The Pectinate Zone is Stiff and the Arcuate Zone Determines Passive Basilar Membrane Mechanics in the Gerbil

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Abstract. The gerbil basilar membrane (BM) differs from other mammalian BMs in that the lower collagen-fiber layer of the pectinate zone (PZ) forms an arch, the upper fiber layer is flat, and ground substance separates the two layers. The role of this arch has been unknown, but can be elucidated by models. In the standard simple beam model (SBM), the upper and lower collagen-fiber layers of the BM are represented as a single layer in both the PZ and the arcuate zone (AZ). In our new arch-beam model (ABM), the upper fiber layer is flat, the lower layer forms an arch in the PZ, and the two layers combine to form the flat portion of the BM in the AZ. This design is incorporated into a 3D finite-element tapered-box model of the cochlea with viscous fluid. We find in the model that the PZ rotates as a rigid body, so its specific properties have little influence, while the AZ thickness and collagen volume fraction primarily determine passive BM mechanics.

INTRODUCTION

The cochlea of the mammalian inner ear exhibits a tonotopic mapping between each input frequency and a corresponding place of maximum mechanical vibration along the length of the cochlea. Higher frequencies excite the basilar membrane (BM) at the basal end of the cochlea near in the stapes, and lower frequencies excite the BM at the apical end near the helicotrema [1]. The gerbil BM differs from that in most other mammals, however, in that the pectinate zone (PZ) consists of distinct upper flat and lower arched bands of collagen fibers ([2] and reviewed in [3]). Between the fiber layers is amorphous ground substance. Previously, the gerbil arch-beam model (ABM) was evaluated in three isolated sections [3]. In this work, we model the ABM configuration for the entire length of the cochlea using the finite-element modeling approach, with viscous fluid (Fig. 1). For comparison, results from a similar finite-element cochlear model that instead uses the classic simple beam model (SBM) for the BM are also presented. The results show that the arch stiffens the PZ so that it rotates as a nearly rigid body, and that the BMs response to the stimulus pressure is dominated by the flexure of the flat arcuate zone (AZ) beam section. Consequently, the geometry (width and thickness) and material properties (volume fraction and Young's modulus) of the AZ fiber bands, not the thickness of the arch, determine passive cochlear mechanics.

METHODS

The ABM and SBM models both have scala fluid on the two sides of the BM. The upper tapered scala vestibule (SV), with dimensions of 1x1 mm at the base, tapers linearly to 0.15x0.4 mm at the apex. Similarly, the lower tapered scala tympani (ST) has dimensions of 1x0.6 mm at the base and tapers linearly to 0.15x0.4 mm at the apex (Fig. 1), similar to [4]. A 0.5 mm length of the BM at the apical end, the helicotrema, is sectioned off and defined as an isotropic material with a Young's modulus of 1e4 GPa to make it softer than the rest of the BM. This creates a pressure gradient that allows quasi-static fluid to flow from the SV to the ST.

Previously, three fluid-viscosity modeling approaches were tested [5]: (1) Visco-acoustics - full Navier-Stokes, (2) Narrow-acoustics - approximations of Navier-Stokes, and (3) Two-layer Visco-Pressure (TLVP) - a thin visco-acoustic layer on both faces of the BM. The TLVP model was shown to be the computationally the fastest and presently used.

In a typical SBM, the upper and lower collagen-fiber layers of the BM are represented as a single layer in both the PZ and AZ. In the present version of the SBM, the BM is represented as a shell with varying thickness and orthotropic material properties that incorporates both the AZ and the PZ (Table 1).

