BASELINE POSITION SHIFTS AND MECHANICAL COMPRESSION IN THE APICAL TURNS OF THE COCHLEA

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Sound-evoked mechanical responses in the apical turns of healthy cochleae are shown to involve both compressive nonlinearity (i.e. growth rates of less than 1dB/dB) and baseline position shifts (i.e. quasi-static displacements). However, at least in the guinea-pig, the frequency and intensity dependencies of the two phenomena differ considerably. A direct link between baseline position shifts and compression can therefore be ruled out. Modelling studies show that the two phenomena could be separate manifestations of a single underlying nonlinearity, but neither one appears to be entirely 'responsible' for the other.

1 Introduction

Both baseline position shifts [1-5] and compressive nonlinearity [6-10] have long histories in the field of cochlear mechanics. Compressive nonlinearity appears to have stood the test of time, and is now considered as an essential characteristic of normal hearing [see 11 for review]. On the other hand, baseline position shifts have had a more dotted history and are rarely considered to be 'normal'. Nonetheless, one recent report has suggested that baseline position shifts and compressive nonlinearity might be linked in the apical turns of the cochlea [5]. In the present report, this suggestion is investigated further: both compression and baseline position shifts are characterised in some detail in the apical turns of the guinea-pig cochlea. The result is the suggestion that baseline position shifts are associated with normal hearing, although they are not tightly linked with all forms of compressive nonlinearity. Both the position shifts and the compression that is seen in in the apical cochlea can be modelled quite realistically using a simple, positive feedback system, much like those that have been used previously to model the more basal regions of the cochlea [12].

2 Methods

Mechanical recordings were made from the apical turn(s) of the cochlear partition in deeply anaesthetised guinea-pigs and chinchillas, using techniques similar to those described previously [13,14]. All of the data presented here were recorded from the highly reflective lipid droplets of the Hensen's cell region of the guinea-pig's organ of Corti.

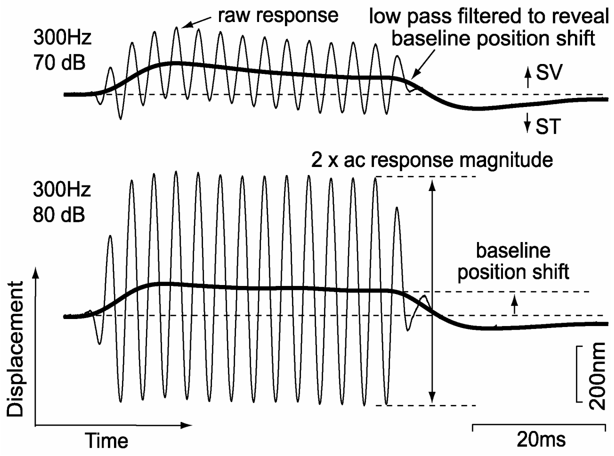

Figure 1. Hensen’s cell vibrations evoked by short tone pips at 70 and 80dB SPL. Each waveform (thin lines) represents the average response to 32 repetitions of a 50ms-long 300Hz stimulus. Baseline position shifts (bold) are revealed by low-pass filtering the waveforms using an 8th-order Butterworth filter with a 100Hz cut-off frequency. SV = scala vestibuli, ST = scala tympani.

3 Results

3.1 Sound-evoked responses include ac and dc components

Baseline position shifts were evident in the Hensen’s cell responses evoked by wide ranges of stimuli. For tonal stimuli, the shifts were quantified by estimating the dc components of the displacement waveforms once a steady state had been achieved (see Fig. 1). Almost all of the shifts were directed towards the scala vestibuli (SV in Fig. 1). Following the termination of a tonal stimulus, the baseline positions of the Hensen’s cells shifted towards the scala tympani. Baseline positions typically returned to their pre-stimulus levels between 20 and 50ms after the termination of a stimulus.

