

Nonlinearities at the apex of the cochlea: Implications for auditory perception

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1 Introduction

Certain aspects of auditory perception are thought to reflect basilar membrane responses, which are nonlinear by virtue of their feedback relationship with outer hair cells. This association between cochlear mechanics and perception (Oxenham and Plack 1997) was originally based on comparisons with the well-characterized mechanical responses recorded from the base of the mammalian cochlea (Ruggero, Rich, Recio, Narayan and Robles 1997). These responses are nonlinear but only around the best frequency (BF) of the recording location. Below BF, responses are linear. However, the assumption that responses are linear below BF does not hold at the apex of the cochlea. Therefore, the purpose of this report is to review what is known about apical inner hair cell (IHC) responses in order to provide an indication of how low and moderate signal frequencies are coded by the basilar membrane-outer hair cell-tectorial membrane (BM-OHC-TM) complex. Because mammalian IHCs supply the inputs to the auditory nerve, their receptor potentials ultimately provide the substrate upon which central auditory processing is based. Results are evaluated for IHCs in turn 3 of the guinea pig cochlea where BFs are ~1 kHz. In other words, recordings are made from regions where a majority of the psychophysical measurements are obtained. Information about the hair cell transducer is provided and compared with results on cochlear mechanics where appropriate. Implications for measurements of auditory compression in human subjects are also discussed.

2 Methods

Inner hair cells were recorded from turn 3 of the guinea pig cochlea using the lateral approach (Dallos, Santos-Sacchi and Flock 1982). Magnitudes of both ac and dc components of the receptor potential were determined offline from FFTs of

averaged response waveforms. In some cases, a half-wave rectified version of the averaged response was obtained by adding together all data points above the baseline in quiet over an integer multiple of cycles and dividing by the total number of points. All procedures were approved by the National Institutes of Health and by Northwestern University's Animal Care and Use Committee.

3 Results and Discussion

In order to emphasize longitudinal variations in cochlear function, basilar membrane responses recorded at the base of the cochlea (Cooper 1998) are shown in Fig. 1A.

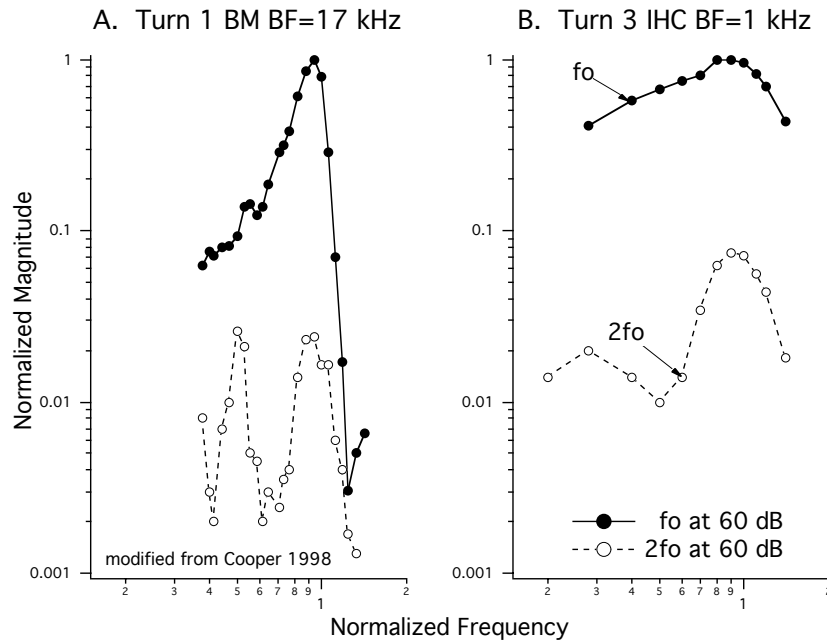


Fig. 1. In part A, basilar membrane data (Cooper 1998, Fig. 2A) are modified to show normalized responses for the fundamental (solid lines). Dashed lines indicate responses at the second harmonic, which are also normalized to the largest fundamental value. Companion IHC data are plotted in panel B. All results were acquired at 60 dB.

