

BASILAR-MEMBRANE MECHANICS AT THE HOOK REGION OF THE CHINCHILLA COCHLEA

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To date, mechanical measurements in chinchilla cochleae are available only for two regions, one at a basal site and the other at the apex (3.5 and 14 mm from the oval window, respectively). We have begun to study basilar-membrane vibrations at the hook region of the chinchilla cochlea, at sites with CF ~15 kHz located ~1.7 mm from the stapes. At this time, results are available only from cochleae substantially traumatized by surgical procedures. Nevertheless, these results reveal basilar-membrane response properties qualitatively similar to those of the 3.5-mm site in healthy preparations. At frequencies well below CF, responses to tones are linear. Around CF, responses exhibit nonlinear behavior: vibration magnitudes grow with stimulus intensity at compressive rates and phases display lags and leads, respectively, at frequencies lower and higher than CF. Phase-vs.-frequency curves consist of a low-frequency segment with shallow slope, a steep-slope segment at frequencies near CF, and a plateau at higher frequencies.

1 Introduction

Although a reasonably complete understanding of cochlear mechanics will require observing basilar-membrane vibration at many sites of the cochlea, anatomical constraints have made it difficult to obtain *in-vivo* recordings from more than one region in any given species. In the case of the chinchilla, measurements have been made at a basal site with characteristic frequency (CF) of 9-10 kHz, located some 3.5 mm from the stapes [e.g., 7-9] and an apical site (CF: 500-800 Hz) located some 14 mm from the stapes [6]. Here we report on basilar-membrane responses to tones recorded at a third site of the chinchilla cochlea, located in its hook region at about 1.7 mm from the stapes.

2 Methods

Methods were similar to those used for *in-vivo* recordings of basilar-membrane vibrations at the 3.5-mm site in chinchilla [8]. To minimize heat loss from the widely exposed cochlea, which lowers cochlear sensitivity, the metal headholder was furnished with an electrical heater. The pinna and bony ear canal were excised to facilitate placement of a speculum, which delivered acoustic stimuli. The tendons of the tensor tympani and stapedius muscles were severed. The basilar membrane was accessed near its basal extreme by removing the posterior rim of the round

window and its membrane. The vibrations of glass microbeads strewn on the basilar membrane were measured with a laser velocimeter coupled to a microscope. All basilar-membrane recordings were made at sites with CFs of 14-16 kHz. Responses could not be measured for stimulus frequencies lower than 3 kHz because at such frequencies they were "masked" by vibrations of the perilymph-air interface induced by ossicular vibration [1, 9]. Middle ear vibrations were also recorded routinely, typically from the incus, near the incudo-stapedial joint or, sometimes, from the stapes. A silver wire electrode in the vicinity of the round window was used to measure compound action potential thresholds (CAP; 10 μ V criterion), which served to assess cochlear sensitivity.

3 Results

As judged from elevations of CAP thresholds, we have not yet succeeded in recording from normal cochleae. Even before removal of the round window membrane, CAP thresholds at frequencies in the vicinity of the CF (\sim 15 kHz) of the

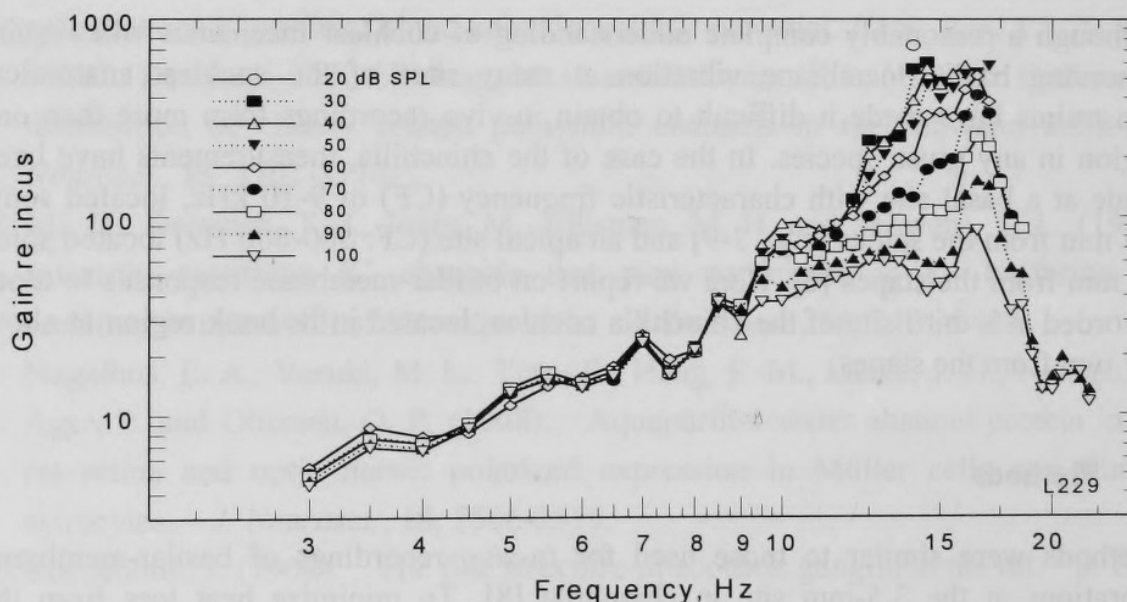


Figure 1. The magnitude of basilar membrane responses to tones as a function of stimulus intensity and frequency, expressed relative to the responses of the incus.

