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Research Paper

Limits on normal cochlear ‘third’ windows provided by previous investigations of additional sound paths into and out of the cat inner ear

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ABSTRACT

While most models of cochlear function assume the presence of only two windows into the mammalian cochlea (the oval and round windows), a position that is generally supported by several lines of data, there is evidence for additional sound paths into and out of the inner ear in normal mammals. In this report we review the existing evidence for and against the ‘two-window’ hypothesis. We then determine how existing data and inner-ear anatomy restrict transmission of sound through these additional sound pathways in cat by utilizing a well-tested model of the cat inner ear, together with anatomical descriptions of the cat cochlear and vestibular aqueducts (potential additional windows to the cochlea). We conclude: (1) The existing data place limits on the size of the cochlear and vestibular aqueducts in cat and are consistent with small volume-velocities through these ducts during ossicular stimulation of the cochlea, (2) the predicted volume velocities produced by aqueducts with diameters half the size of the bony diameters match the functional data within ±10 dB, and (3) these additional volume velocity paths contribute to the inner ear's response to non-acoustic stimulation and conductive pathology.

1. Introduction

Traditional models of cochlear function consider the inner ear to be filled with incompressible fluid and surrounded by rigid incompressible bone, with the exception of two mobile windows: the oval window (OW) and the round window (RW) (Zwislocki, 1950, 1965; Peterson and Bogert, 1950). This view has been supported by animal measurements of the sensitivity of the inner ear to direct sound stimulation at the OW and RW (e.g. Wever and Lawrence, 1950; Voss et al., 1996), and by the similarity of the simultaneous volume displacements of the two windows with sound stimulation of the oval window (Kringlebotn, 1995; Stenfelt et al., 2004). The most telling results of these window stimulation studies are that simultaneous stimulation of the cochlear windows by equal level tones of the same frequency (the magnitude of the sound pressure at the oval, $\boldsymbol{P}_{OW}$, and round window, $\boldsymbol{P}_{RW}$, are equal) 1). produces maximum cochlear response (measured by round-window cochlear microphonic) when the tonal stimuli are exactly out-of-phase ($\angle \boldsymbol{P}_{OW} - \angle \boldsymbol{P}_{RW} = \pm\pi$ radians), and 2). produces a minimum in cochlear microphonic when the two stimuli are exactly in-phase ($\angle \boldsymbol{P}_{OW} = \angle \boldsymbol{P}_{RW}$). Voss et al. (1996) demonstrated that the relative sensitivity of the cochlea to equal sound pressure at the OW and RW was at least 30–40 dB lower than the sensitivity to an equal magnitude sound pressure delivered to just one of the windows. The ratio of these sensitivities is the *Common Mode Rejection Ratio (CMRR),* which is sensitive to additional volume-velocity paths in the ear: In general, the more significant the additional paths, the lower the *CMRR.* Although this relationship between low *CMRR* and significant shunt pathways breaks if the shunts are applied symmetrically in a symmetric system, the inner ear is inherently asymmetric with a relatively high-magnitude impedance of the stapes and its ligament at the OW, and a relatively low-magnitude impedance of the round-window membrane at the RW.

Another factor that limits the *CMRR* is the presence of compressible cochlear contents. Indeed, the contribution of such compressibility is difficult to distinguish from the effect of

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List of variables and abbreviations

C, M or R	an acoustic compliance, mass or resistance
CA	cochlear aqueduct
CMRR	Common Mode Rejection Ratio
OW and RW	oval window and round window respectively
P_{OW}	sound pressure applied to the lateral surface of the oval window
P_{RW}	sound pressure applied to the lateral surface of the round window
P_{ST}	sound pressure in the scala tympani medial to the round window
P_{SV}	sound pressure in the scala vestibule medial to the oval window
U_{CH}	volume velocity through the cochlear partition and helicotrema
U_{RW}	volume velocity of the round window
U_S	volume velocity of the stapes footplate
U_{VA}, U_{CA} and U_{Brain}	volume velocities through the vestibular and cochlear aqueducts and into the braincase respectively
VA	vestibular aqueduct
Z_{Brain}	acoustic impedance associated with compression of the fluids and tissues within the braincase
Z_{CA}	acoustic impedance of the cochlear aqueduct
Z_{CH}	acoustic impedance of the cochlear partition and helicotrema
Z_{RW}	acoustic impedance of the round window
Z_{SAV}	acoustic impedance of the stapes, annular ligament and vestibule
Z_{SC}	acoustic input impedance of the stapes, cochlea, oval window and round window
Z_{VA}	acoustic impedance of the vestibular aqueduct
$\angle X$	phase angle of X
$\lvert X \rvert$	magnitude of X

additional anatomical windows. Shera and Zweig (1992) estimated in humans that equating the compressibility of the cochlear contents with the physical compressibility of water would lead to window stimulation differences that are comparable to the highest *CMRRs* measured by Voss et al. (~40–50 dB).

