

# 1 **Outer hair cell receptor potentials reveal a local resonance in the mammalian cochlea**

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## 10 **SUMMARY**

11 Sensory hair cells, including the sensorimotor outer hair cells, which enable the sensitive,  
12 sharply tuned responses of the mammalian cochlea, are excited by radial shear between the  
13 organ of Corti and the overlying tectorial membrane. It is not currently possible to measure  
14 directly *in vivo* mechanical responses in the narrow cleft between the tectorial membrane and  
15 organ of Corti over a wide range of stimulus frequencies and intensities. The mechanical  
16 responses can, however, be derived by measuring hair cell receptor potentials. We  
17 demonstrate that the seemingly complex frequency and intensity dependent behaviour of  
18 outer hair cell receptor potentials could be qualitatively explained by a two-degrees of  
19 freedom system with a local cochlear partition and tectorial membrane resonances strongly  
20 coupled by the outer hair cell stereocilia. A local minimum in the receptor potential below the  
21 characteristic frequency is always observed at the tectorial membrane resonance frequency  
22 which, however, might shift with stimulus intensity.

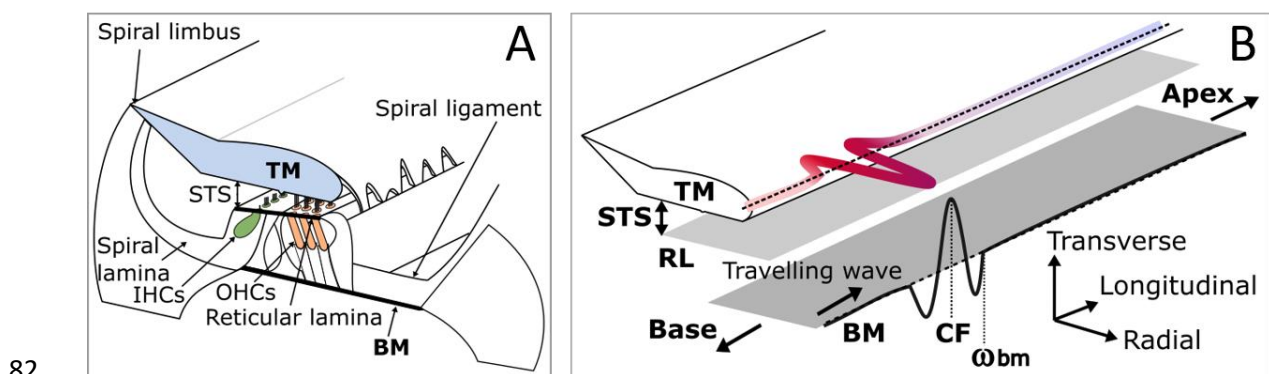
23 **Keywords:** cochlea, cochlear amplifier, cochlear micromechanics, tectorial membrane, outer  
24 hair cell

## 25 **INTRODUCTION**

26 The mammalian cochlea is an impressively sensitive, sharp frequency analyser which works  
27 over a wide range of sound pressure levels (SPLs) exceeding six orders of magnitude (Robles  
28 and Ruggero, 2001). These features are associated with a process called the cochlear  
29 amplifier (Davis, 1983), which amplifies and sharpens cochlear responses to low-level sound

30 stimulation but compresses them at mid to high stimulus levels. Cochlear amplification is  
31 observed only in healthy cochleae and it vanishes once cochlear function is compromised.  
32 The cellular basis of cochlear amplification is the sensory motile outer hair cells (OHCs)  
33 (Figure 1A) (Brownell et al., 1985; Liberman et al., 2002; Ashmore, 2008; Dallos, 2008;  
34 Mellado Lagarde et al., 2008). OHCs are mechanical effectors that change their length in  
35 response to changes in their transmembrane voltage (Ashmore 1987; Santos-Sacchi and  
36 Dilger, 1988). Length changes of the stiff OHCs can generate forces sufficient for minimising  
37 the damping of mechanical responses of cochlear structures surrounded by fluids (Gold,  
38 1948; Lukashkin et al., 2007b; Dong and Olson, 2013). Three rows of OHCs are imbedded in  
39 the sensory organ of Corti (OoC) sitting on top of the extracellular basilar membrane (BM)  
40 that extends the length of the entire spiral cochlea (Figure 1A). The mechano-electrical  
41 transducer (MET) channels of the OHCs are located close to the tips of the OHC sensory  
42 organelles, stereocilia, which form hair bundles that are imbedded in the extracellular  
43 tectorial membrane (TM) that covers the OoC, with the TM inner edge being elastically  
44 attached to the bony spiral limbus (Richardson et al., 2008). The OHC hair bundles provide a  
45 stiff mechanical link between the TM and the reticular lamina (RL) at the apical surface of  
46 the OoC. During radial shear between the TM and RL, the hair bundles are rotated about their  
47 attachment to the apical surface of the OHCs (Figure 1B), which leads to modulation of the  
48 MET current and generation of intra- and extracellular receptor potentials (RP) (Russell,  
49 2008). RP generation results in changes in the OHC transmembrane voltage and associated  
50 OHC length changes. Hair bundles of the other type of sensory cell in the OoC, the inner hair  
51 cells (IHCs), which have rich afferent innervation and provide information to the brain, are  
52 free-standing and excited by flow of fluid entrained in the sub-tectorial space (STS, Figure  
53 1A) during radial shear between the TM and RL (Sellick and Russell, 1980; Patuzzi and  
54 Yates, 1997; Nowotny and Gummer, 2006). The radial shear occurs during transversal BM  
55 vibrations (Figure 1B). The BM mechanical properties are graded and BM vibrations, which  
56 propagate as travelling waves (TWs) along the BM from the high-frequency base to low-  
57 frequency apex, peak at a frequency-specific, characteristic frequency (CF) place, where most  
58 of the TW energy is dissipated (Figure 1B) (von Békésy, 1960). Thus, the BM effectively  
59 functions as a frequency analyser separating constitutive frequency components of sounds in  
60 space and time. The TWs quickly die out at a cochlear place where the BM resonance  
61 frequency  $\omega_{bm}$  (Figure 1B) is equal to the stimulus frequency (von Békésy, 1960). The BM  
62 is not stiff enough to support the TW beyond this point.