basilar-membrane recording site were substantially higher than at lower frequencies (e.g., 60 dB SPL at 16 kHz vs. 34 dB at 11.3 kHz). We have evidence, based on comparisons of CAP thresholds and single-unit thresholds recorded from the same cochleae, that the relatively high CAP thresholds at high stimulus frequencies grossly underestimate (by nearly 40 dB) the sensitivity of auditory-nerve fibers with the same CF [10]. After removing the round window membrane, thresholds were always elevated. We present here responses from a representative cochlea which suffered a 10-dB sensitivity loss at the CF of the basilar-membrane recording site.

At frequencies lower than $\sim 0.7 \cdot \text{CF}$ or higher than $\sim 1.3 \cdot \text{CF}$, basilar-membrane

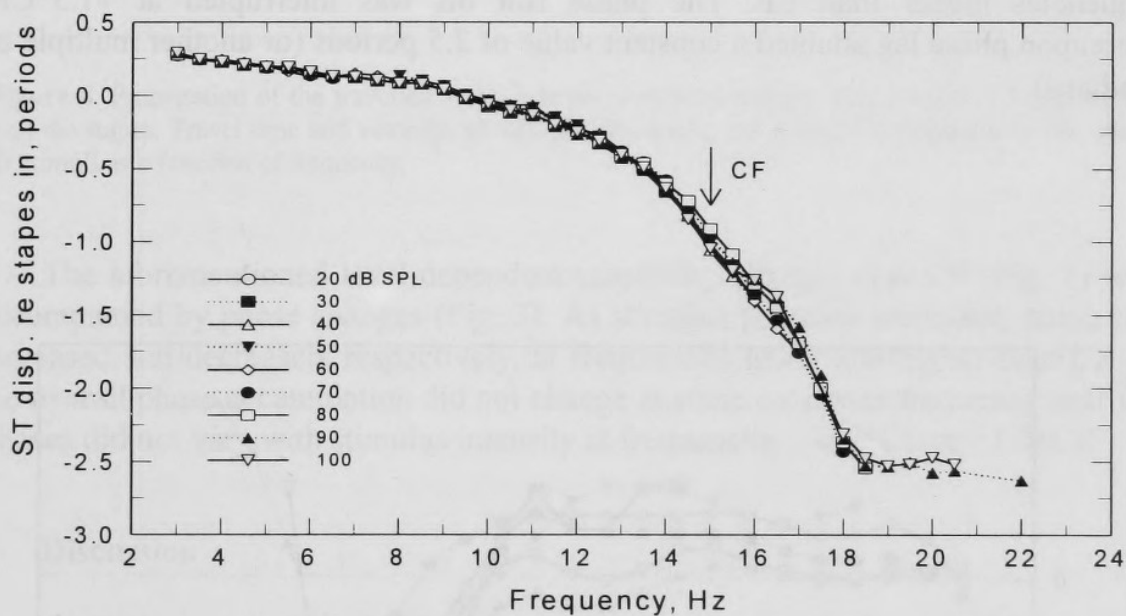


Figure 2. The phases of basilar membrane responses to tones as a function of stimulus intensity and frequency, expressed relative to the responses of the incus.

responses to tones were linear. Around CF, responses grew with stimulus intensity at compressive rates (Fig. 1). As a result, sensitivity (i.e., basilar-membrane vibration magnitudes expressed relative to middle-ear vibration, as in Fig. 1, or stimulus level) for stimulus frequencies near CF were largest at the lowest stimulus levels and became smaller with increasing level. In the cochlea illustrated in Fig. 1, near-CF sensitivity decreased by about 20 dB as stimulus intensity was increased between 30 and 100 dB SPL. In other cochleae (not shown) level-dependent sensitivity changes

ranged from almost nil in cochleae highly traumatized by surgical procedures to 40 dB (not shown).

BM responses could be 1000 times larger than those of middle-ear ossicles for CF stimuli presented at low levels, 30-50 times larger at $\sim 0.7 \cdot CF$ but only a few times larger for lower frequencies (e.g., 4 kHz). Frequency tuning exhibited the familiar pattern of a traveling wave, with the high-frequency slope being much steeper than the low-frequency slope. The steep decline of sensitivity for high frequencies was interrupted by a plateau.

