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Frequency Tuning of Basilar Membrane and Auditory Nerve Fibers in the Same Cochleae

S. Shyamla Narayan,

The Hugh Knowles Center, Audiology and Hearing Sciences Program, Department of Communication Sciences and Disorders, and Institute for Neuroscience, Northwestern University, Evanston, IL 60208–3550, USA.

Andrei N. Temchin,

The Hugh Knowles Center, Audiology and Hearing Sciences Program, Department of Communication Sciences and Disorders, and Institute for Neuroscience, Northwestern University, Evanston, IL 60208–3550, USA.

Alberto Recio, and

Department of Physiology, University of Wisconsin, Madison, WI 53706, USA.

Mario A. Ruggero*

The Hugh Knowles Center, Audiology and Hearing Sciences Program, Department of Communication Sciences and Disorders, and Institute for Neuroscience, Northwestern University, Evanston, IL 60208–3550, USA.

Abstract

Responses to tones of a basilar membrane site and of auditory nerve fibers innervating neighboring inner hair cells were recorded in the same cochleae in chinchillas. At near-threshold stimulus levels, the frequency tuning of auditory nerve fibers closely paralleled that of basilar membrane displacement modified by high-pass filtering, indicating that only relatively minor signal transformations intervene between mechanical vibration and auditory nerve excitation. This finding establishes that cochlear frequency selectivity in chinchillas (and probably in mammals in general) is fully expressed in the vibrations of the basilar membrane and renders unnecessary additional (“second”) filters, such as those present in the hair cells of the cochleae of reptiles.

In mammalian cochleae, the bulk of auditory information is transmitted to the brain via the inner hair cells, which provide the sole synaptic inputs to 90% to 95% of the afferent fibers of the auditory nerve (1). Auditory nerve excitation is triggered by depolarization of inner hair cells upon deflection of their “hair” bundles toward the taller stereocilia (2, 3). Presumably, the forces that deflect the stereocilia bundles are derived from the vibrations of the basilar membrane (BM), but it is not known how these vibrations are transmitted to the inner hair cells (4). Although the BM and auditory nerve fibers are similarly tuned at frequencies close to the characteristic frequency (CF) (5–9), there is no consensus about whether neural threshold corresponds to a constant magnitude of BM displacement, velocity, or some function of these variables.

Until now, comparisons of the response properties of auditory nerve fibers or inner hair cells and the BM have been indirect, involving data from different subjects [with one exception (10)]. For example, a frequency-threshold tuning curve recorded from a single auditory nerve fiber in one subject was compared with BM data from another individual of the same

* To whom correspondence should be addressed. mruggero@nwu.edu.

species (5–7). Alternatively, comparisons have been based on averaged data obtained from two different groups of subjects (8). Considering the variability of both neural [for example, see (11)] and mechanical responses [for example, see (5, 9)], and also the different measurement conditions, such comparisons are bound to lead to imprecise conclusions. To clarify how mechanical vibrations are translated into neural spike trains, we conducted experiments that previously were not successful. We recorded sequentially, under identical conditions, the responses to tones of a BM site and of auditory nerve fibers innervating neighboring inner hair cells in the nearly normal ears of two anesthetized chinchillas (12).

The magnitudes of mechanical and neural responses as a function of stimulus frequency were compared by using tuning curves, which plot the stimulus levels at which a fixed response criterion is reached. In one cochlea, four fibers were encountered with CFs (9.5, 9.3, 8.0, and 7.8 kHz) comparable to the CF of the BM recording site (9.5 kHz). The fiber CFs indicate that they terminated very near the BM recording site or about 0.08, 0.64, and 0.72 mm away, respectively (13). Figure 1A shows tuning curves for the BM and one fiber, selected because its CF coincided with that of the BM site and could be compared with the BM tuning curve directly. At the fiber's CF threshold [13-dB sound pressure level (SPL)], BM vibrations had a peak displacement of 2.7 nm or, equivalently, a peak velocity of 164 $\mu\text{m/s}$. These values were used to plot isodisplacement and isovelocity tuning curves. At frequencies between CF and 1 kHz, there was a good match between neural thresholds and a constant BM velocity. When the entire frequency range of measurements was considered, however, neural thresholds were better fit by mechanical displacements subjected to high-pass filtering at a rate of 3.8 dB per octave. The other three fibers had similar tuning curves, which were well fit (after normalization to the BM CF) by BM displacement high-pass filtered at rates of 4.0, 3.9, and 4.1 dB per octave (14).

In another cochlea, the BM recording site had a CF of 9 kHz and four fibers were found with comparable CFs (9.25, 8.7, 8.1, and 8.0 kHz) and probable terminations 0.10, 0.14, 0.38, and 0.47 mm, respectively, from the BM site. The fiber with CF closest to that of the BM site had a CF threshold of 0.5-dB SPL, at which BM peak vibration was 0.26 nm or 14.6 $\mu\text{m/s}$ (Fig. 1B). As in Fig. 1A, this fiber's thresholds did not correspond to a constant BM displacement. Rather, neural thresholds were well matched by BM displacement high-pass filtered at a rate of 4.8 dB per octave (approaching constant velocity of 14.6 $\mu\text{m/s}$) over almost the entire frequency range of measurements. (Note that velocity curves are shaped like displacement curves high-pass filtered at a rate of 6 dB per octave.) The tuning curves of the three other fibers also were well matched by high-pass filtered BM displacement (at rates of 4.1, 4.3, and 2.7 dB per octave) (14).