63 The intricate structure of the cochlea (Figure 1A) appears to have evolved to enable fine-  
64 tuning of the OHCs responses and ensure optimal cochlear amplification to augment the  
65 stimulation of IHCs and, consequently, to provide adequate auditory information to the brain  
66 (Russell, 2008). Therefore, knowledge of the STS micromechanics is critical for  
67 understanding the workings of the cochlea. Current experimental methods for recording  
68 direct mechanical responses in the narrow cleft between the TM and RL do not have  
69 sufficient resolution *in vivo* to provide unambiguous data on the mechanics in this confined  
70 geometry over a wide range of stimulus frequencies and levels (Nowotny and Gummer,  
71 2006). Fortunately, because the OHC hair bundles are embedded into the TM, and because  
72 the OHC RPs are generated due to radial shear between the TM and RL (Russell, 2008),  
73 measurement of the OHC RP can provide an insight into micromechanics of the STS. The  
74 current study demonstrates that the seemingly complex behaviour of the OHC RP recorded  
75 from a single OHC in the two-dimensional space of stimulus levels and frequencies at the  
76 cochlear base (Figure 2) (Kössl and Russell, 1992; Russell and Kössl, 1992; Levic et al.,  
77 2022) arises from a local resonance in every frequency place. A minimal mechanical  
78 arrangement, which still can explain the OHC RP behaviour, consists of a resonating BM and  
79 TM strongly coupled together via OHC stereocilia, with the TM resonance frequency located  
80 below the BM resonance frequency in every cochlear place (Allen, 1980; Zwislocki, 1980;  
81 Allen and Neely, 1992).



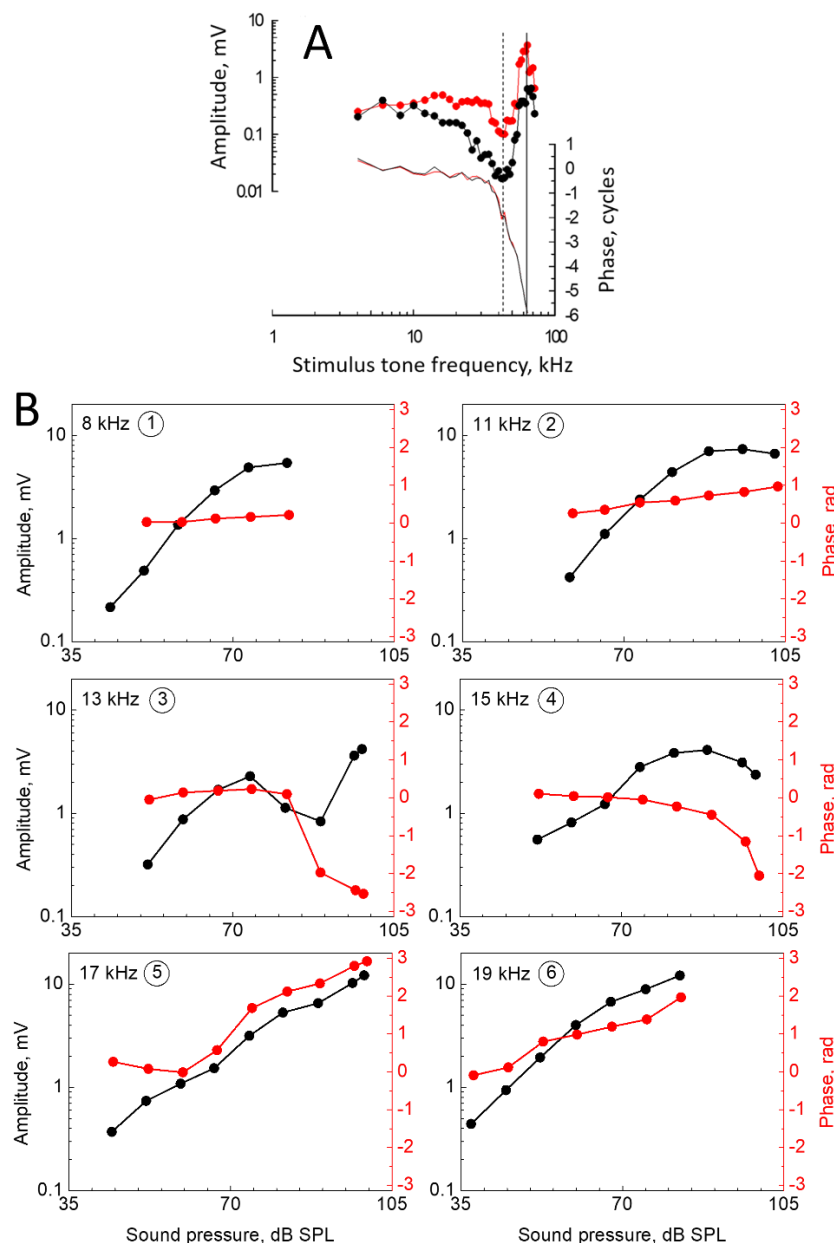
82  
83 **Figure 1. Schematics of the mammalian cochlea and the propagation of travelling wave**  
84 **along its length**

85 BM, basilar membrane; TM, tectorial membrane; STS, subtectorial space; OHCs and IHCs  
86 are inner and outer hair cells, respectively; RL, reticular lamina; CF and  $\omega_{bm}$  are the  
87 characteristic frequency place and BM resonance place for a given stimulus frequency,  
88 respectively.

89 (A) Schematic of the cochlear cross-section showing the relationship between the BM, the  
90 sensory OoC, sitting on top of the BM, and the TM overlaying the OoC. The TM is attached

91 to the OHC sensory stereocilia and the spiral limbus but the IHC stereocilia are free standing  
92 and deflected by flow of fluid in the STS.

93 (B) TW propagation along the BM generates transversal movement of the BM (black wave).  
94 The TW slows down and its amplitude builds up, reaching a maximum at the CF, when the  
95 TW comes to the point where the BM resonance frequency,  $\omega_{bm}$ , is the same as frequency of  
96 the sound stimulation. The TW does not propagate beyond the  $\omega_{bm}$  place towards the  
97 cochlear apex because the stiffness of the BM is insufficient to support the TW. The  
98 transversal BM movement is transformed into radial shearing motion between the TM and  
99 RL (red wave), which, in turn, deflects stereocilia of sensory OHCs and IHCs. Modified from  
100 (Jones et al., 2013).