For click stimuli, baseline position shifts were manifested as response components which did not invert when the polarity of the stimulus was changed from rarefaction to condensation. As shown in Figure 2, these non-inverting, or common-mode click-evoked components showed signs of oscillatory behaviour on a much longer timescale than the conventional (i.e. best-frequency related, ac) oscillations of the apical partition. The initial portions of the click-evoked baseline position shifts were always directed towards the scala vestibuli. Fourier transformation of the click-evoked response components (not illustrated) revealed the baseline position shifts to have a low-pass corner frequency of less than 50Hz, and the ac response components to have a low-pass corner frequency of around 600Hz.

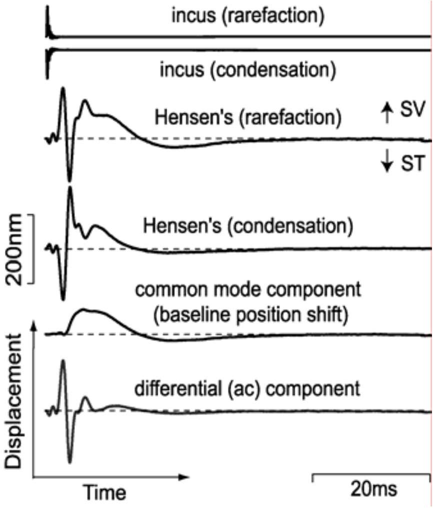

Figure 2. Hensen's cell vibrations evoked by rarefaction and condensation clicks at peak-equivalent levels of ~80dB SPL. Each waveform represents the average response to 250 clicks. Baseline position shifts are revealed by averaging the responses to the rarefaction clicks with those to the condensation clicks. The differential (i.e. ac) response components are revealed by subtracting the responses to the condensation clicks from those to the rarefaction clicks, and dividing by two. Control responses, as recorded from the incus in the middle ear, are shown in the top two traces. SV = scala vestibuli, ST = scala tympani.

3.2 *Compressive nonlinearity*

Both ac and dc response components exhibited compressive nonlinearity over certain ranges of frequency and intensity. That is, under certain conditions, both the oscillatory responses and the baseline position shifts grew at rates of less than 1dB/dB when the intensity of a sound was increased. The baseline position shifts behaved relatively simply in this respect, as illustrated in Figures 3 and 4: Over much of the frequency range which was effective in evoking responses in the apical turn (from 25 to over 600Hz), the shifts first became clear (> ~10nm) at ~50-60 dB SPL. They then grew at rates of between 1 and 2 dB/dB up to ~70-80dB SPL before saturating at levels of between ~50 and 200nm.

The oscillatory (i.e. ac) response components exhibited compression over much narrower frequency ranges than the baseline position shifts. The strongest ac compression was observed in a very narrow frequency region (typically between

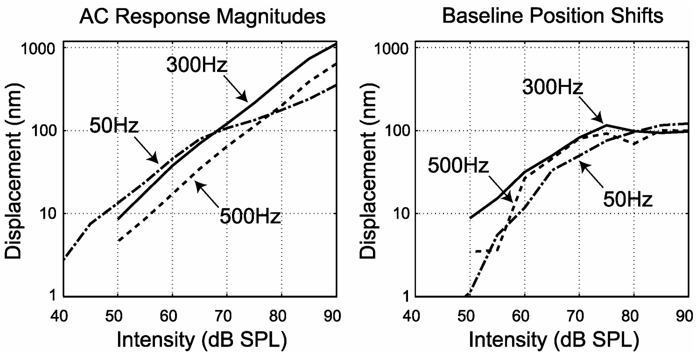

Figure 3. Input-output functions for ac (i.e. oscillatory) and dc response components evoked by short tone-pips at 3 frequencies (cf. Fig. 1)

