

Birds have a single ossicle, consisting of an extracolumella attached to the tympanic membrane, a columella and a footplate. Figure 1 shows the ossicles from a duck and a gannet, with a human incus for comparison. Birds are creatures 'designed' for flight and some species also dive under water. One might expect that they would have a mechanism for protecting the cochlea from changes in static pressure.

We therefore decided to investigate the motion of the avian ossicle during changes in static pressure. The anatomy of the avian middle ear is also of interest because of its similarity to the reconstructed human middle ear, although there are some important differences.[3]

Materials and methods

Experiments were carried out on fresh birds' heads. The birds used in the study had died of natural causes (these birds included a glaucous gull (*Larus hyperboreus*), a rock dove (*Columba livia*) and a gannet (*Morus basanus*)) or been killed for food (pheasants (*Phasianus colchicus*)). The heads were removed and frozen as soon after death as possible.

The middle ear was accessed via a postaural approach. Sufficient bone was removed to expose the medial surface of the tympanic membrane, the extracolumella and the lateral portion of the columella (Figure 2). This also allowed visualization of the stapedius muscle. After the initial experiments had been completed, more bone was removed from the oval window niche in the pheasant and rock

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Accepted for publication: 11 April 2006.

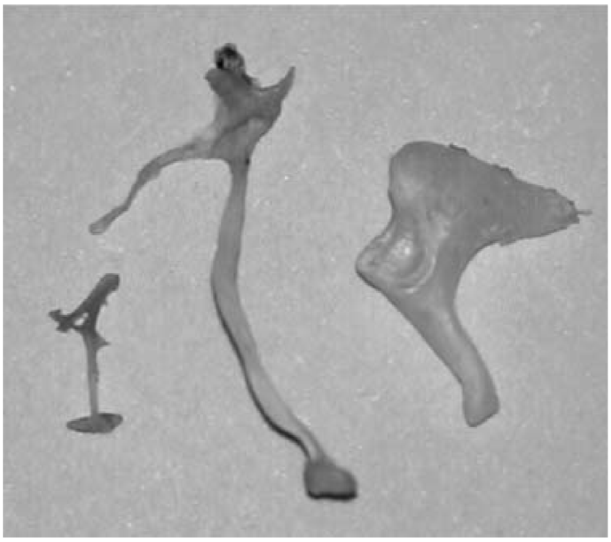

FIG. 1
Ossicle from a mallard duck (*Anas platyrhynchos*) (left) and an atlantic gannet (*Morus basanus*) (centre), with a human incus (right) for comparison.

dove to allow visualization of the footplate. In the rock dove, the vestibule was opened and motion of the footplate was observed from its medial side (Figure 3). A plastic tube was placed in the external auditory meatus and cemented to its bony opening with epoxy resin to produce an air-tight seal (Figure 4).

Specimens were placed in a temporal bone holder and the external auditory meatus was connected to an Amplaid 720 manual impedance meter (Amplaid Ltd, Spa, Italy) via a three way connector. The third channel was connected to a digital pressure gauge (Testo Ltd, Alton, Hampshire, UK. Dazzle Multimedia Inc., Freemont, CA, USA) so that the pressure delivered by the impedance meter could be checked for accuracy. The impedance meter was used to alter the pressure in the external auditory

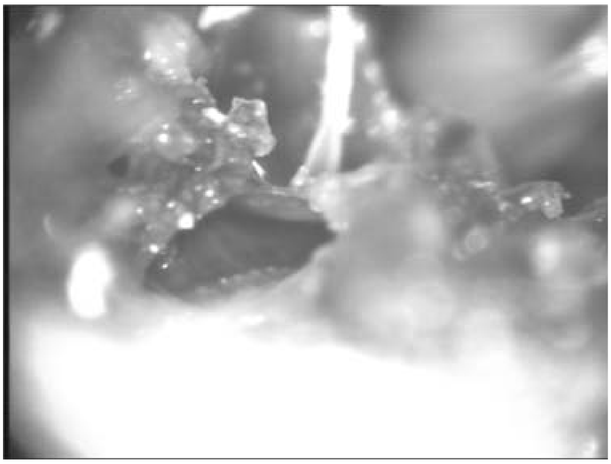

FIG. 3
View of the middle ear via a post-aural approach in the rock dove (*Columba livia*). The vestibule has been opened and the underside of the footplate can be seen. A rocking motion was evident during changes in static pressure.

meatus. This produced movements of the tympanic membrane and ossicular chain analogous to those occurring during changes in middle-ear pressure. The movements of the intact avian ossicular chain during +100 to −100 dPa pressure sweeps were recorded as digital clips, using the Dazzle DVC 80 device (Testo Ltd, Alton, Hampshire, UK. Dazzle Multimedia Inc., Freemont, CA, USA).