101

102 **Figure 2. Outer hair cell receptor potentials recorded in mouse and guinea pig cochleae**

103 (A) The 70 dB SPL isolevel frequency functions of the intracellular (black) and extracellular  
104 (red) receptor potentials recorded from the mouse cochlea. The data were compensated for

105 recording electrode low-pass filter characteristics. Vertical solid lines indicate CF; dotted line  
106 indicate the frequency of amplitude minimum observed about half an octave below the CF.  
107 Phase was corrected for middle ear transfer characteristics (Dong et al., 2013), sound system,  
108 and recording electrode. Modified from (Levic et al., 2022).

109 (B) Amplitude (black) and phase (red) receptor potential level functions recorded  
110 extracellularly from a guinea pig OHC (CF is 18 kHz) at the frequencies indicated within  
111 each panel. The amplitude was compensated for the single-pole, low-pass filtering of the  
112 recording electrode (corner frequency is 3.5 kHz). Numbers in circles in each panel identify  
113 frequencies with relative positions as indicated in Figure 4C. Modified from (Kössl and  
114 Russell, 1992).

## 115 RESULTS

### 116 Linear Passive System

117 A minimal micromechanical model which still qualitatively reproduces the behaviour of the  
118 OHC RP is an Allen-Zwislocki-Neely type model (Allen, 1980; Zwislocki, 1980; Allen and  
119 Neely, 1992) in which the TM is able to resonate radially due to its elastic attachments to the  
120 OHC stereocilia and the spiral limbus (Figure 1A). For this model, each cross-section of the  
121 OoC with attached TM could be represented by a schematic shown in Figure 3A (see Allen  
122 (1980) for the equivalent of this schematic and a mechanical system with the TM-RL shear).

123 The system in Figure 3A is described by the following equations

$$124 \quad M_{\text{bm}} \frac{d^2 X_{\text{bm}}}{dt^2} + \eta_{\text{bm}} \frac{dX_{\text{bm}}}{dt} + K_{\text{bm}} X_{\text{bm}} - K_c \Delta X = P(t); \quad (1)$$

$$125 \quad M_{\text{tm}} \frac{d^2 X_{\text{tm}}}{dt^2} + \eta_{\text{tm}} \frac{dX_{\text{tm}}}{dt} + K_{\text{tm}} X_{\text{tm}} + K_c \Delta X = 0, \quad (2)$$

126 where a harmonic external force  $P(t) = P_a \sin(\omega t)$  of frequency  $\omega$  and amplitude  $P_a$  is  
127 applied to the BM, and  $M_{\text{bm}}$  denotes the entire cochlear partition mass.  $\Delta X = X_{\text{tm}} - X_{\text{bm}}$  is  
128 the relative displacement between the OoC and TM which excites the OHCs and, as a first  
129 approximation for small  $\Delta X$ , could be used to make estimates of the OHC RP behaviour.

130 Substituting the characteristic parameters,

$$131 \quad \omega_{\text{bm}} = \sqrt{\frac{K_{\text{bm}}}{M_{\text{bm}}}}, \quad \omega_{\text{tm}} = \sqrt{\frac{K_{\text{tm}}}{M_{\text{tm}}}}, \quad \omega_c = \sqrt{\frac{K_c}{M_{\text{tm}}}}, \quad \zeta_{\text{bm}} = \sqrt{\frac{\eta_{\text{bm}}}{M_{\text{bm}}}},$$
$$132 \quad \zeta_{\text{tm}} = \sqrt{\frac{\eta_{\text{tm}}}{M_{\text{tm}}}}, \quad (3)$$

133 the system of equations (1, 2) may be rewritten as

134 
$$\frac{d^2 X_{\text{bm}}}{dt^2} + \zeta_{\text{bm}} \frac{dX_{\text{bm}}}{dt} + \omega_{\text{bm}}^2 X_{\text{bm}} - \omega_c^2 \Delta X \left( \frac{M_{\text{tm}}}{M_{\text{bm}}} \right) = \frac{P(t)}{M_{\text{bm}}}; \quad (4)$$

135 
$$\frac{d^2 X_{\text{tm}}}{dt^2} + \zeta_{\text{tm}} \frac{dX_{\text{tm}}}{dt} + \omega_{\text{tm}}^2 X_{\text{tm}} + \omega_c^2 \Delta X = 0. \quad (5)$$