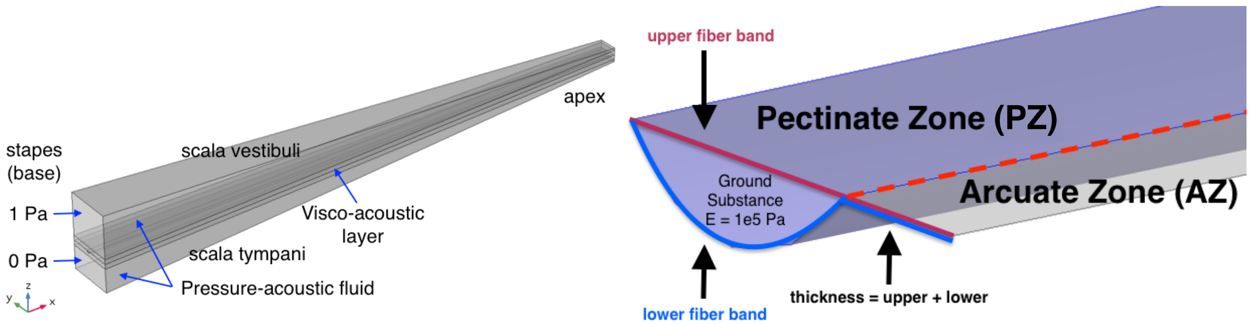

FIGURE 1. Left - Arch-beam model (ABM) with anatomically based scala vestibuli and scala tympani areas. The box tapers linearly from base to apex. The simple beam model (SBM) has identical geometry, but without the arch. The BM in the SBM is a shell with a varying volume fraction. The SBM responses are calculated along a line down the center of the BM. Right - Close-up view of the arch in the pectinate zone (PZ) of the ABM, along with the flat arcuate zone (AZ). All ABM responses are calculated along the junction of the AZ and PZ (red dashed line).

TABLE 1. SBM Model Parameters

	Value	**Units**
Length l	12	mm
Scala Vestibuli Area	Base = 1, Apex = 0.06	mm^2
Scala Tympani Area	Base = 0.6, Apex = 0.06	mm^2
Speed of Sound c	1500	m/s
Density ρ	1850	$\frac{kg}{m^3}$
Young's modulus E bone	10e9	Pa
Poisson's Ratio γ	0.49	-
Basilar Membrane		
Fiber Volume Fraction $v_f(x)$	$-0.0127x + 0.0141$	-
Ey	(1e9-1e5)$*v_f$+1e5	-
Young's Moduli E	1e5, Ey, 1e5	Pa
Shear Moduli G	1e5/3, Ey/3, 1e5/3	Pa
Thickness	$(0.0094x/L + 0.011) * 10^{-3}$	mm
Width $w(x)$	$(0.15x/L + 0.15) * 10^{-3}$	mm
Density ρ	1000	$\frac{kg}{m^3}$
Poisson's Ratio	0	-
Scala Fluid		
Dynamic Viscosity μ	7e-4	$Pa \cdot s$
Density ρ	1000	$\frac{kg}{m^3}$
Helicotrema		
Young's modulus E	1e4	Pa
Shear modulus G	1e4/3	Pa

For the ABM representation (Table 2), the upper collagen-fiber layer is a flat shell (red line in the right panel of Fig. 1), while the lower shell layer forms an arch in the PZ (blue line). The two fiber layers combine to form the flat portion of the BM in the AZ. The PZ arch is a parametric curve, and the ground-substance gel between the layers is a solid with a low Young's modulus (1e5 Pa), consistent with calculations of 1.4e5 Pa for ground substance[6]. The PZ width is defined as 2/3 of the total BM width. Fiber-layer thicknesses were measured by Schweitzer[2]. The bottom shell is defined as a parametric surface with a height and a radius, both a function of the cochlea length. We use 1 GPa as the Young's modulus for collagen. The volume fraction in the layers is assumed to be 0.5, which gives an effective Young's modulus of 5e8 Pa given that the Young's modulus of the BM ground substance is a much smaller 1e5 Pa.

TABLE 2. Parameters for the ABM. Other model parameters are the same as for the SBM shown in Table 1

	Value	Units
Basilar Membrane		
Fiber Volume Fraction v_f	0.5	-
Ey	1e9 $*v_f$	*Pa*
Young's Moduli E	1e5, Ey, 1e5	*Pa*
PZ Thickness, upper band	$(21.6x^2 - 0.3961x + 0.002) * 10^{-3}$	*mm*
PZ Thickness, lower band	$(10.6x^2 - 0.2779x + 0.002) * 10^{-3}$	*mm*
AZ Thickness	PZ upper + PZ lower band	*mm*
Young's modulus Ground Substance	1e5	*Pa*
Arch height $h(x)$	$(2.6x + 0.0299) * 10^{-3}$	*mm*
Radius $r(x)$	$(\frac{w}{2}^2 + h^2)/(2h)$	*mm*

An input pressure of 1 Pa is applied to the base of the scala vestibuli, and 0 Pa is applied to the base of the scala tympani to approximate the round window. Several frequencies (1, 5, 10, and 20 kHz) are applied to the stapes and solved in the frequency domain for BM velocity. All other boundaries are defined as a hard wall.

