Unraveling the mystery of hearing in gerbil and other rodents with an arch-beam model of the basilar membrane

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Supporting Information

Methods, Tables and Figures

1. The model for point-load measurements

An analytical formulation is developed to predict the large-deflection response of the BM under point-load measurements. For mathematical simplicity, the support due to the outer pillar is considered to be stiff enough to allow any deflection, without losing much accuracy for the deflection at the center of the arch. Figure 1C shows the resulting simplified model, where $k_a$ represents the effective spring stiffness of the arcuate zone and the SSL. The ground substance is modeled as an incompressible gel with the effect of providing a uniform internal pressure $p$ on the arch (lower fiber band) as well as the flat beam (upper fiber band). The effective diameter $d$ of the model is taken as equal to the diameter of the probe, since there is negligible longitudinal coupling between adjacent filaments\textsuperscript{1}.

1.1 Lower fiber band: the circular arch

It is appropriate to consider von Karman-type geometric nonlinearity due to large deflections for the present purpose. For the shallow circular arch, with circumferential axis $\theta$ and thickness axis $z$, the Langrangian strain $\varepsilon_\theta$ at a point $P(\theta, z)$ is given by\textsuperscript{2}

$$\varepsilon_\theta = \frac{u_\theta}{R} + \frac{w_\theta}{R} + \frac{1}{2} (\frac{w_\theta}{R})^2 - z \frac{w_{\theta \theta}}{R^2} = \varepsilon_0 + z\kappa,$$

where a subscripted comma denotes a partial differentiation. $u_\theta$ and $w_\theta$ are the in-plane and transverse displacements of the middle surface ($z = 0$) along $\theta$ and $z$ directions, respectively. $\varepsilon_0$ and $\kappa$ denote the membrane strain at the arch’s midsurface and its curvature, respectively. $R$ is the radius of the midsurface of the arch. Neglecting the transverse shear strain (for $\gamma_{\theta z} \approx 0$) as per Love’s thin shell theory assumptions, the principle of virtual work for the arch with a point load $Q$ applied at its center, reduces to

$$\int_V \sigma_\theta \delta \varepsilon_\theta dV + \int_S b_p \delta w_0 - Q \delta w_c = 0$$

for all kinematically admissible virtual displacements $\delta u_\theta$ and $\delta w_0$. $V$ and $S$ denote, respectively, the volume and arc length of the arch. $\sigma_\theta$ denotes the circumferential normal stress and $w_c$ is the central deflection at $\theta = 0$. Substituting Eq. (1) into Eq. (2) and performing integration over the thickness of the arch yields

$$\int_S \left[ N_\theta \left( \delta u_{0,s} + \frac{1}{R} \delta w_0 + w_{0,s} \delta w_{0,s} \right) - M_\theta \delta w_{0,ss} + \bar{p} \delta w_0 \right] ds - Q \delta w_c = 0,$$

where $s = R\theta$, $\bar{p} = b_p$, and $N_\theta$ and $M_\theta$ are the membrane and bending stress resultants, respectively, given by

$$N_\theta = \int_{-t_1/2}^{t_1/2} b \sigma_\theta dz \quad \text{and} \quad M_\theta = \int_{-t_1/2}^{t_1/2} b z \sigma_\theta dz.$$  

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The integral in Eq. (3) is expressed in terms of variations \( \delta u_0 \) and \( \delta w_0 \) by applying integration by parts when necessary, which yields

\[
\int_S \left[ -N_{\theta,s} \delta u_0 + \frac{N_{\theta}}{R} \delta w_0 - \left( N_{\theta} w_{0,s} \right)_s \delta w_0 - M_{\theta,ss} \delta w_0 + \bar{p} \delta w_0 \right] ds + \left[ N_{\theta} \delta u_0 + \frac{N_{\theta} w_{0,s} \delta w_0 + M_{\theta,s}}{R} \right]_{s=0}^s - Q \delta w_c = 0. \tag{5}
\]