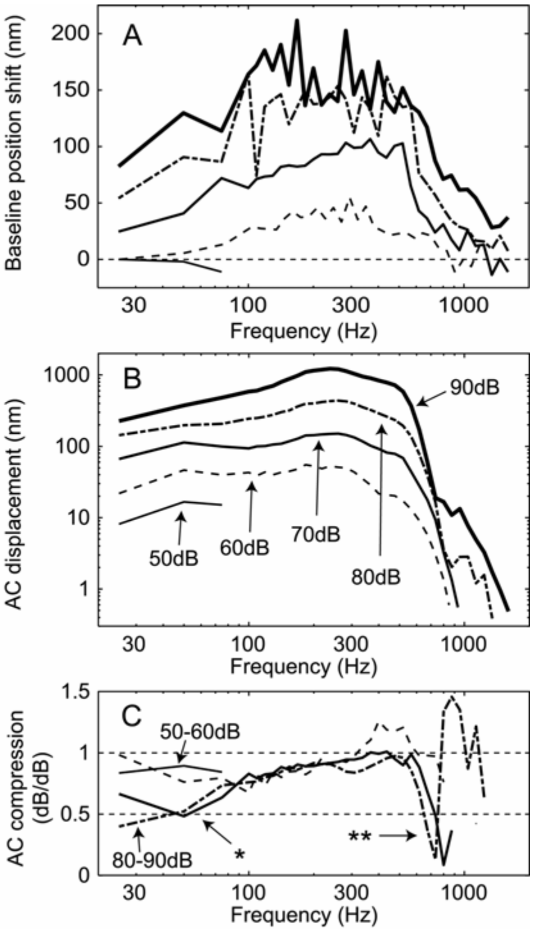

Figure 4. Frequency dependence of baseline position shifts and ac compression: (A) dc and (B) ac response component amplitudes evoked by short tone-pips at five intensities (50-90dB SPL, as indicated in B). (C) Growth rates of ac response components across the four intervening intensity ranges (thin solid line = 50-60dB, thicker solid line = 70-80dB, etc). Asterisks indicate separate regions of moderate (*) and strong (**) compression.

600
and 900Hz) on the high-frequency cut-off slope of the Hensen's cells' transfer functions (cf. ** in Fig. 4C). This is the same region that often has nonmonotonic or "notchy" input-output functions (not illustrated), suggesting that the compression might be achieved by cancelling out two (or more) driving forces. Such input-output functions also result in regions of expansive nonlinearity, as illustrated by the growth rates of >1dB/dB in Figure 4C. Another region of ac compression was observed at extremely low frequencies (<100Hz, cf. * in Fig. 4C). This is the same frequency region where the baseline position shifts become dominant in the spectra of the click-evoked responses.