Phase-vs.-frequency curves (re stapes or incus) exhibited the well-known traveling-wave pattern of accumulating phase lag, with three distinct segments (Fig. 2). For frequencies $< 0.8-0.9 \cdot CF$, the curves had a shallow constant slope equivalent to a delay of $\approx 40 \mu s$. Phase accumulation was rapid at frequencies flanking CF, with a slope equivalent to a delay of $\approx 350 \mu s$. The phase accumulation at CF amounted to 0.5-1.5 periods, with an additional 1-2 periods of lag at frequencies higher than CF. The phase roll off was interrupted at $\sim 1.3 \cdot CF$, whereupon phase lag attained a constant value of 2.5 periods (or another multiple of π radians).

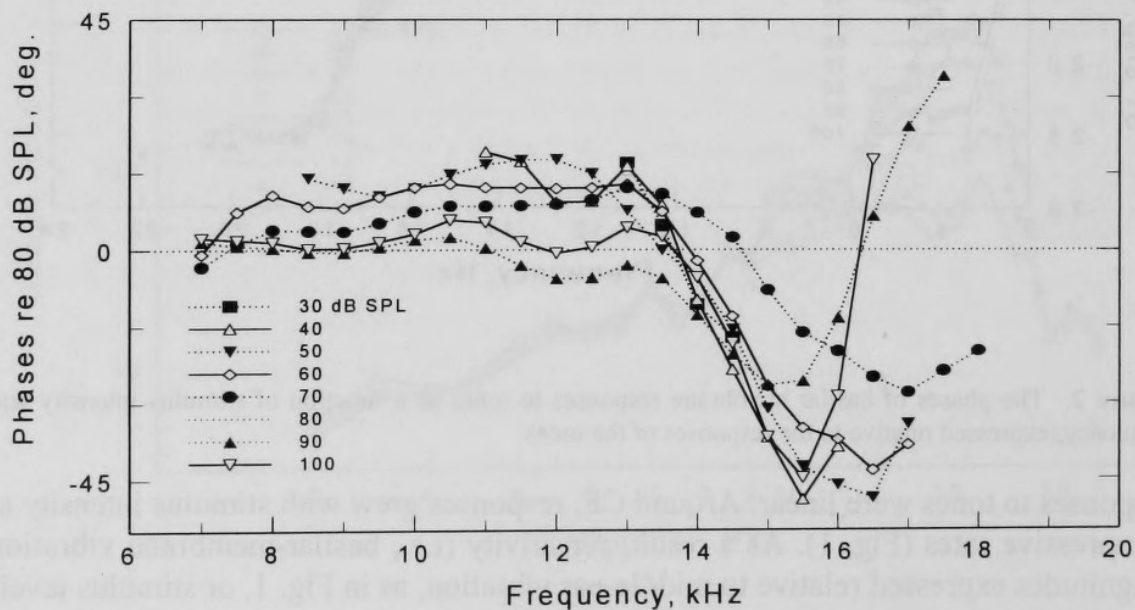


Figure 3. The variation of response phase as a function of stimulus frequency and level. To emphasize the level changes, phases are normalized to the responses to 80-dB tones.