Since the virtual displacements are arbitrary, their coefficients in the integrand of Eq. (5) must vanish separately. This yields the governing equations of equilibrium of the arch under large deflection:

\[
N_{\theta,s} = 0, \quad \Rightarrow \quad N_{\theta} = \text{constant} = \pm \bar{N}_1, \quad \bar{N}_1 > 0; \tag{6}
\]

\[
M_{\theta,ss} - \frac{N_{\theta}}{R} + \left( N_{\theta} w_{0,s} \right)_s + \bar{p} = 0. \tag{7}
\]

The variationally consistent boundary conditions are the prescribed values of one of the factors of each of the following products appearing in Eq. (5):

\[
N_{\theta} \delta u_0, \quad \left( N_{\theta} w_{0,s} + M_{\theta,s} \right) \delta w_0, \quad \text{and} \quad M_{\theta} \delta w_{0,s}. \tag{8}
\]

In the present problem, considering symmetry, the boundary conditions are

\[
\text{at} \ s = 0: \quad w_{0,s} = 0, \quad \text{and} \quad M_{\theta,s} = Q/2, \quad \text{and}
\]

\[
\text{at} \ s = \pm S/2: \quad w_0 = 0, \quad \text{and} \quad M_{\theta} = 0. \tag{9}
\]

From Eq. (6), \( N_{\theta} \) is constant, which can be compressive or tensile depending on the relative values of \( Q \) and \( p \).

**Case 1: \( N_{\theta} < 0 \)**

From its definition in Eq. (4), \( M_{\theta} \) can be related to \( w_0 \) as \( M_{\theta} = -E_1 w_{0,ss} \), where \( I_1 \) is the moment of inertia of the arch cross-section about its neutral axis along the direction perpendicular to the \( \theta-z \) plane. Substituting this relation into Eq. (7) yields

\[
w_{0,sss} + \mu_1^2 w_{0,ss} = \mu_1^2 \bar{p}_1/R, \tag{10}
\]

where \( \mu_1^2 = \bar{N}_1/E_1 \) and \( \bar{p}_1 = (\bar{p}R + \bar{N}_1)/\bar{N}_1 \). Its solution satisfying the boundary conditions can be obtained as

\[
w_0 = -\frac{\bar{Q}}{\mu_1^2 \bar{r}_0} \{ \tan \bar{s}_0 \cos \bar{s} - \bar{s}_0 - H(s)(\sin \bar{s} - \bar{s}) \} - \frac{\bar{p}_1}{\mu_1^2 R} \left\{ 1 - \frac{\cos \bar{s}}{\cos \bar{s}_0} + \frac{s_0^2}{\bar{s}^2} \right\}. \tag{11}
\]

where \( \bar{s} = \mu_1 s, \bar{s}_0 = \mu_1 S/2, \bar{Q} = QRS/4E_1, \) and \( H(s) \) is the Heaviside step function defined by \( H(s) = \{ -1 \text{ when } s < 0 \} \). The central deflection \( w_c \) at \( s = 0 \) is obtained from Eq. (11) as

\[
w_c = -\frac{\bar{Q}}{\mu_1^2 \bar{r}_0} \{ \tan \bar{s}_0 - \bar{s}_0 \} - \frac{\bar{p}_1}{\mu_1^2 R} \left\{ 1 - \frac{1}{\cos \bar{s}_0} + \frac{s_0^2}{\bar{s}^2} \right\}. \tag{12}
\]

The area displacement \( (A_s) \) of the arch is obtained as

\[
A_s = \int_{-S/2}^{S/2} w_0 ds = -\frac{\bar{Q}}{\mu_1^2 \bar{r}_0} \left\{ \frac{1}{\cos \bar{s}_0} - \frac{s_0^2}{2} - 1 \right\} - \frac{2\bar{p}_1}{\mu_1^2 R} \left\{ \bar{s}_0 - \tan \bar{s}_0 + \frac{s_0^2}{3} \right\}. \tag{13}
\]