Other physical investigations of additional volume-velocity paths out of the cochlea are comparisons of the volume displacement of the OW and RW when the OW is stimulated by stapes motion (Kringlebotn, 1995; Stenfelt et al., 2004). Though the data suggest window volume displacements can differ by as much as 40% (up to 3 dB), this near equality is used as evidence against the importance of additional cochlear sound pathways.

Our interest in investigating the contribution of additional normal sound pathways in the inner ear (besides the OW and RW) comes from recent clinical data by Coletti and others, who use direct mechanical stimulation of the RW as a treatment for conductive hearing loss (Colletti et al., 2006; Beltrame et al., 2009; Tringali et al., 2009). This work suggests that direct RW stimulation can help patients with multiple conductive disorders, including those with immobilized stapes footplates. Such reports are contrary to the two-window incompressible cochlear model that predicts immobilization of either OW or RW produces a total conductive hearing loss that cannot be effectively treated by stimulation of the other window.

A further contradiction of the two-window models is that RW occlusion, which should produce a large 60 dB+ hearing loss, appears to have inconsistent effects on hearing. Tissue grafts placed on the RW in patients actually appear to improve hearing (Houghson, 1937). Reports of patients with RW atresia (bony closure of the window) usually describe hearing losses of only 20–40 dB (Linder et al., 2003; Borrmann and Arnold, 2007). There are also a number of animal measurements (e.g. Tonndorf and Tabor, 1962; Nageris et al., 2012; Cai et al., 2013) that suggest that RW immobilization produces less-than-total reductions in ossicularly conducted hearing, with losses of only 20–45 dB.

Other evidence for the existence for additional sound pathways in and out of the cochlea comes from studies investigating non-ossicular sound conduction to the inner ear. Stenfelt et al. (2004) demonstrated a frequency-dependent inequality of the volume displacements of the OW and RW produced by bone-conducted vibrations of a human temporal bone, while Tonndorf and Tabor (1962), and Chhan et al. (2016) demonstrated that RW or OW immobilization produced relatively small decreases in the cochlear response in animals stimulated by bone-conduction vibrators. Finally, using mechanical stimulation of the RW in a human cadaveric preparation, Stieger et al. (2013) detected sound flow through an additional sound pathway located on the vestibular side of the cochlea.

The purpose of this paper is to use a model based on cochlear anatomy and physiological measurements in domestic cat, together with independent physiological measurements of the *CMMR* in the same species (Voss et al., 1996) to place anatomical and physiological limits on the effect of additional sound pathways on the response of the ear to stimulation of the RW and OW.

2. Methods

We use the cat inner ear, because we know much about its anatomy, acoustics and macromechanics; data also exist that describe how the cochlear microphonic (a measure of the sensory mechanism in the ear) is affected by simultaneous stimulation of the OW and RW in cat (Voss et al., 1996). An existing model (Lynch et al., 1982) is modified by the addition of an anatomically realistic cochlear aqueduct (CA) and vestibular aqueduct (VA), where these fluid-filled connections between the cochlea and the brain are often hypothesized to act as additional sound pathways into and out of the inner ear (e.g., Gopen et al., 1997; Sohmer et al., 2000; Stenfelt, 2015; Elliott et al., 2016). The modified model is used to predict the effect of these additional windows on the cochlea's response to sound stimulation of both windows. We also use the model to predict 1) difference in the RW and OW volume velocities when one window is stimulated, and 2) the effect of window fixations on cochlear sensitivity.

2.1. *The baseline model of stapes and cochlear input impedance in cat*

In the two-window model of Lynch et al. (Fig. 1 and Table 1), the input impedance of the inner ear, Z_{SC}, is the series combination of three impedances:

$$Z_{SC} = Z_{SAV} + Z_{CH} + Z_{RW} \tag{1}$$

where the impedance of the stapes, annular ligament and the fluid within the vestibule is