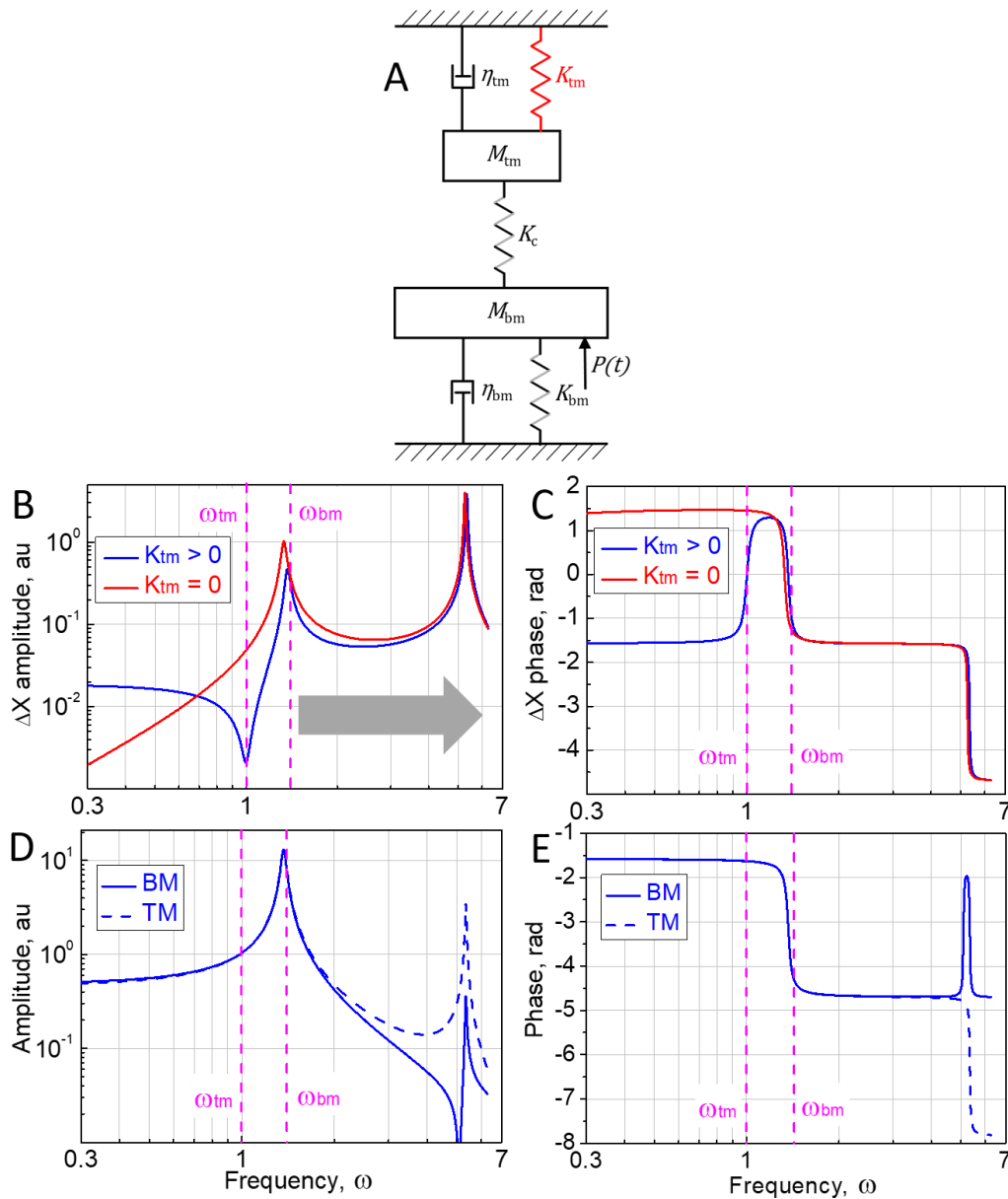
136 We refer to  $\omega_{\text{bm}}$  and  $\omega_{\text{tm}}$  as the BM and TM resonance frequency, respectively, for the rest  
137 of the paper. For the chosen relationships between the model parameters, which are in line  
138 with those measured experimentally and used in other modelling studies (e.g. see Meaud and  
139 Grosh, 2014; Nankali et al., 2022),  $\Delta X$ , i.e. relative displacement between  $M_{\text{tm}}$  and  $M_{\text{bm}}$ ,  
140 demonstrates a local minimum at frequency  $\omega_{\text{tm}}$  (Figure 3B). The minimum should result in  
141 a decrease in OHC excitation and, in turn, in a local minimum in the OHC RP observed about  
142 half an octave below the CF (Figure 2A). The minimum always occurs at the TM resonance  
143 frequency  $\omega_{\text{tm}}$ , where the TM has a minimal impedance determined only by the viscous  
144 damping and, hence, minimal load on the OHC stereocilia, and its frequency position does  
145 not depend on the properties of the driven oscillator, i.e. the BM (see question 1 and an  
146 answer to it in the Supplemental Information for detailed derivation). The  $\Delta X$  minimum  
147 becomes more pronounced with decreasing TM damping so that  $\Delta X \rightarrow 0$  at frequency  $\omega_{\text{tm}}$   
148 when  $\zeta_{\text{tm}} \rightarrow 0$ .

149 For the chosen model parameters, the minimum/antiresonance is not observed in the BM and  
150 TM responses for frequencies below  $\omega_{\text{bm}}$  (Figure 3D).  $\Delta X$  is stiffness dominated below the  
151 minimum (Figure 3C).  $\Delta X$  becomes mass dominated at the amplitude minimum and a  
152 corresponding phase transition of  $\pi$  is observed (also see Equation S24 in the Supplemental  
153 Information). The corresponding phase transition is also observed near the minimum of the  
154 experimentally measured OHC RP (Figure 2A).  $\Delta X$  becomes stiffness dominated close to the  
155 first normal mode of vibrations near  $\omega_{\text{bm}}$  where local maximums of the BM and TM  
156 displacements (Figure 3D) and  $\Delta X$  (Figure 3B) are observed, and where the  $\Delta X$  phase angle  
157 returns to  $-\pi/2$  (Figure 3C, Equation S24 in the Supplemental Information). It should be  
158 noted that the system of equations (4, 5) does not include the TW observed in the cochlea.  
159 Therefore, a large phase roll-off due to TW propagation (Figure 2A) is not observed in the  
160 model responses. The phase demonstrates only a transition up to 180 degrees (Figure 3C) for  
161 the mass-dominated responses between  $\omega_{\text{tm}}$  and  $\omega_{\text{bm}}$ , which is similar to that seen in figure 3  
162 of Allen (1980). Also, because the model does not include TW, a sharp decline in the  
163 amplitude of the OHC RP above the CF (Figure 2A) is not observed in the model presented



164 in Figure 3A. In the real cochlea, the TWs quickly die out at a cochlear place where the BM  
165 resonance frequency  $\omega_{\text{bm}}$  is equal to the stimulus frequency (Figure 1B) and responses for  
166 frequencies above  $\omega_{\text{bm}}$  cannot be recorded (von Békésy, 1960). This frequency region is  
167 indicated by horizontal grey arrows in Figures 3B, 4B. Hence, the second normal mode,  
168 which is shifted to frequencies well above  $\omega_{\text{bm}}$  due to strong elastic coupling  $K_c$  between  
169  $M_{\text{tm}}$  and  $M_{\text{bm}}$ , is not observed *in vivo* (see question 2 and an answer to it in the Supplemental  
170 Information for detailed derivation).