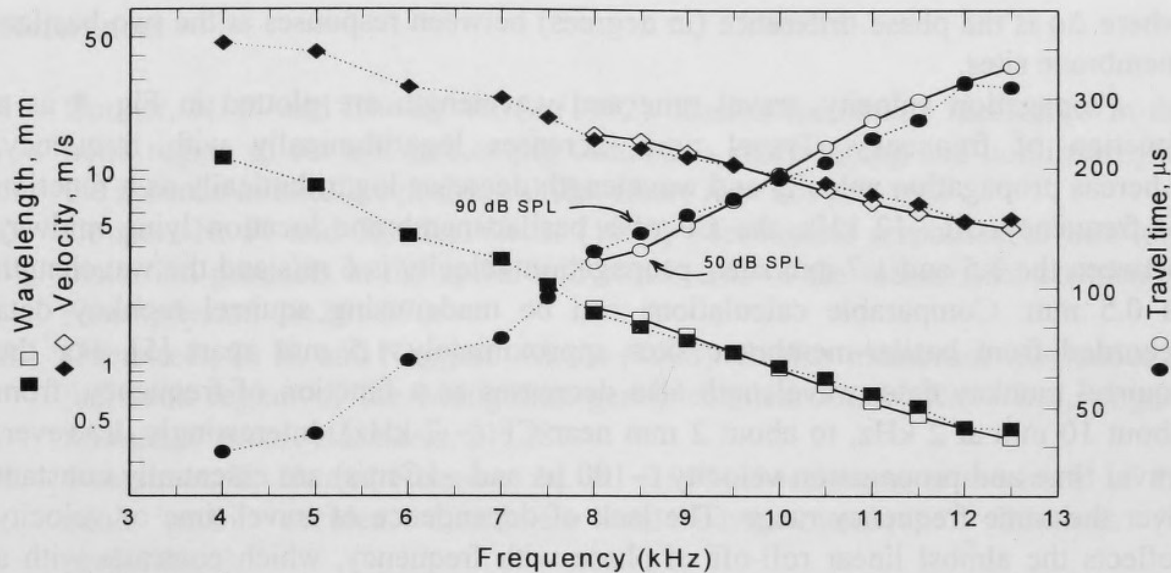


Figure 4. Propagation of the traveling wave between basilar-membrane sites located 1.7 and 3.5 mm from the stapes. Travel time and velocity, as well as wavelength, are plotted for responses to 50- and 90 dB stimuli as a function of frequency.

The aforementioned level-dependent sensitivity changes near CF (Fig. 1) were accompanied by phase changes (Fig. 3). As stimulus intensity increased, phase lags increased and decreased, respectively, at frequencies lower and higher than CF but the overall phase accumulation did not change at some crossover frequency near CF. Phases did not vary with stimulus intensity at frequencies $< 0.7 \cdot CF$ or $> 1.3 \cdot CF$.

4 Discussion

Combining the present vibration data for the 1.7-mm site of the chinchilla cochlea with comparable basilar-membrane data for the 3.5-mm site [e.g., 9], we computed some characteristics of the traveling wave in the intervening 1.8 mm using the following equations:

$$\text{travel time} = (\Delta\phi / 360) * \text{period}, \quad (1)$$

$$\text{propagation velocity} = 1.8\text{mm} / \text{travel time}, \quad (2)$$

$$\text{wavelength} = 1.8\text{mm} * (360 / \Delta\phi), \quad (3)$$

where $\Delta\phi$ is the phase difference (in degrees) between responses at the two basilar-membrane sites.

Propagation velocity, travel time and wavelength are plotted in Fig. 4 as a function of frequency. Travel time increases logarithmically with frequency, whereas propagation velocity and wavelength decrease logarithmically as a function of frequency. At ~ 12 kHz, the CF of a basilar-membrane location lying midway between the 3.5 and 1.7 mm sites, propagation velocity is 6 m/s and the wavelength is 0.5 mm. Comparable calculations can be made using squirrel monkey data recorded from basilar-membrane sites approximately 1.5 mm apart [5]. For the squirrel monkey data, wavelength also decreases as a function of frequency, from about 10 mm at 2 kHz, to about 2 mm near CF (~ 7 kHz). Interestingly, however, travel time and propagation velocity (~ 100 μ s and ~ 16 m/s) are essentially constant over the same frequency range. The lack of dependence of travel time or velocity reflects the almost linear roll-off of phase with frequency, which contrasts with a continuously accelerating phase lag in the present results in chinchilla (Fig. 2).

Basilar-membrane responses at the 1.7-mm site of the chinchilla cochlea resemble qualitatively, in essentially every respect, those at the 3.5-mm site in the same species [9]. However, the available responses at the 1.7-mm site are less sensitive and exhibit less compressive nonlinearity than at the 3.5-mm location. For example: basilar-membrane vibration magnitudes exceed stapes vibration by 73-78 dB and 55 dB, respectively, at the 3.5-mm and 1.7-mm sites. The intensity-dependent changes of gain at CF were 55-69 dB at the 3.5-mm site but did not exceed 40 dB at the 1.7-mm site. The differences are due, at least in part, to greater surgical damage in the recordings from the hook. Nevertheless, it is also possible that sensitivity and nonlinearity are weaker in the hook region even in entirely normal chinchilla cochleae.

The magnitude of peak basilar-membrane gain at the hook region of the chinchilla -- 55 dB re ossicular motion -- is comparable to gains reported for hook locations in cat and guinea pig cochleae, 42 and 48 dB respectively [1]. In the gerbil, the gains are only about 22 dB in insensitive cochleae [11] but they reach 40-58 dB in healthier cochleae [3-4]. The intensity-dependent change of gain at the 1.7-mm site of chinchilla (<40 dB) is also comparable with corresponding measurements at the hook region of gerbil, cat and guinea pig cochleae (20-30, 36 and 19 dB, respectively). In making these cross-species comparisons, it is important to keep in mind that the recording sites have different CFs in different species: 15 kHz in chinchilla (e.g., Fig. 1), and 30, 33 and 35-38, respectively, in guinea pig [1,2], cat [1] and gerbil [3-4].

5 Acknowledgements

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