



Research Paper

Non-tip auditory-nerve responses that are suppressed by low-frequency bias tones originate from reticular lamina motion

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ABSTRACT

Recent cochlear mechanical measurements show that active processes increase the motion response of the reticular lamina (RL) at frequencies more than an octave below the local characteristic frequency (CF) for CFs above 5 kHz. A possible correlate is that in high-CF (>5 kHz) auditory-nerve (AN) fibers, responses to frequencies 1–3 octaves below CF (“tail” frequencies) can be inhibited by medial olivocochlear (MOC) efferents. These results indicate that active processes enhance the sensitivity of tail-frequency RL and AN responses. Perhaps related is that some apical low-CF AN fibers have tuning-curve (TC) “side-lobe” response areas at frequencies above and below the TC-tip that are MOC inhibited. We hypothesized that the tail and side-lobe responses are enhanced by the same active mechanisms as CF cochlear amplification. If responses to CF, tail-frequency, and TC-side-lobe tones are all enhanced by prestin motility controlled by outer-hair-cell (OHC) transmembrane voltage, then they should depend on OHC stereocilia position in the same way. To test this, we cyclically changed the OHC-stereocilia mechano-electric-transduction (MET) operating point with low-frequency “bias” tones (BTs) and increased the BT level until the BT caused quasi-static OHC MET saturation that reduced or “suppressed” the gain of OHC active processes. While measuring cat AN-fiber responses, 50 Hz BT level series, 70–120 dB SPL, were run alone and with CF tones, or 2.5 kHz tail-frequency tones, or side-lobe tones. BT-tone-alone responses were used to exclude BT sound levels that produced AN responses that might obscure BT suppression. Data were analyzed to show the BT phase that suppressed the tone responses at the lowest sound level. We found that AN responses to CF, tail-frequency, and side-lobe tones were suppressed at the same BT phase in almost all cases. The data are consistent with the enhancement of responses to CF, tail-frequency, and side-lobe tones all being due to the same OHC-stereocilia MET-dependent active process. Thus, OHC active processes enhance AN responses at frequencies outside of the cochlear-amplified TC-tip region in both high- and low-frequency cochlear regions. The data are consistent with the AN response enhancements being due to enhanced RL motion that drives IHC-stereocilia deflection by traditional RL-TM shear and/or by changing the RL-TM gap. Since tail-frequency basilar membrane (BM) motion is not actively enhanced, the tail-frequency IHC drive is from a vibrational mode little present on the BM, not a “second filter” of BM motion.

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1. Introduction

The high sensitivity and frequency selectivity of mammalian hearing is due to active processes in outer hair cells (OHCs) that

enhance cochlear mechanical responses to sound (reviewed in Dallos et al., 1996; Guinan et al., 2012). This enhancement, termed “cochlear amplification,” has been attributed to an increase in basilar-membrane (BM) motion and that was thought to fully account for the sensitivity and frequency selectivity of auditory-nerve (AN) fiber responses (Narayan et al., 1998; Ashmore et al., 2010). In contrast to this widely-held view, recent mechanical measurements show that at low sound levels the reticular lamina (RL) moves more and is enhanced by active processes more than is the BM (Lee et al., 2016; Ren et al., 2016). Since the RL is closer to inner-

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hair-cell (IHC) stereocilia than the BM, RL motion can be expected to have a more direct influence than BM motion in driving IHCs (Guinan, 2012).

IHC stereocilia are deflected primarily by fluid motion, but the cochlear structural motion(s) that produce this fluid motion are poorly understood (Guinan, 2012). Classically, the drive to IHC stereocilia was attributed to direct radial shear between the RL and the tectorial membrane (TM) (ter Kuile, 1900). With the more recent knowledge that IHC stereocilia are not imbedded in the TM, IHC stereocilia must be deflected by fluid forces and this has usually been attributed to fluid-drag from RL-TM radial shear (e.g. Sellick and Russell, 1980; Freeman and Weiss, 1990a, 1990b). However, in addition to this shear drive, oscillating changes in the width of the RL-TM gap can cause oscillating fluid flow within the gap that also deflects IHC stereocilia (Steele and Puria, 2005; Nowotny and Gummer, 2006, 2011; Guinan, 2012). Thus, both radial RL motion (causing shear) and transverse RL motion (causing RL-TM gap changes), as well as other micromechanical motions, may be involved in driving IHC stereocilia. Active-process enhancement of these RL motions could enhance AN responses.

BM measurements in high-CF regions show that active-process enhancement of tone-evoked BM motion is restricted to within an octave of CF (Robles and Ruggero, 2001). In contrast, RL motion is enhanced over a much wider frequency range extending to frequencies more than an octave below CF (called “tail” frequencies) (Ren et al., 2016; Lee et al., 2016). This finding raises several questions: What is the relationship of the enhanced RL motion to the drive to IHCs? Does the enhanced tail-frequency RL motion produce enhanced excitation of AN fibers? Is the active-process that enhances tail-frequency RL motion the same active process that cochlear-amplifies BM motion at CF?