Since \( N_{\theta} \) is constant, the membrane strain \( \varepsilon_0 \) can be computed as \( \varepsilon_0 = -\frac{\bar{N}_1}{E_1 \bar{r}_1} = -\mu_1^2 \bar{r}_1^2, \) with \( \bar{r}_1 = \sqrt{I_1/b} \). Integrating this and noting that \( u_0(-S/2) = 0 \) yields the lateral displacement at the outer-pillar end \( (s = S/2) \) as

\[
u_0(S/2) = -\mu_1^2 \bar{r}_1^2 S - \frac{1}{R} \int_{-S/2}^{S/2} w_0 ds - \frac{1}{2} \int_{-S/2}^{S/2} (w_{0,s})^2 ds, \tag{14}
\]

which should be equal to the deformation of the spring of stiffness \( k_\alpha \):

\[
u_0(S/2) = -k_\alpha (N_1 - N_2), \tag{15}
\]
where $N_2$ is the tensile force in the flat beam. We introduce an effective length $L_e$ for the spring constant $k_a$ such that $k_a = Eb(t_1 + t_2)/L_e$. Substituting the expression of $w_0$ from Eq. (11) into Eqs. (14) and (15) yields

\[ A_1 \bar{Q}^2 + B_1 \bar{Q} + C_1 = 0, \tag{16} \]

where

\[ A_1 = \frac{1}{4s^2} \left[ 3 - 3\tan \frac{s_0}{s_0} + \tan^2 \frac{s_0}{s_0} \right], \]

\[ B_1 = \frac{1}{s^2} \left[ 2\bar{p}_1 - 1 - (2\bar{p}_1 - 1) + 1 - \frac{\bar{p}_1}{2} \right] \frac{s_0^2}{2}, \]

\[ C_1 = \left( \frac{s_0}{\lambda} \right)^2 \left[ 1 + \frac{t_1 L_e}{s} \right] + D_1 - 4 \frac{N_2 L_e R^2}{Et^3}, \]

\[ D_1 = \frac{1}{4s^2} \left[ 3 - 3\tan \frac{s_0}{s_0} + \tan^2 \frac{s_0}{s_0} \right], \tag{17} \]

with $s = S^2/4t_1 R$ and $t = t_1 + t_2$.

**Case 2: $N_\theta > 0$**

In this case, $N_\theta = N_1$, with $N_1 > 0$, for which the governing differential equation for $w_0$ becomes

\[ w_{0,ssss} - \mu_1^2 w_{0,ss} = -\mu_1^2 \bar{p}_1 / R, \tag{18} \]

where $\bar{p}_1 = (-\bar{p}R + N_1)/\bar{N}_1$. Equations (11)–(13) and the coefficients of Eq. (16) take the following forms:

\[ w_0 = \frac{q}{\mu_1^2 R s_0} \left\{ \tanh \frac{s_0}{s_0} \cosh \frac{s_0}{s_0} - H(s) \left( \sinh \frac{s_0}{s_0} - s_0 \right) \right\} + \frac{\bar{p}_1}{\mu_1^2 R} \left[ 1 - \frac{\cosh s_0}{\cosh s_0} - \frac{s_0^2}{2} \right], \tag{19} \]

\[ w_0 = \frac{q}{\mu_1^2 R s_0} \left\{ \tanh \frac{s_0}{s_0} - s_0 \right\} + \frac{\bar{p}_1}{\mu_1^2 R} \left[ 1 - \frac{1}{\cosh s_0} - \frac{s_0^2}{2} \right], \tag{20} \]

\[ A_2 = \frac{2q}{\mu_1^2 R s_0} \left\{ \frac{1}{\cosh s_0} + \frac{s_0^2}{2} - 1 \right\} + \frac{2\bar{p}_1}{\mu_1^2 R} \left[ \tanh \frac{s_0}{s_0} - s_0 + \frac{s_0^2}{3} \right], \tag{21} \]