Thus, at near-threshold stimulus levels, the frequency tuning of auditory nerve fibers both cochleae closely resembled that of BM displacement modified by high-pass filtering. However, neural tuning curves lacked the high-frequency plateaus (Fig. 1, arrows) often demonstrable in BM responses (7–9, 15–17).

The question of how BM mechanics determines auditory nerve excitation has often been posed in terms of the existence of a “second filter,” which receives its input from (but does not feed back on) the BM (the “first filter”) and transforms poorly tuned and insensitive vibrations into well-tuned and sensitive responses of hair cells and auditory nerve fibers (10, 18, 19). Indeed, electrical second filters (resonances due to interactions of ionic channels in the basolateral membranes of hair cells) exist in the cochleae of turtles (20). In the case of mammals, however, the discovery that BM responses are, in fact, well tuned and sensitive (5, 6, 8) has convinced many that a second filter is unnecessary (21). The common current view is that the vibrations of the BM are boosted by a mechanical feedback from the organ of Corti (22), perhaps involving somatic electromotility of the outer hair cells (23).

However, the lack of consensus regarding the correspondence between BM vibration and auditory nerve excitation has permitted a lingering defense (24) of second filter models or even denials that BM vibrations participate in stimulation of the auditory nerve (25). The present results show that the tuning of auditory nerve fibers closely approximates that of BM vibrations (Fig. 1) and thus demonstrate that there is no need for a second filter.

Only one previous investigation studied auditory nerve fibers and the BM in the same cochleae (10). That investigation yielded results strikingly different from the present ones: sharply tuned and sensitive responses of auditory nerve fibers were obtained from cochleae in which BM vibrations were insensitive and poorly tuned. In retrospect, it seems apparent that the method used to measure BM vibrations induced severe but localized cochlear damage and that the neural recordings came from fibers connected to sites other than those where vibrations were measured.

Other comparisons of frequency tuning in auditory nerve fibers and at the BM have been indirect. Those involving BM recordings from reasonably healthy cochleae have yielded diverse results, some indicating that neural thresholds correspond to a constant BM displacement (7, 26) and others favoring a sensitivity to velocity (5) or a combination of displacement and velocity (8). The present findings are consistent with the latter study (8) and with another that noted that the “tails” of tuning curves of inner hair cells are less sensitive than those of outer hair cells or BM displacement (27).

In conclusion, although the BM and auditory nerve fibers are similarly tuned at threshold levels, certain transformations do intervene between BM vibration and auditory nerve excitation. These transformations (high-pass filtering and removal or attenuation of the high-frequency magnitude plateau) may arise from micromechanical interactions of the organ of Corti, the tectorial membrane, and the endolymph in the subtectorial space (28) or from electrical processes in the inner hair cells, including filtering by the basolateral membrane and synaptic effects of extracellular potentials (29).

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33. All animal procedures were approved by Northwestern University's Animal Care and Use Committee. Each chinchilla was deeply anesthetized with diallyl barbituric acid in urethane. The left pinna was resected and the head was attached to a metallic holder. A calibrated miniature microphone, with its tip placed within 2 mm of the eardrum, was used for in situ determination of SPLs (expressed relative to 20 μ Pa). The auditory bulla was opened widely and a gross electrode, which recorded compound action potential thresholds of responses to tone pips, was placed on the round window. Both middle-ear muscles (cochlea L208) or only the tensor tympani (L199) was detached. Then the surgical preparations necessary for microelectrode recording from auditory nerve fibers (31) and for measuring BM vibrations with a laser velocimeter (32) were made consecutively. After the otic capsule was opened and reflective microbeads were dropped onto the

BM, the otic capsule hole was covered with a window (made from slide coverslip glass) to minimize motion of the perilymph (7). Stimuli for BM recordings were 128 to 512 repetitions of gated tones (5 to 100 ms in duration, presented every 53 to 500 ms). BM tuning curves were computed from velocity-intensity functions (resolution: 5 or 10 dB, 100 to 1000 Hz) by interpolating at each frequency the response magnitude corresponding to neural threshold at CF. Frequency-threshold tuning curves of auditory nerve fibers were measured with 50-ms tone pips, presented every 100 ms, by an automated procedure (11). They had a resolution of 32 frequency steps per octave near CF and 8 steps per octave at lower frequencies.

Fig. 1.

Frequency tuning of responses to tones of BM sites and auditory nerve fibers with similar CF. (**A** and **B**) Comparison of the frequency-threshold tuning curve for one fiber (filled symbols connected by thin solid line) with iso-displacement and isovelocity mechanical tuning curves (open circles connected by dashed line and thick solid line, respectively). In (**A**) another curve (open squares connected by solid lines) indicates the result of high-pass filtering the displacement curve at a rate of 3.8 dB per octave. The tip of the BM tuning-curve in (**B**) appears spuriously narrow because of the low-frequency resolution of data sampling [1000 Hz, versus 250 Hz in (**A**)]. The fibers had spontaneous activity of 11.2 (**A**) and 76.3 (**B**) spikes per second (33).