The active process that produces BM cochlear amplification at CF arises from OHC somatic motility. One way to study the effects of OHC active processes is to change OHC properties by stimulating medial olivocochlear (MOC) efferents that synapse on OHCs. Using electrical stimulation of MOC efferents, Stankovic and Guinan (1999, 2000) found that for cat AN fibers with CFs >5 kHz, AN responses were inhibited by MOC activity for near-threshold, tail-frequency tones 1–3 octaves below CF (e.g. Fig. 1A). BM motion, in contrast, is little changed by MOC stimulation at frequencies an octave or more below CF (Cooper and Guinan, 2006; Guinan and Cooper, 2008). Stankovic and Guinan attributed the MOC inhibition of tail-frequency AN responses to MOC efferents changing cochlear micromechanics (i.e. the inhibition was not due to a

change in BM motion). However, they were not able to say which cochlear structures had tail-frequency motions that were MOC inhibited. We now hypothesize that actively-enhanced RL motion is inhibited by MOC activity and this is what reduces AN tail-frequency responses.

An alternate to MOC stimulation for modifying OHC active processes is to use high-amplitude, low-frequency “bias” tones that produce large deflections of OHC stereocilia. Deflections of OHC stereocilia open and close OHC mechano-electric transduction (MET) channels and the resulting currents change OHC transmembrane voltage and OHC length, and the OHC length changes produce cochlear amplification. The slope of the OHC-current vs. stereocilia-deflection curve sets cochlear-amplification gain with higher slopes producing more amplification (Cai and Geisler, 1996c). A high-amplitude, low-frequency “bias tone” (BT) can quasi-statically push the OHC MET functions into low-slope, saturating edge regions (e.g., in Fig. 1C for a test tone much higher in frequency than the BT: from test-frequency variations around point “a” to variations around point “b”). During a BT-response phase in the low-slope region, the (temporary) effect of the BT is to decrease the MET slope seen by the higher-frequency test tone and thereby decrease or “suppress” the amplification of test-tone responses (OUT,b is smaller than OUT,a in Fig. 1C). Thus, the BT suppresses test-frequency responses whenever the BT quasi-statically moves OHC stereocilia into low-slope MET regions (Fig. 1C). When the OHC MET function is asymmetric (which it is along most of the cochlea in cats – Nam and Guinan, 2016), one low-slope MET edge is reached at a lower BT sound level than the other, which results in one gain reduction per bias-tone cycle and a modulation of the test-tone response that has a large first harmonic of the BT frequency. The BT phase at which this happens is termed the “major suppression phase.” At higher bias-tone levels, stereocilia deflections reach the low-slope regions on both ends of the MET function and there are two gain reductions per bias-tone cycle and modulation of the test-tone response has a large second harmonic of the BT frequency. Many experiments have provided evidence consistent with these bias-tone effects on responses to low-level tones near CF (Sachs and Hubbard, 1981; Sellick et al., 1982; Javel et al., 1983; Patuzzi et al., 1984a, b; Rhode and Cooper, 1993; Cooper, 1996; Cai and Geisler, 1996a, 1996b; Rhode, 2007; Nam and Guinan, 2016).

The MOC inhibition of AN responses to tail-frequency tones is consistent with the hypothesis that the motion driving these responses was amplified. If this amplification is by the same OHC

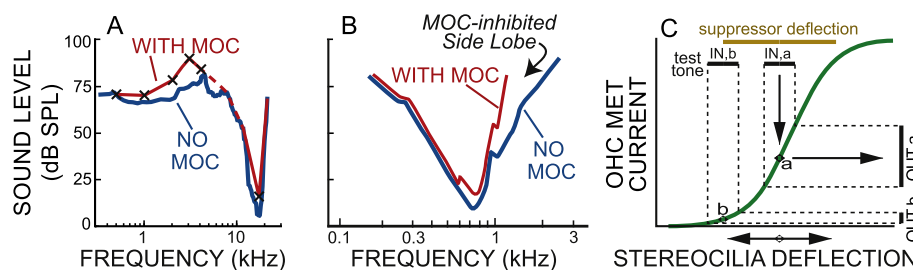


Fig. 1. **A, B:** Tuning curves (TCs) from cat auditory-nerve fibers with and without excitation of medial olivocochlear (MOC) efferents. **A:** A tail-frequency inhibition. **B:** A side-lobe inhibition. **C:** Bias-tone suppression of outer-hair-cell (OHC) mechano-electric transduction (MET) current variation at the test-tone frequency. In **C**, the horizontal lines at top represent the stereocilia-deflection excursions produced by a low-frequency suppressor tone (top line), and by a much-higher-frequency test tone (lower lines). The black line labeled IN,a shows the test-frequency input excursion when the suppressor is not present (this excursion is about point “a” of the MET function represented by the curved line), and the black line labeled IN,b shows the input excursion when the suppressor-produced OHC deflection is at one edge of its excursion (this test-frequency excursion is about point b). The vertical lines at right represent the corresponding OHC-MET-current output excursions at the test-tone frequency. When the suppressor response is at the extreme of its excursion, the output MET current variation at the test-tone frequency is reduced from its no-suppressor value. **A** was derived from Fig. 6 of Stankovic and Guinan (1999). The no-MOC TC is from their Fig. 6A and the with-MOC TC was derived from the no-MOC TC and the level-shifts from the other panels of their Fig. 6 (shown as X’s here). To fill in the TC, we assumed no MOC inhibition at the upper edges of the TC tip; the dashed line represents a tail region with no MOC-inhibition data. **B** is a stylized version of AN-fiber TCs from Guinan and Gifford (1988) (shown in Guinan, 2011).

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