\[ A_1 = \frac{1}{4s^2} \left[ 3 - 3\tan \frac{s_0}{s_0} + \tan^2 \frac{s_0}{s_0} \right], \tag{22a} \]

\[ B_1 = \frac{1}{s^2} \left[ 2\bar{p}_1 - 1 - (2\bar{p}_1 - 1) + 1 - \frac{\bar{p}_1}{2} \right] \frac{s_0^2}{2}, \tag{22b} \]

\[ C_1 = \left( \frac{s_0}{\lambda} \right)^2 \left[ 1 + \frac{t_1 L_e}{s} \right] + D_1 - 4 \frac{N_2 L_e R^2}{Et^3}, \tag{22c} \]

\[ D_1 = \frac{1}{4s^2} \left[ 3 - 3\tan \frac{s_0}{s_0} + \tan^2 \frac{s_0}{s_0} \right]. \tag{22d} \]

### 1.2 Upper fiber band: the flat beam

The flat beam representing the upper fiber band is subjected to a uniform pressure $p$ and an axial tension $N_2$. Its governing equation of equilibrium can be obtained in terms of the deflection $w_0^b$, following the same procedure as for the arch:

\[ w_{0,xxxx}^b - \mu_2^2 w_{0,xx}^b = -\mu_2^2 \bar{p}_2, \tag{23} \]

where $\mu_2^2 = N_2/EI_2$ and $\bar{p}_2 = p/N_2 = p/\mu_2^2 E I_2$; with $I_2$ being the moment of inertia of the beam section. The solution of Eq. (23) satisfying the boundary conditions, $w_0^b = w_{0,xx}^b = 0$ at $x = L_p/2$ and $w_0^b = w_{0,xxx}^b = 0$ at $x = 0$, is obtained as

\[ w_0^b = \frac{p_2}{\mu_2^2} \left[ 1 - \frac{\cosh x}{\cosh x_0} + \frac{x^2}{2} - \frac{x_0^2}{2} \right], \tag{24} \]

where $x = \mu_2 x$ and $x_0 = \mu_2 L_p/2$. The area displacement $A_b$ is obtained as

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Also, equating the axial displacement at \( x = L_p/2 \) to the shortening of the end spring \( k_a \) yields
\[
\mu_2^2 r_2^2 L_p - \frac{1}{2} \int_{L_p/2}^{L_p} \left( w_{b,0,x}^b \right)^2 \, dx = - \frac{(N_2 - N_3) L_e}{E b t},
\]
with \( r_2 = \sqrt{l_2/bt_2} \). Substituting \( w_{b,0}^b \) from Eq. (24) into Eq. (26) leads to
\[
\vec{r}_2 = \frac{2 x_0}{\sqrt{\lambda_b}} \left[ \frac{x_0^2}{\lambda_b} + (\mu_2^2 l_2 - \mu_1^2 l_1) \frac{L_e}{b t} \right]^{1/2},
\]
where \( \lambda_b = L_p/2r_2 \) and
\[
\Gamma = 5 \frac{\tanh x_0}{x_0} - \frac{1}{\cosh^2 x_0} + \frac{2}{3} x_0^2 - 4.
\]
Equations 1–28 are implemented in a custom MATLAB script.

### 1.3 Coupling of the arch and the beam

The deformations of the arch and the beam are coupled by the fact that the area displacements, \( A_s \) and \( A_b \), respectively, are related to each other. Considering incompressibility of the ground substance and total-mass conservation at a given cross section of the PZ arch, the two area displacements should be equal. However, under point loading, some amount of the ground substance in the loaded region may be pushed away to adjacent areas. To account for this, the area displacements are related as
\[
A_b = c A_s, \quad 0 \leq c \leq 1,
\]
where \( c \) is the volume-dispersal factor. A model for this effect has been developed in which the pectinate zone is treated as an elastic tube. The result for reasonable tissue properties that \( c \) is around 0.8. However, in the present calculations, the effect of various values for \( c \) are also considered. The unknowns in the arch-beam-ground substance system are \( \mu_1, \mu_2, \) and \( \bar{r} \), which are obtained by solving the system of nonlinear equations (16), (27), and (29). The solution is obtained iteratively using a displacement-controlled approach (finding \( Q \) for a given \( w_c \)).