Results

In birds, the extracolumella is attached to the tympanic membrane away from its centre. In all the avian species we studied, an increase in the pressure within the external auditory meatus resulted in medial displacement of the drum and extracolumella. This motion was not fully transmitted to the columella because of tilting of the extracolumella and flexion at the joint between the extracolumella and

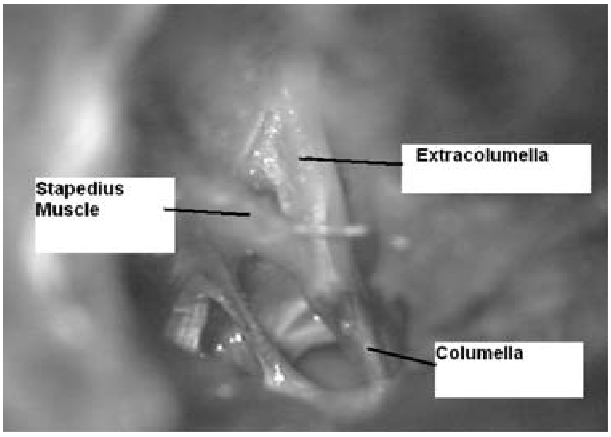

FIG. 2
View of the middle ear via a post-aural approach in the glaucous gull (*Larus hyperboreus*). Movement at the joint between the columella and extracolumella could be seen during changes in static pressure.

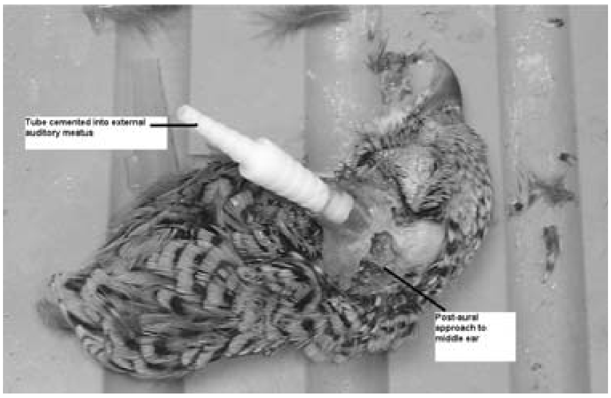

FIG. 4
Experimental apparatus. A tube for connection to the impedance meter has been cemented into the external auditory meatus of a pheasant (*Phasianus colchicus*). The middle ear has been opened via a post-aural approach so that the motion of the ossicle can be observed.

columella (see video of Figure 2 at http://www.jlo.co.uk). This tilting of the extracolumella was least marked in the gannet. The movement of the footplate within the oval window of the rock dove was a rocking motion around its anterior edge (see video of Figure 3 at http://www.jlo.co.uk).

Discussion

In the avian middle ear, the tilting of the extracolumella during changes in static pressure appears to be a protective mechanism to minimize medial displacement of the footplate into the vestibule. Nevertheless, in the cadaveric preparations used in this study, there was still significant displacement of the columella and footplate in this direction. However, this motion produced rocking of the footplate rather than direct displacement into the vestibule. Significant displacements were produced with much smaller pressure changes than those employed in human temporal bone studies.

The joint between the columella and extracolumella is the site of attachment of the stapedius muscle to the extracolumella. Anteriorly, there is a ligament which is so arranged that it will tighten when the stapedius muscle contracts. If the muscle contracts, the flexion at the joint will be increased and there will be less displacement of the columella in the medial/lateral plane. Assuming that such a reflex pathway exists, this would enhance the protective effect of the mechanism described above. It might be expected that birds whose ears were subjected to larger changes in static pressure might have larger stapedius muscles. Although the gull had a larger muscle than the pigeon or pheasant, the gannet stapedius muscle was very small, especially considering that it was by far the biggest species studied.

- **Deterioration in cochlear function following ossiculoplasty is an uncommon event and appears more likely following total rather than partial ossicular replacement**
- **Changes in static pressure move prostheses and tend to drive the footplate into and out of the vestibule**
- **In the avian ear, the single ossicle moves in such a way that the footplate tilts during changes in static pressure**
- **A novel incus/stapes replacement which connects the malleus head to the stapes footplate avoids direct movement into and out of the vestibule during changes in static pressure *and may protect the inner ear from trauma***

Most avian species possess a mechanoreceptor in the middle ear called the paratympanic organ. This is thought to be a baroreceptor[4] and could be involved in the mechanism proposed above. The stapedius muscle of the chicken (*Gallus gallus*) contracts in response to the bird's own vocalizations.[5] There is no acoustic reflex,[5] and vocalization-related stapedius muscle activity is more marked in young birds than in adults, suggesting that it has a role in vocal development.[6]

The gannet was the most interesting species studied because it flies higher than the pheasant or pigeon and also swims under water when hunting for fish. When diving from height it can hit the water at 60 miles an hour.[7] It regularly dives to a depth of 60 feet when pursuing fish.[7] Of the species studied, it was therefore the one in which cochlear damage was most likely to occur as a result of static pressure changes. The ossicle of the gannet is longer than a human incus, but the footplate and extracolumella are proportionately smaller than those found in the other species studied. The tympanic membrane is small and indistinguishable from the skin of the external auditory meatus. The gannet's vocal repertoire is limited and, because of its size and natural habitat, it probably relies little on hearing to avoid predators. The structural adaptations observed in its middle ear probably represent a compromise between these requirements.

Acknowledgements

We thank Professor Eric Abel for advice on setting up our static pressure experiments.

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Dr R P Mills takes responsibility for the integrity of the content of the paper.
Competing interests: None declared