Measurements for both fundamental and second harmonic responses were normalized to the largest value measured at the fundamental. By also plotting results on a normalized frequency scale, it is possible to compare Cooper's mechanical data with those from third-turn IHCs. Mechanical responses recorded at the fundamental show the tip and tail configuration of basilar membrane tuning

curves obtained in healthy preparations at the base of the cochlea. In contrast, second harmonic responses exhibit a bimodal frequency distribution such that one peak occurs when the stimulus is at $BF/2$ (8.5 kHz). In this case, the primary is below BF and, therefore, receives little amplification. The second harmonic, however, is amplified because it coincides with BF where the cochlear amplifier has its largest gain. Cooper refers to this response pattern as amplified distortion. When the stimulus is at BF (17 kHz), responses are highly nonlinear but the second harmonic at 34 kHz receives no amplification because it is well above BF . Cooper refers to this second peak as distorted amplification.

In contrast to Cooper's results from the base of the cochlea, data from an IHC with BF at 1 kHz show only one peak, as in Fig. 1B. These different distribution patterns are consistent with the knowledge that apical mechanical and hair cell responses are nonlinear throughout the response area (Rhode and Cooper 1996) and that filter shapes are relatively symmetrical with no well defined tip and tail segments. Hence, it is not surprising that two peaks are not found in apical IHC responses because amplified distortion should be much less prominent in IHCs with low BF s. Although not shown here, data at 80 dB do not display individual peaks, i.e., the second harmonic is expressed throughout the response area for both IHC and basilar membrane responses.

As alluded to earlier, mechanical nonlinearities measured at the base of the cochlea are frequency specific with the result that basilar membrane responses are linear for inputs well below BF . Based on this assumption, psychophysical estimates of compression were obtained in human subjects by measuring the growth of masking for maskers at and below signal frequency. Unfortunately, the assumption of linearity below BF is untenable at the apex of the cochlea where both mechanical and IHC responses are nonlinear throughout the response area. Therefore, this assumption was abandoned and psychophysical experiments redesigned. Results published earlier this year (Plack and Drga 2003; Lopez-Poveda, Plack and Meddis 2003) indicate that the compression observed in human subjects at low frequencies is ~ 0.2 dB/dB. This value is similar to that measured at higher frequencies but greater than the ~ 0.5 dB/dB observed in apical mechanical responses by Rhode and Cooper (1996). Although Plack and colleagues speculate that compression in human subjects might originate centrally, IHC data shown in Fig. 2 suggest otherwise.

In this example, the average value of the half-wave rectified IHC response is plotted as a function of SPL. This average voltage provides a reasonable representation of the signal inducing transmitter release because it represents a combination of both ac and dc components of the receptor potential. Data points are plotted with circles for two IHCs with BF s at ~ 1000 Hz. The compression is ~ 0.1 dB/dB, i.e., much greater than the 0.5 dB/dB observed in apical mechanical responses measured from the tectorial membrane by Rhode and Cooper. These latter results, shown with the thick line, are plotted using the ordinate on the right. Also included are results for the cochlear microphonic (CM) recorded in the organ of Corti (OC) fluid space and plotted with squares using the left ordinate. This gross

ac response grows at ~ 0.2 dB/dB. In fact, the CM is more compressive than are the mechanical data. Assuming that the BM-OHC-TM complex is tightly coupled, then this observation suggests that mechanical responses at the apex may still be compromised, in spite of the efforts made to acquire the data.

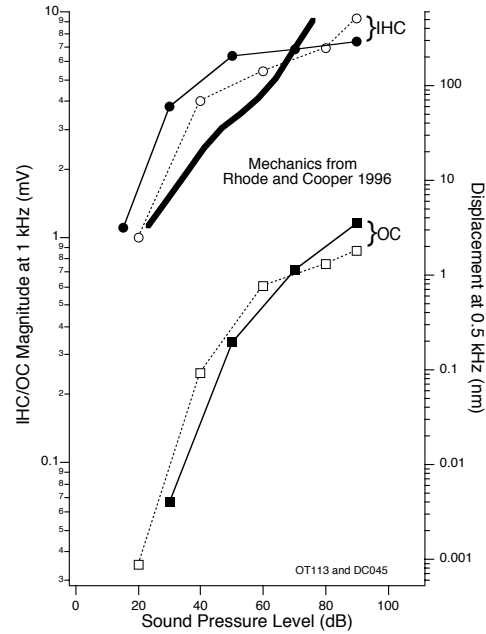


Fig. 2. Input-output functions are plotted for IHC (circles), OC (squares) and mechanical (solid line) responses. The mechanical data were collected from the tectorial membrane at 500 Hz (Rhode and Cooper 1996, Fig. 7). IHC and OC responses were obtained at 1000 Hz.