171 The role of the TM limbal attachment  $K_{\text{tm}}$  for OHC excitation was investigated  
172 experimentally by Lukashkin et al. (2012) and modelled by Meaud and Grosh (2014). Similar  
173 sensitivity and sharpness of BM tuning were found in wild-type mice and mutant mice with  
174 the TM detached from the spiral limbus. It was suggested that the elasticity of the TM  
175 attachment to the spiral limbus is not a crucial factor for exciting the OHCs near their CF, and  
176 that the OHCs must be excited by the inertial load provided by the TM mass at CF to  
177 effectively boost the mechanical responses of the cochlea. Indeed, while the  $\Delta X$  minimum is  
178 not observed in model responses when  $K_{\text{tm}} = 0$  (Figure 3B, see question 3 and an answer to  
179 it in the Supplemental Information for detailed derivation),  $\Delta X$  response is mass dominated  
180 and the phase angle is similar in both cases,  $K_{\text{tm}} > 0$  and  $K_{\text{tm}} = 0$ , between  $\omega_{\text{tm}}$  and  $\omega_{\text{bm}}$   
181 (Figure 3C). In the real cochlea, this frequency range corresponds to stimulus frequencies  
182 below the CF where the non-linear cochlear amplification gradually builds up (Nilsen and  
183 Russell, 1999; Robles and Ruggero, 2001; Zheng et al., 2007; Dong and Olson, 2013; Lee et  
184 al., 2016) and, thus, the  $\Delta X$  phase angle and OHC excitation timing are optimal for cochlear  
185 amplification to occur. Therefore, similar  $\Delta X$  excitation phase/timing for conditions  $K_{\text{tm}} = 0$   
186 and  $K_{\text{tm}} > 0$  (Figure 3C), with  $K_{\text{tm}} = 0$  simulating mutants with the TM detached from the  
187 spiral limbus, supports the conclusion that the OHCs must be excited by the inertial load  
188 provided by the TM mass at CF to effectively boost the mechanical responses of the cochlea  
189 (Gummer et al., 1996; Lukashkin et al., 2010; Lukashkin et al., 2012; Meaud and Grosh,  
190 2014; Nankali et al., 2022).



191

192 **Figure 3. A schematic of cochlear cross-section with resonating tectorial membrane and**  
 193 **its responses to harmonic excitation  $P(t)$ .**

194 (A) A schematic showing the relationship between the mechanical elements in a cochlear  
 195 cross-section.  $M_{tm}$  is the TM mass and  $M_{bm}$  denotes the entire cochlear partition mass;  $K_{tm}$   
 196 and  $K_{bm}$  are stiffnesses of the TM limbal attachment and BM stiffness respectively;  $K_c$  is  
 197 elastic coupling between the TM and BM due to OHC stereocilia;  $\eta_{tm}$  and  $\eta_{bm}$  denote  
 198 viscous damping of the TM and BM respectively. See the main text for more details.

199 (B) Amplitude and (C) phase responses for the relative displacement,  $\Delta X$ , between the BM  
 200 and TM.

201 (D) Amplitude and (E) phase responses of the BM and TM.

202 Vertical dashed magenta lines indicate  $\omega_{tm}$  and  $\omega_{bm}$  as defined by equation (3). Responses  
 203 for the condition  $K_{tm} = 0$  in panels (D) and (E) are not shown because at the given resolution  
 204 they are superimposed with responses when  $K_{tm} > 0$ . Horizontal grey arrow in panel (B)



205 indicates the frequency range where *in vivo* responses are not recorded because the BM TW  
206 does not propagate beyond the  $\omega_{\text{bm}}$  place towards the cochlear apex (Figure 1B).

207 The following parameters were used to calculate the responses:  $M_{\text{tm}} = 1$ ,  $M_{\text{bm}} = 10$ ,  $\omega_{\text{tm}} = 1$ ,  
208  $\omega_{\text{bm}} = 1.4$ ,  $\omega_{\text{c}} = 5$ ,  $\zeta_{\text{tm}} = \zeta_{\text{bm}} = 0.05$ ,  $P_{\text{a}} = 10$ .

209

## 210 **Active Nonlinear System**

211 The cochlear amplifier is introduced as a nonlinear damping ( $\eta_{\text{n}}$  in Figure 4A) which  
212 includes a level-independent positive damping and a level-dependent negative damping  
213 component (Gold, 1948; Elliott et al., 2015) demonstrated experimentally (Lukashkin et al.,  
214 2007b) so that

$$215 \quad \zeta_{\text{bm}} = \zeta_{\text{bm}}^+ + \zeta_{\text{bm}}^- \quad (6)$$

216 and

$$217 \quad \zeta_{\text{tm}} = \zeta_{\text{tm}}^+ + \zeta_{\text{tm}}^-, \quad (7)$$

218 where  $\zeta^+$  and  $\zeta^-$  are corresponding positive and negative components for the BM and TM  
219 damping. The cochlear amplifier emerges from the OHC length changes which are controlled  
220 by changes in the voltage across the OHC basolateral membrane (Ashmore 1987; Santos-  
221 Sacchi and Dilger, 1988). The transmembrane voltage changes, in turn, are generated by the  
222 MET current which is modulated when the OHC hair bundles are rotated about their  
223 attachment to the OHC apical cuticular plate due to the relative displacement between the  
224 OoC and TM (Russell, 2008). In this case, the OHC MET current is a function of  $\Delta X$ . As a  
225 first approximation this function could be describes by a sigmoidal nonlinearity/Boltzmann  
226 function