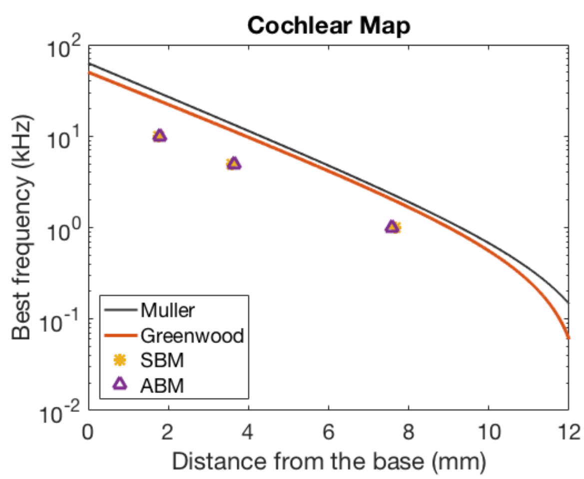

FIGURE 2. Greenwood [7] and Muller's [8] cochlear maps are fits to the measured locations on the BM corresponding to the maximum amplitude for a given frequency in the active cochlea. The present SBM and ABM calculations for the passive cochlea are about an octave lower.

RESULTS

The SBM parameters were adjusted so that their place–frequency mappings at three input frequencies (1, 5, and 10 kHz) are similar to those of the ABM and the Greenwood [7] and Muller [8] maps in Fig. 2. For the SBM, the BM responses are calculated along a line down the center of the BM, and for the ABM the responses are calculated along a line marking the junction between the PZ and AZ regions, as shown in Fig.1. For both the ABM and the SBM, the frequency–place maps are about an octave below the measured (in-vivo) maps, as is to be expected for a passive cochlea (Fig. 2).

To determine the sensitivity of the AZ vs. the PZ in the ABM, their volume fraction (v_f) and thickness were varied. The left panel of Fig. 3 shows that a reduction of the v_f from 0.5 to 0.01 in the AZ (green + symbols and dash-dotted green line) basally shifts the location of the maximum frequency to a much greater extent than the same reduction in v_f in the PZ (green o symbols and dashed green line). Similarly, reducing and increasing the thickness of the AZ by a factor of 2 (cyan and red + symbols, respectively, in the right panel) has a much greater effect than reducing and increasing the thickness of the PZ by a factor of 2 (cyan and red o symbols, respectively). Overall, decreasing parameters of the PZ (o symbols) results in smaller shifts to the left (less stiff) than varying the parameters for AZ (+ symbols), suggesting that the ABM is more sensitive to parameter changes in the AZ than to parameter changes in the PZ.

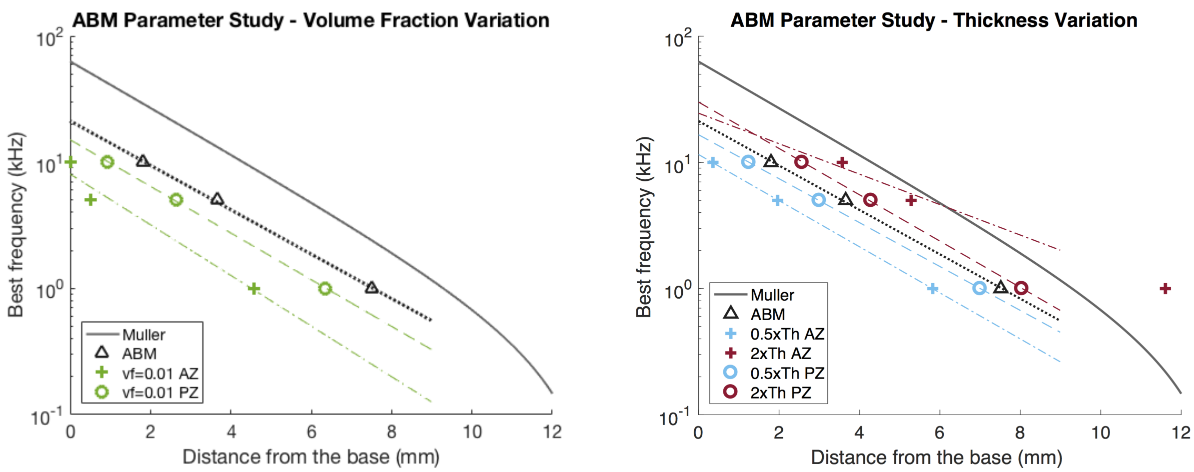

FIGURE 3. A parameter study of the ABM, varying the volume fraction (v_f, left) and thickness (right) of the AZ and PZ shows that the AZ primarily determines the cochlear map.