### 1.4 Effects of the soft cell cover

The fact that the soft cells on the scala-tympani side of the BM affect the force–deflection curve under point loading has been demonstrated by Miller. Like the ground substance, these cells too can be approximated as an incompressible fluid layer with a low shear strength under pressure loading. Under a point force, however, these cells would act as a soft spring, which would deflect the most until fully compressed. The final load–deflection behavior would be that of this spring and the nonlinear spring representing the load–deflection curve of the arch-beam-ground substance system, acting in series. Denoting the thickness and the spring stiffness of the soft cell layer as \( t_{cell} \) and \( k_{cell} \), respectively, the effective deflection \( w_e \) for a given force \( Q \) will be
\[
w_e = \begin{cases} 
Q/k_{cell} + w_c & \text{when } Q/k_{cell} < t_{cell} \\
t_{cell} + w_c & \text{when } Q/k_{cell} \geq t_{cell}
\end{cases}
\]

### 2. The model for pressure-load behavior

For pressure loading, the model shown in Fig. 1D is considered without the spring support \( (k_a) \) at the outer-pillar foot. The ground substance is modeled as a solid of very low elastic modulus and a Poisson’s ratio close to 0.5 (not exactly 0.5 to avoid numerical difficulties). Since the soft cell cover will act as an incompressible layer under pressure loading, it will not affect the deflection. Only the linear stiffness corresponding to the physiological range of deflections is of importance here. Hence, a linear analysis is
performed using the commercial finite-element software COMSOL. The lower and upper fiber layers are modeled using curved and flat beam elements, and the ground substance using plane stress elements.

The volume compliance $C$ is computed as

$$C = \frac{\Delta A}{p_o},$$

(31)

where $\Delta A$ is the area displacement of the BM subjected to a differential pressure $p_o$, computed from the deflection $w$ as $\Delta A = \int_0^{L_p+L_a} w dx$. The BM is covered with soft cells that are in contact with extracellular fluid, both of which have similar density and acoustical properties. Consequently, for modeling, the soft cells can be replaced by fluid. Based on these assumptions, Puria and Steele obtained the best frequency $f$ of the BM as a plate immersed in fluid. Following this formulation, the best frequency of the BM can be estimated from its volume compliance as

$$f = \frac{1}{\pi} \sqrt{\frac{1}{\pi p_f c^2}},$$

(32)

where $\rho_f$ is the fluid density and $f$ is in Hz.
3. SI Tables

### Table S1: Predicted frequency ratios calculated from the Simple Beam Model for the guinea pig and gerbil from basal to apical ends.

|                | Guinea pig | Gerbil         |
|----------------|------------|----------------|
|                | Basal end  | Apical end     | Ratio (Base/Apex) | Basal end  | Apical end | Ratio (Base/Apex) |
| Fiber vol. fraction \((v_f)\)^a | 0.08       | 0.01           | 8                 | 0.16^a     | 0.0083^a   | 19.3             |
| BM PZ width \((L_p)\), µm | 80         | 180            | 0.44              | 148^b–93.6^e | 211^b–214^e | 0.07–0.44         |
| BM thickness \((t_f)\), µm | 7          | 1              | 7                 | 22.6^b     | 56.5^b     | 0.40             |
| Point stiffness^c ratio | -          | -              | 32213             | -          | -          | 3.6–14.5          |
| Resonant frequency ratio | -          | -              | 400               | -          | -          | 2.7–8.7           |
| Auditory Range, Hz | 50,000     | 54             | 926               | 60,000     | 100        | 600             |

^a approximated from the ratio of fiber band thickness^5 to overall thickness^6

^b extrapolated to basal and apical ends from measurements at three locations given in Edge et al.^6

^c extrapolated to basal and apical ends from measurements at three locations given in Schweitzer et al.^5

^d Point stiffness \(\propto \frac{v_f t^3}{\rho_f L_p^2}\)

^e Taken from the fiber density measured in cat by Cabezudo^7.

