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Deformation of avian middle ear structures under static pressure loads, and potential regulation mechanisms

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ABSTRACT

Static pressure changes can alter the configuration and mechanical behavior of the chain of ossicles, which may affect the acoustic transfer function. In mammals, the Eustachian tube plays an important role in restoring ambient middle ear pressure, hence restoring the acoustic transfer function and excluding barotrauma of the middle and inner ear. Ambient pressure fluctuations can be potentially extreme in birds and due to the simple structure of the avian middle ear (one ossicle, one muscle), regulation of the middle ear pressure via reflexive opening of the pharyngotympanic tube appears all the more important. In this study the deformations of the chicken (*Gallus gallus domesticus*) middle ear structures, as a result of middle ear pressure alterations, are quantified, using micro-CT scanning. It was experimentally tested whether reflexive opening of the pharyngotympanic tube to restore ambient middle ear pressure is present in chicken and mallard (*Anas platyrhynchos*) and whether this mechanism depends on sensing middle ear pressure indirectly via deformations of the middle ear components or sensing the middle ear pressure directly. A translation of the columella footplate was observed when middle ear pressure was kept at 1 kPa and −1 kPa relative to ambient pressure. Deformation of the tympanic membrane was larger than the columella footplate translation. Bending and deformation of the extracolumella was observed. Opening of the pharyngotympanic tube occurred at random pressure for both chicken and mallard when middle ear pressure was raised and lowered by 1.5 kPa relative to ambient pressure. We also did not find a difference in middle ear venting rate when middle ear pressure was held constant at 0.5, 1, 1.5, −0.5, −1 and −1.5 kPa for chickens and at 1, 2, 4, −1, −2 and −4 kPa for mallards. As a result, no statement can be made about pressure within the avian middle ear being measured directly or indirectly. Our experiments do not support the presence of a short-loop reflexive control of pressure equilibration via the pharyngotympanic tube. However, it is still possible that triggering this loop requires additional sensorial input (e.g. visual, vestibular) or that it occurs voluntarily (being controlled at a higher brain level).

1. Introduction

When tetrapods made the transition from water to land the development of the middle ear (ME) structures was essential to match the acoustic impedance between the outside air and the fluid-filled inner ear. Without the mechanical impedance match 99.9% of sound energy would be lost due to reflection (Møller, 1974). The ME ossicles are contained in an air-filled cavity with a mostly rigid wall and one opening is sealed off by the tympanic membrane. A connection between the ME cavity and the nasopharynx exists both in mammals (Eustachian tube) and in birds (pharyngotympanic tube). In mammals it has been shown that the Eustachian tube is closed most of the time. In normal conditions it occasionally injects small volumes of nasopharyngeal gas into the middle ear. When, mostly due to external circumstances, very large pressure differences develop between the ME cavity and the ambient pressure, it has the function of a protective valve (Dirckx et al., 2013) and can release over- or underpressure. The main pressure regulation mechanism in the mammal ear is a complex interplay between eardrum deformations, Eustachian tube gas injection and, most importantly, gas exchange over the mucosa covering the inner walls of the ME cavity and the air cells in the mastoid. In birds, a mucosa-lined mastoid is not present. However, the ME cavity and air cavities in the skull (connecting the two MEs) are covered with mucosa so gas exchange can be present. It could be that the pharyngotympanic tube

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might play a more prominent role in ME pressure regulation.

The mammalian ME contains three bony ossicles (malleus, incus and stapes), two muscles (tensor tympani muscle and stapedius muscle) and some ligaments (anterior and superior mallear ligament; posterior incudal ligament and the annular ligament) to transmit (and modulate) the sound waves from the tympanic membrane to the inner ear. The ME cavity is also enclosed within one single bony structure and the only connection to the pharynx is via the Eustachian tubes, one at each side of the head (Møller, 1974; Rosowski, 1996; Ades et al., 2012). The mammalian ME is subjected to slow and sudden pressure changes due to changes in ambient pressure (e.g. changing altitude, diving in water etc.). These pressure changes may cause a pressure differential over the tympanic membrane resulting in deformations of the tympanic membrane, thus altering the configuration and mechanical behavior of the chain of ossicles. This may affect the acoustic transfer function (Murakami et al., 1997; Teoh et al., 1997; Lee and Rosowski, 2001; Dirckx et al., 2006). When pressure changes are extreme (cfr. underwater diving: 10.1 kPa/m), barotrauma of the ME and inner ear can occur (e.g. rupture of the tympanic membrane, the inner ear membranes, oval and round window) (Melamed et al., 1992). The articulated multiple ossicles, muscles and ligaments of the ME enable to (partly) compensate for these altered mechanics, but cancelling the pressure differentials over the tympanic membrane is a more direct way to restore the normal transfer.

The effects of static pressure changes on the mammalian ME are well known and described (Hüttenbrink, 1988; Dirckx and Decreamer, 1991; Dirckx et al., 2006). During experiments conducted by Dirckx et al. (2006) on cadaveric rabbits' temporal bones, where ambient pressure was altered from −2.5 to 2.5 kPa, the umbo (of the tympanic membrane) was displaced by 0.165 mm while the stapes amplitude was only 0.034 mm. In humans the complex interplay between gas exchange processes, eardrum deformation and, to some extent, Eustachian tube action regulates the pressure differences between the ME cavity and ambient pressure (Dirckx et al., 2013). In the human middle ear, it has been shown that both over- and underpressure can develop over time and that normal Eustachian tube action does not reset the pressure to ambient conditions (Padurariu et al., 2016). Under normal conditions these Eustachian tubes are closed. During reflexive behaviors, including swallowing and yawning, muscles will enable gas transfer through the Eustachian tube between the ME and the pharynx (Siedentop et al., 1968; Rosowski and Merchant, 2000). Therefore, a baroreceptor function is premised at the level of the ME but the exact appearance and sites of these receptors are still under debate (Rockley and Hawke, 1992). For example, Nagai and Tono (1989) and Nagai et al. (1989) reported mechanoreceptors (Vater-Pacinian corpuscles) in the tympanic membrane and ME which are suggested to be sensitive to deformations of the tympanic membrane which may play a role in Eustachian tube action.