We next examined the spatial responses of the BM for four input frequencies (1, 5, 10, and 20 kHz) and the frequency response at given spatial point of the ABM and SBM and compared them to published data from Ren and Nuttall [9].

Figure 4 left column, shows the magnitude and phase of the BM spatial responses for the ABM and SBM. Peak locations are nearly identical in both models, as seen in the cochlear map (Fig. 2), but with sharper apical-side roll-off observed in the SBM. The phase slope increases as the wave approaches the characteristic frequency, indicating a traveling wave in both models. For the ABM, the amplitude and phase roll-off are less steep than for the SBM due to the longitudinal coupling of the gel, which is defined as an isotropic material with E = 1e5 Pa, while the BM layer of the SBM is exclusively dictated by the volume fraction.

The frequency response is generated by running a series of frequencies and extracting the normalized velocity at the 10 kHz best-frequency location (from the cochlear map). The ABM frequency response generally matches well with the SBM at the 10 kHz best-frequency location in magnitude and phase (Fig.4, right panel). However, the peak in both are higher than in the experimental data from Ren and Nuttall[9] by about a factor of about 2-3. Part of this discrepancy could be due to differences in the radial location of the calculation (near the peaks) and measurement (some what arbitrarily) points.

DISCUSSION

Nearly all previous models of the cochlea represent the BM as a simple beam or a plate (e.g., [10], [11]). This is valid for some animals like guinea pig and human, where the upper and lower fiber bands are parallel [12]. This is not the case for a family of gerbils, mouse, and possibly other rodents, however[3]. A recent analysis suggests that for these animals an ABM formulation is important to capture their BM mechanics[3]. However, that model analysis

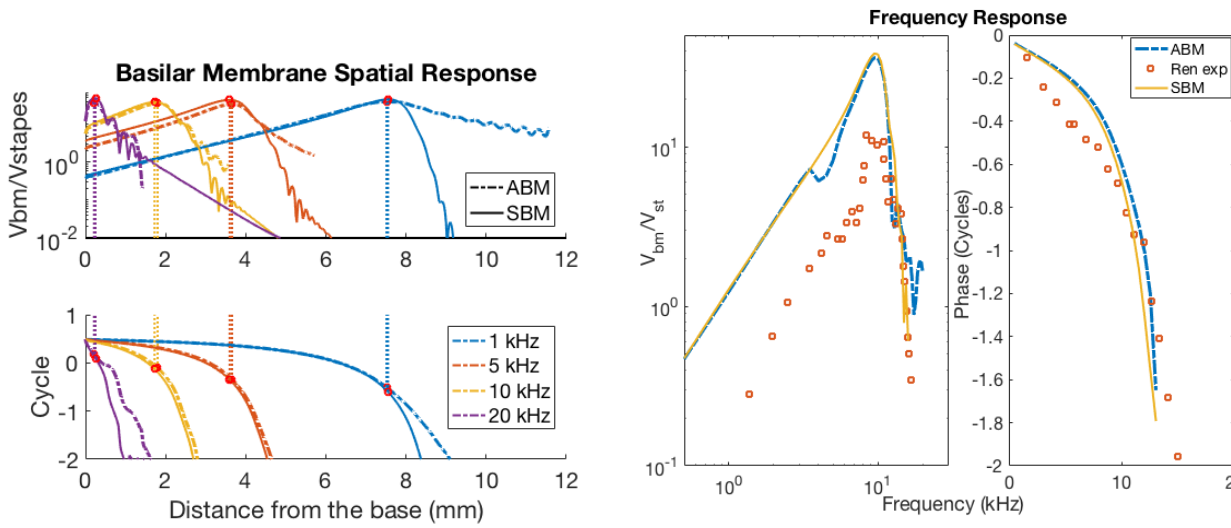

FIGURE 4. Left - Normalized Vbm/Vstapes magnitude and phase plots of the AZ for the SBM and ABM. The locations of the peak amplitudes and corresponding phase are circled in red. Right - Normalized velocity and phase vs. frequency measured at x=2.57 mm from the base (the best-frequency location at 10 kHz) compared to experimental data at 80 dB SPL Ren and Nuttall[9].