^f As an approximation, 2/3 of the total BM width is given^7. Extrapolation of Tuedt and Richter^8 gives higher value of 100 µm at the basal end of the guinea pig.

### Table S2: Geometry parameters and measured and ABM point stiffness for gerbil BM.

|                | Location | Basal turn | Middle turn | Apical turn |
|----------------|----------|------------|-------------|-------------|
| Distance from base, mm | 2.8      | 6.0        | 10.3        |
| Width of PZ \((L_p)\), µm | 168.0    | 192.0      | 207.3       |
| Height \((h)\), µm | 35.0      | 49.7       | 55.3        |
| Lower fiber band thickness \((t_1)\), µm | 1.49     | 0.90       | 0.45        |
| Upper fiber band thickness \((t_2)\), µm | 1.01     | 0.35       | 0.16        |
| Measured plateau stiffness, N/m | 0.79     | 0.15       | 0.017       |
| ABM-Estimated plateau stiffness, N/m | 0.78     | 0.15       | 0.019       |

^a from Edge et al.^6

^b interpolated at given locations from measurements in Schweitzer et al.^5

^c \(k = 0.95 \times 10^{(10.24–4.43x)/20}\), where \(x\) is the distance from the base in mm [Fig. 3 of Emadi et al.^9]
### Table S3: ABM volume compliance and best frequency of gerbil BM

| Location                      | Basal turn | Middle turn | Apical turn |
|-------------------------------|------------|-------------|-------------|
| Distance from base, mm        | 2.8        | 6.0         | 10.3        |
| Total width $(L)^a$, µm       | 175        | 224         | 287         |
| Volume compliance, m²/TPa     | 0.20       | 3.34        | 93.27       |
| Estimated best frequency, kHz | 12.8       | 3.11        | 0.59        |
| Best frequency$^b$, kHz       | 15.1       | 3.64        | 0.45        |

$^a$from Schweitzer et al.$^5$

$^b$from Greenwood$^{10}$

### Table S4: ABM volume compliance and best frequency of house mouse

| Location                      | Basal turn | Middle turn | Apical turn |
|-------------------------------|------------|-------------|-------------|
| Distance from base, mm        | 4.3        | 2.13        | 0.97        |
| Width of PZ $(L_p)^a$, µm     | 95         | 110         | 115         |
| Width of AZ $(L_a)^a$, µm     | 39         | 51          | 58.5        |
| Height $(h)^a$, µm            | 14.1       | 14.0        | 9.8         |
| Lower fiber layer thickness, µm | 1.7      | 0.9         | 0.46        |
| Upper fiber layer thickness, µm | 1.3       | 0.35        | 0.18        |
| Volume compliance, m²/TPa     | 0.037      | 0.86        | 10.8        |
| Estimated best frequency, kHz | 29.7       | 6.1         | 1.73        |
| Best frequency$^b$, kHz       | 34.1       | 5.3         | 1.8         |

$^a$from Keiler and Richter$^{11}$

$^b$from Greenwood$^{10}$
4. SI Figures

SI Figure S1: Basilar membrane total width as function of %distance from the base as measured by Plassmann et al.\textsuperscript{12} for 5 species of the gerbillinae rodent family.

SI Figure S2: Same as SI Fig S1 but with the pectinate zone (PZ) thickness plotted.

SI Figure S3: Same as SI Fig S1 but with the arcuate zone (AZ) thickness plotted.
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