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Spatial distribution of electrically induced high frequency vibration on basilar membrane

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Abstract

We reported that the electrically evoked basilar membrane (BM) vibration at frequencies above the best frequency (BF) showed a lowest BM velocity magnitude, called a "dip", in the velocity–frequency spectra, indicating a cancellation. In the present study, we measured the high frequency BM motion as functions of the longitudinal and radial locations. Measurements were taken at three longitudinal locations in the first turn and the hook region: 14.9, 15.8 and 16.8 mm from the apex, corresponding to the BFs of 17, 21.3 and 28.0 kHz calculated from Greenwood [J. Acoust. Soc. Am. 87, 2592], and at different radial locations across the width of the BM. It was found that the dip frequency (DF) varied with the longitudinal and radial locations. In the longitudinal direction, the average value of the DF was 49.6, 55.6 and 72.8 kHz, respectively. Thus, the longitudinal distribution of the high frequency BM vibration was correlated with the BF. In the radial direction, there was consistent variation of the response spectrum such that the dip was mainly evident in the pectinate zone of the BM. These results imply that the high frequency BM motion is related to mechanical properties of the cochlear partition, including the outer hair cells (OHCs) themselves. Data also indicate different vibration modes across the width of the organ of Corti.

Keywords: Electromotility; Vibration; High frequency; Laser Doppler velocimeter; Cochlea; Basilar membrane; Outer hair cells; Guinea pig

1. Introduction

The outer hair cells (OHCs) of mammalian organ of Corti are able to convert electrical fluctuation of their transmembrane potential to cell length variation. This, the so-called OHC electromotility, has been demonstrated in isolated OHC experiments (Brownell et al., 1985; Kachar et al., 1986; Ashmore, 1987; Santos-Sacchi and Dilger, 1988; Frank et al., 1999). The motility is fast enough to follow changes in the membrane potential at auditory and ultrasonic frequencies (Dallos and Evans, 1995b; Frank et al., 1999). The OHC electromotility in vivo is considered to function within a cycle-by-cycle sound amplification mechanism by feeding back mechanical energy with the correct phase to the basilar membrane (BM) to enhance vibration or drive the BM. It has been shown in vivo that electrical stimulation applied into the cochlea can evoke otoacoustic emissions (Hubbard and Mountain, 1983; Nuttall and Ren, 1995; Ren et al., 1996; Nuttall et al., 2001) and induce BM motion (Xue et al., 1995; Nuttall et al., 2003; Grosh et al., 2004).

Based on the membrane resistance and capacitance of OHCs, a low-pass membrane filtering will occur, restricting the OHC electromotility force or stiffness change at high frequencies (Housley and Ashmore, 1992; Santos-Sacchi, 1992; Preyer and Gummer, 1996).

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Nevertheless, OHC electromotility was observed at least up to 79 kHz in an isolated OHCs experiment (Frank et al., 1999). Our previous in vivo studies have shown a high frequency BM motion above the best frequency (BF) extending to 100 kHz evoked with electrical stimulation at the round window (RW) or across the cochlear duct (Nuttall et al., 2003; Grosh et al., 2004). In these studies, the velocity magnitude spectrum above BF showed a low of BM velocity, called a "dip", at a frequency around 50 kHz when the measurement was taken at a location about 14.9 mm from the apex (a BF location of 17 kHz). We defined the dip frequency (DF) as the frequency with the lowest magnitude and a rapid phase transition. A different pattern of BM motion evoked with electrical stimulation was also observed at the tunnel of Corti compared to the OHC region (Grosh et al., 2004).

These results showed that the OHC electromotility evoked with electrical stimulation has sufficient force to move the BM at such high frequencies (Nuttall et al., 2003; Grosh et al., 2004). The different radial pattern of the electrically evoked high frequency BM motion was assumed due to the asymmetrical mechanical properties of the organ of Corti and the involvement of the OHC electromotility, the test for which was by salicylate-induced reduction of the BM responses (Grosh et al., 2004).

Studies have revealed that the motility of OHC is based on a membrane protein motor that directly converts electrical energy to mechanical force (Zheng et al., 2000; Dallos and Faker, 2002). Conformational transitions of this membrane protein motor accompany charge transfer across the membrane resulting in mechanical displacement of membrane. The electrical and mechanical changes are coupled, analogous to piezoelectricity (Iwasa, 2001). Piezoelectric OHC models have been proposed for the lateral membrane motor of OHC (Mountain and Hubbard, 1994; Tolomeo and Steele, 1995; Weitzel et al., 2003). A recent equivalent circuit made for the OHC that includes piezoelectricity showed a greater mechanical admittance at high frequencies than one containing only the membrane resistance and capacitance (Weitzel et al., 2003). This model predicted resonance at ultrasonic frequencies that is inversely proportional to cell length (Weitzel et al., 2003).

We hypothesized that the longitudinal and radial patterns of high frequency vibration should depend on the mechanical properties of the cochlear partition. These mechanical properties will result from the variation of the length of OHCs, the width and stiffness of the BM and other cellular components. To test this hypothesis, we measured the BM vibration evoked by acoustic and electrical stimulation at three longitudinal locations of approximately 28.0, 21.3 and 17.0 kHz of the BFs. We also measured the BM vibration at different radial locations across the width of BM at the above longitudinal sites. This study extends our previous work (Nuttall et al., 2003; Grosh et al., 2004) with a more detailed investigation of the longitudinal and radial pattern of the electrically induced BM motion at the basal turn and hook areas.

2. Materials and methods

2.1. Animal preparation

Young pigmented guinea pigs ($n = 15$) with normal hearing (strain 2, NCR, obtained from the Charles River Laboratory, weighing 250–350 g) were divided into three groups with five animals, each for the different longitudinal measurements. In general, the BM data were collected only from one longitudinal location per animal with a single exception as mentioned below. Surgical and experimental protocols used in animals were approved by the Institutional Animal Care and Use committee of Oregon Health and Science University and complied with the animal-use standards of the National Institutes of Health. Animals were anesthetized with a combination of ketamine (40 mg/kg) and xylazine (10 mg/kg), injected intramuscularly. Surgical anesthesia level was maintained with the same dosage administered intramuscularly hourly or as needed based on a positive paw-pinch reflex. A tracheotomy was performed and a ventilation cannula was inserted into the trachea to facilitate spontaneous respiration. Core body temperature of the animals was maintained at 38 ± 1°C with a heated blanket and cochlear temperature was additionally controlled by a heated head holder and a lamp. The lateral part of the external ear canal was removed, and the remaining bony part of the ear canal was connected to a coupler containing a pair of condenser microphones (Bruel and Kjaer, 1/2 in., Model 4134) used as speakers to deliver acoustic stimuli. The auditory bulla on the left side was exposed through a ventral and post-auricular approach. Subsequent surgery was performed under the aid of a dissecting microscope. The bulla was widely opened and the middle ear muscle tendons were transected. A ball electrode made of a Teflon coated silver wire (0.075 mm in diameter) was placed on the RM membrane of the cochlea and a silver–silver chloride wire was inserted into neck tissues as a reference electrode, which was used to monitor cochlear sensitivity by the acoustically evoked compound action potential. This RW electrode was also used as one pole of the electrically stimulating electrodes.

A small observation hole in the bone over the scala tympani (ST) of the basal turn was carefully created to access the BM. The velocity of BM was measured at distinct longitudinal locations on the basal turn or the hook area at distances of 16.8, 15.8 and 14.9 mm from the apex, corresponding to 28, 21.3 and 17 kHz of BFs calculated according to Greenwood (1990). These