was limited to several isolated cross-sections of the cochlea. Building on that recent work, we present a full-length finite-element model of the Mongolian-gerbil cochlea using an arch for the PZ with a gel between the upper and lower fiber layers that extends to a flat beam in the AZ. The ABM is compared to a similar finite-element model with a simple beam representation for the BM.

Cochlear maps for both models are similar (Fig. 2), suggesting that the SBM and ABM have similar volume compliance. Upper and lower fiber-layer v_f and thickness parameter variations in the AZ and PZ show that the ABM is more sensitive to parameter changes in the AZ, suggesting that the AZ dimensions and material properties primarily determine passive BM mechanics in the gerbil (Fig. 3 and [3]). Radial-profile displacement measurements indicate that the PZ moves as a stiff beam with a peak displacement near where the AZ and PZ meet [13]. This observation is consistent with the present model.

The frequency responses of the models are validated against data at the 10 kHz location (Fig. 4, right column). New passive measurements at frequencies below 3–4 kHz from the gerbil apical turns [14] will allow further tests of this gerbil cochlear model.

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COMMENTS AND DISCUSSION

Jong-Hoon Nam:

1. As the BM dominates cochlear physics, better understanding the behavior of the BM may be crucial. I liked [the] recent Kapuria paper (that has a similar theme to this MS), especially the discussion was insightful. What is the essential reason for this model to have more physiological phase accumulation as compared to Yoon et al.'s? I suppose that it is due to the mass of the ground substance.

   Author Reply: In the Kapuria *et al.* [3] paper, we developed analytic models for discrete cross sections of the gerbil cochlea, whereas for the present analysis we developed finite-element models for the cochlea from base to apex (e.g., Fig. 1). In the preliminary manuscript, the best-frequency locations for the ABM and the SBM were slightly different, resulting in phase differences between the two model results. In this revised manuscript, the best-frequency locations are better aligned, which produces similar phase accumulations for the two models (Fig. 4).

2. Do you have any thoughts of why the gerbil cochlea has different BM geometry from other species? Or, I meant to say that this model may be useful for comparative study.

   Author Reply: The late Dave Mountain also challenged us with this question nearly a decade ago, and we are still trying to understand the reasons with multiple approaches including model comparisons with mammals like guinea pig and human that don't have a PZ arch. As discussed in Kapuria *et al.*, another area of interest is developmental studies of the arch.

3. Do you know if the arcuate zone has the collagen fiber layer(s), too? It is unclear in the Schweitzer paper. Seen under the light microscope, aligned fiber-like patterns are apparent only in the pectinate zone.

   Author Reply: The collagen fibers continue from the flat AZ to the arched PZ (Fig. 1). The only measurements of the upper and lower fiber-band layer thicknesses come from Lisa Schweitzer [2]. She showed that the collagen-fiber-layer thickness of both bands changes during development.

4. Have you observed the longitudinal space constant of your BM?

   Author Reply: No, we have not. But it is worth looking at for a future publication.

John Stockie:

1. A nice example of how a finite element calculation can study a fine geometrical feature like the arched-beam structure discussed in the gerbil cochlea. This is clearly moving beyond other simpler beam or plate models of the BM, but is it possible to comment nonetheless on how significant these ”arching” effects are in comparison with other physical features of simpler 1D/2D beam models? I’m thinking about components of beam models (many discussed in other papers in this proceedings) such as longitudinal coupling, BM thickness, parameter variations in the radial direction, etc.
   Author Reply: Thank you John. A good answer to your excellent question(s) requires more parametric studies. What we can say at this point is that in the ABM the overall BM thickness seems to be less important and the thickness of the fiber bands matters most [3]. The arch configuration makes the PZ stiff and thus radially moves the peak of the traveling wave from the center of the BM in the SBM towards the AZ and PZ junction in the ABM. The ground substance is modeled as an isotropic elastic material, which supplies longitudinal coupling. This has a significant effect on the 1 kHz spatial response (left column, Fig. 4).