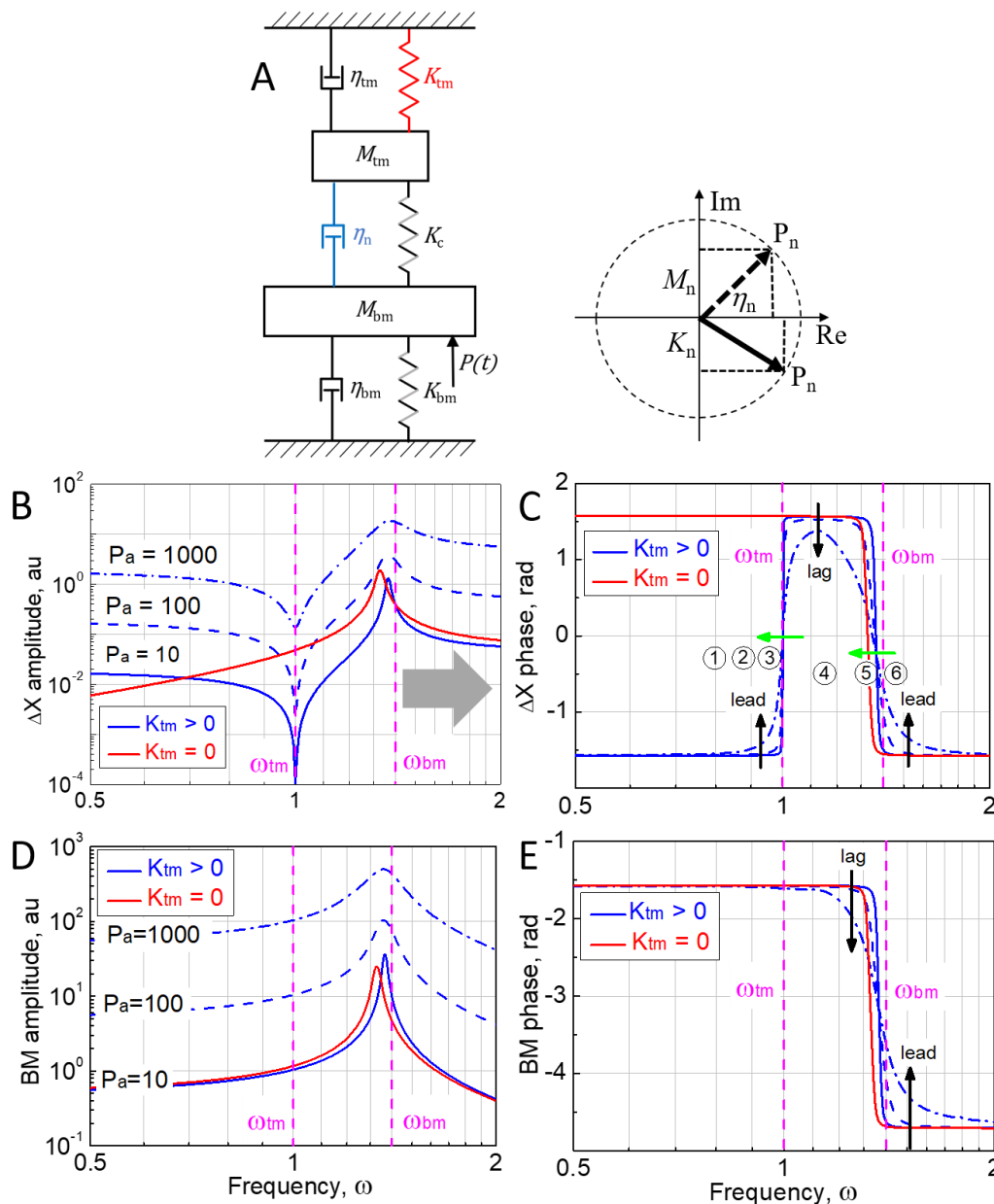
$$227 \quad N(\Delta X) = \frac{1}{1 + e^{a_1(x_1 - \Delta X)}}, \quad (8)$$

228 where  $N(\Delta X)$  is the MET nonlinearity,  $a_1$  sets the slope of the function, and  $x_1$  is the position  
229 of maximum slope. Therefore, the negative damping for both the BM and TM could be  
230 defined as

$$231 \quad \zeta^- = -\gamma \frac{dN(\Delta X)}{d\Delta X}, \quad (9)$$

232 where  $\gamma$  is the transfer ratio relating the change in the OHC receptor potential to resultant  
233 negative damping developed by the OHCs. To find numerical solutions of equations (4-9) in

234 the time domain,  $\gamma$  was taken to be  $\gamma = 4(\zeta^+ - 0.0001)$  for both the BM and TM to ensure  
 235 that the total damping is always positive.



236

237 **Figure 4. Response of the active model with nonlinear damping to harmonic excitation**

238 (A) A schematic showing the relationship between the mechanical elements in a cochlear  
 239 cross-section.  $M_{tm}$  is the TM mass and  $M_{bm}$  denotes the entire cochlear partition mass;  $K_{tm}$   
 240 and  $K_{bm}$  are stiffnesses of the TM limbal attachment and BM stiffness respectively;  $K_c$  is  
 241 elastic coupling between the TM and BM due to the OHC stereocilia;  $\eta_{tm}$  and  $\eta_{bm}$  denote  
 242 viscous damping of the TM and BM respectively;  $\eta_n$  is a nonlinear damping due to action of  
 243 the OHCs. Only  $P_a = 10$  response for  $K_{tm} = 0$  is shown. Insert in (A) illustrates a situation  
 244 when the nonlinear, level-dependent OHC force  $P_n$  is out of phase with the damping force  $\eta_n$ .  
 245 In this case a nonlinear, level-dependent stiffness  $K_n$  (if  $P_n$  lags  $\eta_n$ ) or mass  $M_n$  (if  $P_n$  leads  
 246  $\eta_n$ ) associated with the OHC action is observed. See the main text for more details.

247 (B) Amplitude and (C) phase responses of the relative displacement,  $\Delta X$ , between the BM  
248 and TM for different amplitudes  $P_a$  of the harmonic force  $P(t)$ .  $P_a$  is indicated for each  
249 curve. Responses for the condition  $K_{tm} = 0$  are shown only for  $P_a = 1$ . Vertical black arrows  
250 in (C) show changes in the  $\Delta X$  phase with increasing  $P_a$ , i.e. the stimulus level. Numbers in  
251 circles in (C) identify presumed frequency positions of the corresponding experimental  
252 responses (Figure 2B) relative to  $\omega_{tm}$  and  $\omega_{bm}$ . Green horizontal arrows in (C) shows a  
253 presumed shift of  $\omega_{tm}$  and  $\omega_{bm}$  to lower frequencies due to changes in  $K_n$ . See inset in (A).

254 (D) Amplitude and (E) phase angle of BM responses for different amplitudes  $P_a$  of the  
255 harmonic force  $P(t)$ .  $P_a$  is indicated for each curve. Responses for the condition  $K_{tm} = 0$  are  
256 shown only for  $P_a = 1$ . Vertical black arrows in (E) show changes in the BM phase responses  
257 with increasing  $P_a$ , i.e. the stimulus level.

258 Vertical dashed magenta lines indicate  $\omega_{tm}$  and  $\omega_{bm}$  as defined by equation (3). A horizontal  
259 grey arrow in (B) indicates the frequency range where *in vivo* responses are not recorded  
260 because the BM TW does not propagate beyond the  $\omega_{bm}$  place towards the cochlear apex  
261 (Figure 1B).