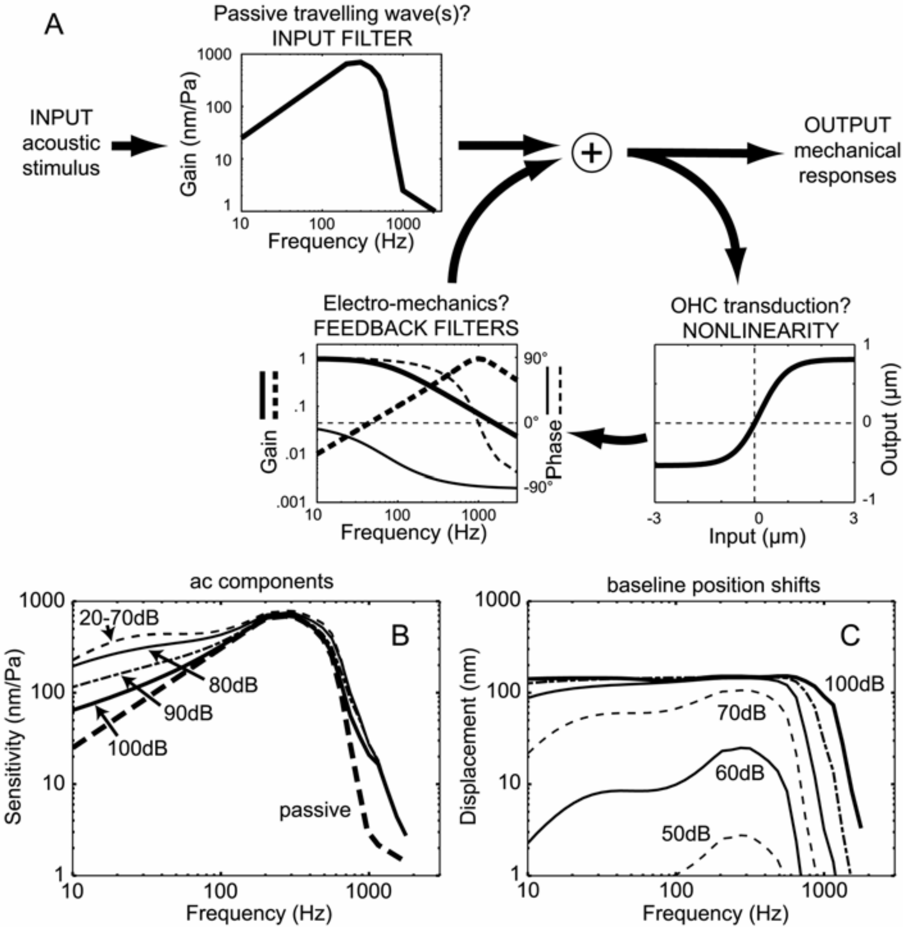

Figure 5. A positive-feedback model (A) that can account for both compressive nonlinearity (B) and baseline position shifts (C) in the apical turn of the cochlea. The model has two filters in its feedback pathway: one is a second-order band-pass filter (dashed lines; bold = gain, thin = phase) centered just beyond the input filter's cut off frequency (1kHz). The other is a first-order low-pass filter (solid lines) with a cut-off frequency of 70Hz. The model's only nonlinearity consists of a first-order Boltzman function [cf. ref. 15].

3.3 Physiological vulnerability

Both the baseline position shifts and the low-frequency ac compression were vulnerable to physiological insult. Both phenomena were only observed in near-intact, in vivo preparations, and both were reversibly affected by anoxia. Both phenomena were obliterated when Reisnner's membrane was ruptured.

4 Models and Discussion

The finding that baseline position shifts are evoked across a wide range of stimulus frequency allows us to tease them apart from the phenomenon of ac compression. This separation was not possible in previous studies at the apex of the chinchilla cochlea [5], where the ac compression is more powerful and more widespread than it is in guinea-pigs. To some extent, this separation serves to confirm the earlier separation of ac compression and baseline position shifts that was suggested by recordings from the basilar membrane in the basal turns of the cochlea [4]. However, the link between the separation in the apex and that in the base of the cochlea must be made with caution. To date, there is no evidence that either (i) the baseline position shifts that we see at the level of the Hensen's cells can also be seen at the level of the basilar membrane (in the apex), or (ii) that the absence of baseline position shifts on the basilar membrane in the base of the cochlea means an absence of baseline position shifts elsewhere in the organ of Corti (e.g. on the reticular lamina in the basal turns of the cochlea).

Turning now to the origins of the apical-turn compression and the baseline position shifts, our findings appear reasonably consistent with the predictions of a positive-feedback model (Fig. 5) of the type used previously to explain mechanics in the basal turns of the cochlea [12]. The positive feedback of this model serves to amplify the responses to low intensity stimuli more than those to high intensity stimuli, due to the saturating nature of the nonlinearity in the feedback loop. The nonlinearity needed to account for the apical turn data has to be slightly more asymmetric than that commonly used to account for basal turn mechanics, and the filtering in the feedback loop also has to be more complex than it does in the base [compare Fig. 5A to the model in ref. 15]. However, there is no need to consider either the feedback filter or the nonlinearity as having a single origin in the cochlea. As suggested in Fig. 5A, perhaps there are actually two feedback loops in the apical cochlea – one responsible for generating the baseline position shifts (and generating low-frequency compression as a by-product), and another for generating (high-frequency) compression.

Acknowledgments

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