In birds, the ME contains one ossicle with a bony shaft (the columella) and a cartilaginous, trifurcated distal end (the extracolumella), some ligaments (ascendens ligament, drumtubal ligaments, Platner's ligament and annular ligament) and one muscle (stapedius muscle) (Smith, 1904; Starck, 1995; Saunders et al., 2000) (Fig. 1A). The MEs at both sides of the head are connected to each other by intracranial air-filled cavities and the interaural pathway which is part of the Y-shaped pharyngotympanic tube (Fig. 1B). Increasing the pressure outside one ear makes the tympanic membrane of the contralateral ear bulge out (Wada, 1923; Schwartzkopff, 1955; Counter and Borg, 1979) (Fig. 2). The avian MEs are also connected with the pharynx via the pharyngotympanic tube, which is also closed (Saunders et al., 2000) (Fig. 2). Under normal conditions ME pressure slowly decreases 20 Pa below ambient pressure. When this pressure is reached, venting of the ME (opening of the pharyngotympanic tube) occurs. As such, depending on the species, regular venting of the ME occurs at constant ambient pressures, every 20–180 s (Larsen et al., 1997, 2016).

However, much larger pressure differentials than a few tens of Pa/s are likely to occur as a result of birds' behavior. Many species frequently climb and descend several hundreds of meters in a relatively short time span. The bar-headed goose (*Anser indicus*), for instance, can bridge altitude differences of 6000 m starting at sea level in one flight (total pressure drop of ± 54 kPa (Hawkes et al., 2011), and stoop-dive flights of peregrine falcons, reaching speeds as high as 100 m/s (e.g. Ponitz et al., 2014), go along with pressure rates of change above 1 kPa/s (own estimates). In case of plunge-diving birds, such as gannets, these rates of change may even rise to several tens of kPa/s (based on, e.g., Brierley and Fernandez, 2001; Capuska et al., 2011). Due to the simple structure of the ME (one ossicle, one muscle), the capability to compensate for the inherently affected mechanical transfer by adjusting the properties of the chain connecting the tympanic membrane with the inner ear seems to be much less in birds, compared to the mammalian ME. Therefore, given the potentially large and fast ambient pressure fluctuations, the possibility to effectively regulate the ME pressure via reflexive opening of the pharyngotympanic tube appears all the more important.

If reflexive pressure equilibration via pharyngotympanic tube ventilation is present in birds, there is also a need for a system that can sense the pressure changes in the ME. Whatever the sensor is, from the mechanical point of view it could theoretically function in two different ways: either it senses the ME pressure directly, or it relies on the stress or strain changes that emerge when the mechanical chain of the ME

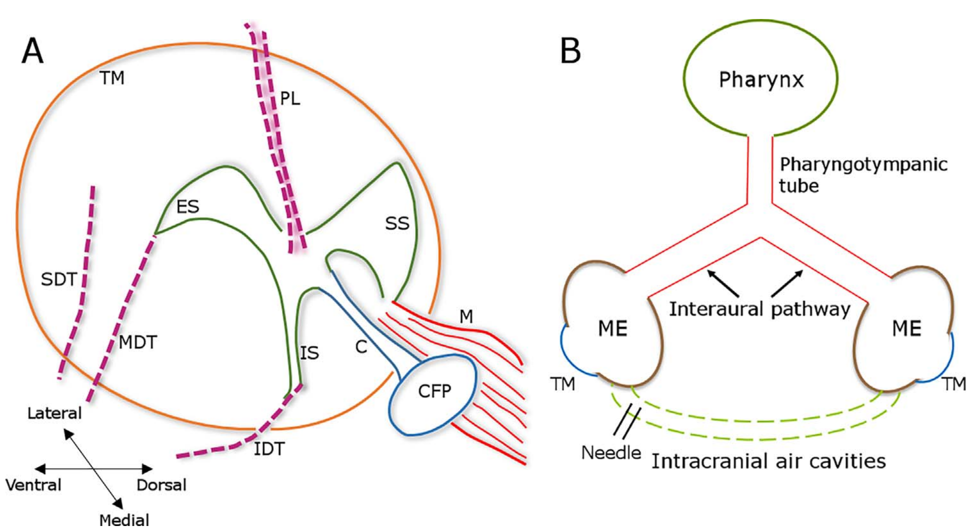

Fig. 1. (A) Medial view of the middle ear (ME) components: tympanic membrane (TM), columella (C), columella footplate (CFP), extrastapedius (ES), infrastapedius (IS), suprastapedius (SS), Platner's ligament (PL), superior drumtubal ligament (SDT), medial drumtubal ligament (MDT), inferior drumtubal ligament (IDT) and tympanic muscle (M). Deduced from Smith (1904). (B) Schematic overview of the connections between pharynx and middle ears (ME), with pharyngotympanic tube, interaural pathway and intracranial air cavities.