262 The following parameters were used to calculate the responses:  $M_{tm} = 1$ ,  $M_{bm} = 10$ ,  $\omega_{tm} = 1$ ,  
263  $\omega_{bm} = 1.4$ ,  $\omega_c = 5$ ,  $\zeta_{tm}^+ = \zeta_{bm}^+ = 0.15$ ,  $x_1 = 0$ ,  $a_1 = 1$ .

264 Responses of the active model to harmonic excitation  $P(t) = P_a \sin(\omega t)$  for different  
265 amplitude  $P_a$  are shown in Figure 4. Only responses below and around  $\omega_{bm}$  are shown  
266 because the BM TW does not propagate beyond the  $\omega_{bm}$  place towards the cochlear apex  
267 (horizontal grey arrow in Figure 4B). Therefore, the second normal mode (see question 2 and  
268 an answer to it in the Supplemental Information for detailed derivation), which is shifted to  
269 frequencies well above  $\omega_{bm}$  due to strong elastic coupling  $K_c$  between  $M_{tm}$  and  $M_{bm}$ , is not  
270 shown in Figure 4 (compare Figure 3B and 4B). An active model, which includes only local  
271 BM/TM resonances, provides an impressively good qualitative description of the  
272 experimental data for the OHC receptor potentials (Figure 2) despite the absence of global  
273 phenomena like the BM TW or elastic/hydronechanical coupling along the cochlea. The RP  
274 minimum seen about half an octave below the CF in isolevel RP responses recorded for a  
275 stimulus level of 70 dB SPL to ensure the recording of responses over a wide frequency range  
276 (Figure 2A) is less sharp than the model minima recorded for smaller  $P_a$  (Figure 4B).

277 However, the model minimum becomes less sharp for  $P_a = 100$  when the nonlinear model  
278 amplification becomes saturated (see question 1 and an answer to it in the Supplemental  
279 Information for the assessment of the depth of the local minimum at  $\omega_{tm}$  for varying TM  
280 damping).

281 The active local resonance model provides an explanation of the seemingly complex level-  
282 dependent OHC RP amplitude and phase behaviour observed in experiments (Figure 2B,  
283 Kössl and Russell, 1992) assuming that  $\omega_{tm}$  was situated around 13 kHz, i.e. about half an

284 octave below the CF of 18 kHz. Indeed, in this case, the phase angle does not depend on the  
285 stimulus level when the stimulus frequency is 8 kHz and well below  $\omega_{tm}$  (panel 1 in Figure  
286 2B and frequency point 1 in Figure 4C). There is a small phase lead with level (leftmost black  
287 vertical arrow in Figure 4C) for the stimulus frequency of 11 kHz which is situated closer to  
288 but still below  $\omega_{tm}$  (panel 2 in Figure 2B and frequency point 2 in Figure 4C) but the phase  
289 lead is larger (rightmost black vertical arrow in Figure 4C) for the stimulus frequency of 19  
290 kHz above the  $CF/\omega_{bm}$  (panel 6 in Figure 2B and frequency point 6 in Figure 4C). The phase  
291 behaviour reverses and the phase lags with level (middle vertical black arrow in Figure 4C)  
292 for the stimulus frequency of 15 kHz situated between the  $\omega_{tm}$  and  $CF/\omega_{bm}$  (panel 4 in  
293 Figure 2B and frequency point 4 in Figure 4C). A reversal of phase behaviour is observed  
294 with increasing the stimulus level for 13 kHz (small lead to lag) situated just below assumed  
295  $\omega_{tm}$ , and 17 kHz (small lag to lead) situated just below the  $CF/\omega_{bm}$  in panels 3 and 5 in  
296 Figure 2B, respectively. At the same time, this reversal of the phase behaviour for both  
297 stimulus frequencies are associated with phase transitions which are close to  $180^\circ$ . The near-  
298  $180^\circ$  phase transition at 13 kHz is steeper than the transition observed for 17 kHz which is  
299 expected because of a steeper phase slope near  $\omega_{tm}$  (Figure 4C). An amplitude notch in the  
300 OHC RP level function is, however, observed only for 13 kHz stimulus (panel 3 in Figure  
301 2B) and it is absent at 17 kHz. In terms of the active model (Figure 4A), the observed  
302 nonmonotonic amplitude and phase behaviour is explained by presumed shifts of  $\omega_{tm}$  and  
303  $\omega_{bm}$  to lower frequencies with increasing the stimulus level (green horizontal arrows in  
304 Figure 4C). Indeed, the low-frequency shift of maximum responses near the CF is well-  
305 documented (e.g. Robles and Ruggero, 2001) and a low-frequency shift of the TM resonance  
306 was suggested from observation of different indices of cochlear responses associated with  
307  $\omega_{tm}$  (Lukashkin et al., 2007a). Therefore, if 13 kHz (panel 3 in Figure 2B) is situated just  
308 below  $\omega_{tm}$  (frequency point 3 in Figure 4C) for low stimulus levels but it appears above  $\omega_{tm}$   
309 for high stimulus levels then the  $\Delta X$  amplitude (i.e. the OHC RP amplitude) would fall into  
310 the amplitude minimum at  $\omega_{tm}$  and eventually recover from it with increasing stimulus level.  
311 In this case not only a reversal of the phase behaviour and a steep phase transition but also an  
312 amplitude notch in the OHC RP level functions should be observed. The amplitude notch in  
313 the OHC RP level functions should not be observed during reversal of the phase behaviour  
314 and corresponding phase transition for responses to the 17 kHz stimulus (panel 5 in Figure  
315 2B) if this stimulus frequency is situated just below the  $CF/\omega_{bm}$  (frequency point 5 in Figure  
316 4C) at low stimulus levels but appears above  $CF/\omega_{bm}$  for high stimulus levels due to a low-

317 frequency shift of  $\omega_{\text{bm}}$  because there is no a local amplitude minimum associated with the  
318  $\Delta X$  frequency responses near  $\omega_{\text{bm}}$  (Figure 4B).