The compression observed in IHCs with low BFs reflects a combination of mechanical distortion, as well as that associated with the hair cell transducer. In other words, it is not possible to separate mechanical and hair cell nonlinearities. This contrasts with measurements at the base of the cochlea where compression at BF is dominated by frequency-specific nonlinearities associated with cochlea mechanics. Compression below BF, however, is dominated by the asymmetry of the hair cell transducer. By making mechanical and hair cell measurements at the base of the cochlea, Patuzzi and Sellick (1983) were able to demonstrate that the nonlinearity associated with the hair cell transducer is frequency independent.

Figure 3 serves to document the degree of asymmetry associated with the IHC transducer for cells with high and low BFs. Iso-response functions are compared here for an IHC in turn 1, with BF at 17,000 Hz, and for an IHC in turn 3, with BF at 1,000 Hz. Data, plotted on the right, were taken from Russell and Sellick (1978). The iso-response functions in turn 1 indicate that the 2 mV criterion value for both

ac and dc components is achieved at the same sound pressure level, in this case, 9 dB at BF. AC values were obtained by compensating for low-pass filtering by the IHC's basolateral membrane and by the recording apparatus. This adjustment allows the sensitivity of the IHC transducer to be estimated. Data from turn 3 are plotted on the left. Although criterion ac values are produced at about the same level as in the base, a higher sound pressure level is required to produce the 2 mV criterion dc response. This implies that while IHCs with low and high BFs are similar in sensitivity, they differ in their asymmetry. This possibility was demonstrated in pseudotransducer functions obtained from IHCs with low and high BFs. These data indicate that third-turn IHCs are more symmetrical than IHCs recorded at the base of the cochlea (Cheatham and Dallos 2000, Fig. 1). These observations suggest that apical IHC responses are linear to a higher sound pressure level than are basal IHC responses. In contrast, IHCs with high BFs produce dc responses at near-threshold levels, thereby assuring transmitter release and communication with the auditory nerve.

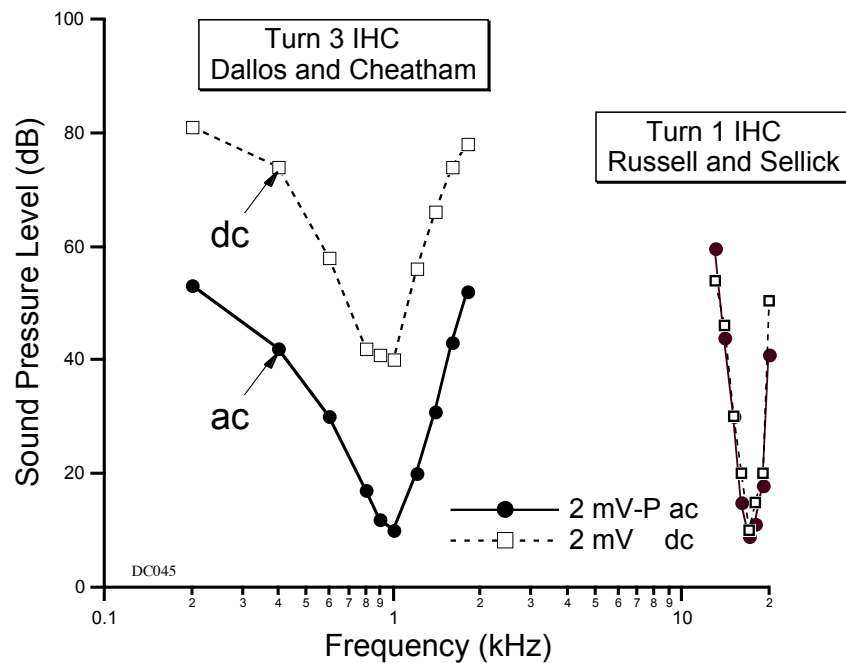


Fig. 3. Iso-response functions for ac and dc receptor potentials recorded in turn 3 and turn 1 of the guinea pig cochlea. The basal-turn data are taken from Russell and Sellick (1978, Fig. 7B, #222). Both ac curves were compensated for filtering by the cell's basolateral membrane; the basal-turn data were also compensated for filtering by the recording apparatus.

4 Conclusions

Results indicate that several stages of preprocessing in the cochlea are nonlinear and that all must be considered as sources of compression observed psychophysically. Because mechanical data recorded at the apex may still be compromised, it is not possible to determine whether the compression observed psychophysically at low frequencies is a reflection of mechanical and/or hair cell nonlinearities. We can state, however, that it is not necessary to assume that the compression observed in human subjects at low frequencies originates centrally. This is because the compression measured at the IHC level exceeds that observed psychophysically at low stimulus frequencies.

Acknowledgments

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