319 A local resonance active cochlear model which includes only nonlinear negative damping  
320 (Figure 4A) does not reproduce the suggested low-frequency shift of  $\omega_{\text{tm}}$  and  $\omega_{\text{bm}}$  at high  
321 stimulus levels (green arrows in Figure 4C). The low-frequency shift of the TM and BM  
322 resonances would occur quite naturally if the nonlinear, level-dependent OHC force  $P_n$  is out  
323 of phase with the damping force  $\eta_n$  (Figure 4A, insert). In this case nonlinear, level-  
324 dependent stiffness  $K_n$  or inertial  $M_n$  projections associated with the OHC action that  
325 correspond to the imaginary parts of the impedance are observed for mechanical components  
326 of the system (e.g. see Kolston et al., 1990). Changes in the projections  $K_n$  or  $M_n$  due to  
327 changes in the phase angle of  $P_n$  or variation of its amplitude with increasing stimulus level,  
328 would lead to changes in the imaginary part of the components' impedances, thus changing  
329 frequencies  $\omega_{\text{tm}}$  and  $\omega_{\text{bm}}$ . Changes in the effective masses or stiffnesses of the system  
330 components, and, hence, shifts of  $\omega_{\text{tm}}$  and  $\omega_{\text{bm}}$ , might also be explained by a spread of  
331 excitation along the cochlea due to stiffening of the TM or/and entraining larger masses of  
332 cochlear fluids with increasing stimulus levels (see Discussion for more details). Also, the  
333 shift may be a product of OHC efferent activation (Guinan, 2018) but it should still be  
334 associated with changes in the imaginary part of the impedances, i.e. the effective  
335 stiffness/mass changes, even in this case.

336 It is worth noting that the minimal local resonance active cochlear model with negative  
337 damping (Figure 4A) also qualitatively reproduces experimental level dependent behaviour of  
338 the BM phase. It has been known for a long time that the phase angle of BM responses  
339 lags/leads with levels for frequencies below/above the CF/ $\omega_{\text{bm}}$ , respectively (Robles and  
340 Ruggero, 2001). Exactly this type of phase behaviour is observed for the local resonance  
341 active cochlear model with negative damping (black vertical arrows in Figure 4E).

## 342 **DISCUSSION**

343 The objective of this study is to find a minimal mechanical system which still can  
344 qualitatively explain the behaviour of the OHC RP *in vivo*. It is demonstrated that a local  
345 resonance of a strongly coupled TM and BM as suggested by (Allen, 1980; Zwislocki, 1980;  
346 Allen and Neely, 1992) and experimentally recorded by (Gummer et al., 1996; Lee et al.,  
347 2016) is sufficient to explain the phenomenology of the seemingly complex changes in the  
348 OHC RP amplitude and phase recorded close to OHCs *in vivo* for wide range of frequencies

349 and levels of acoustic stimulation (Kössl and Russell, 1992; Russell and Kössl, 1992; Levic et  
350 al., 2022). Moreover, the model reveals that the nonmonotonic amplitude behaviour (i.e. local  
351 minima/maxima) of experimentally recorded cochlear responses generated due to radial shear  
352 between the TM and OoC at frequencies below the CF, is observed at the TM resonance  
353 frequency and the frequency position of these minima/maxima does not depend either on the  
354 properties of the pressure driven part of the system (i.e. the BM with the OoC sitting on its  
355 top) or the degree of coupling between the TM and OoC. The model confirms that the shear  
356 between the TM and OoC is mass dominated in the frequency region associated with  
357 nonlinear cochlear amplification and a corresponding phase transition is observed for this  
358 frequency region between  $\omega_{tm}$  and  $\omega_{bm}$  (Figure 3C, 4C), where the timing of OHC  
359 stimulation is optimal for cochlear amplification. An obvious conclusion is that the timing is  
360 suboptimal for cochlear amplification and sharpened frequency tuning of mechanical  
361 responses of the cochlear partition outside of the range of between  $\omega_{tm}$  and  $\omega_{bm}$ , despite the  
362 finding that OHCs are stimulated over a wider frequency span than  $[\omega_{tm}, \omega_{bm}]$  as judged by  
363 the reticular lamina active responses (Ren et al., 2016; He et al., 2022).

364 There is no need for global phenomena, e.g. TW or elastic/hydronechanical coupling along  
365 the cochlea, to explain the experimental data on the OHC RP (Figure 2B). In fact, addition of  
366 global phenomena to the local resonance model can smear sharp antiresonance/resonance in  
367 the system as discussed below. This, however, does not destroy the effect of local resonance.  
368 Its signature could still be seen in various types of cochlear responses (Lukashkin et al.,  
369 2010). Addition of the TW to the local resonance model, which includes independent TM  
370 resonance at frequencies below the BM resonance, provides a good fit to the neural data  
371 (Allen, 1980; Allen and Neely, 1992; Allen and Fahey, 1993). A notch of insensitivity seen in  
372 the neural data at a frequency about half an octave below the CF (Lieberman, 1978; Allen,  
373 1980; Liberman and Dodds, 1984; Taberner and Liberman, 2005; Temchin et al., 2008)  
374 resembles a similar notch in the OHC RP (Figure 2A) and in neural suppression tuning  
375 curves (Lukashkin et al., 2007a). The notch disappears in mutants with the TM detached from  
376 the spiral limbus (Lukashkin et al., 2012), confirming its origin (compare with the red curve  
377 for  $K_{tm} = 0$  in Figure 3B). It was also suggested that the amplitude and phase dependence of  
378 the distortion product otoacoustic emission (DPOAE) on the ratio of the two primary  
379 stimulus tones ( $f_1$  and  $f_2$ ,  $f_2 > f_1$ ) used to evoke the DPOAEs, reflected band-pass filtering of  
380 the DPOAEs by the mechanical filter associated with the local TM resonance. Amplitude  
381 maxima for DPOAEs of different order (i.e.  $2f_1-f_2$ ,  $3f_1-2f_2$ ,  $4f_1-3f_2$ ) are observed at the



382 same frequency which is independent of the  $f_2/f_1$  ratio (Brown et al., 1992; Allen and Fahey,  
383 1993) and the phase of DPOAE of different order changes from lag to lead at the same  
384 frequency when the levels of primaries are increased (Lukashkin and Russell, 2003;  
385 Lukashkin et al., 2007a).

386 The local minimum in sensitivity of the OHC RP at frequencies about half an octave below  
387 the CF (Figure 2A) and corresponding amplitude notches associated with steep phase  
388 transitions (panel 3 in Figure 2B) are more sharply tuned in intracellular OHC RP recordings  
389 or extracellular recordings in the closest vicinity of OHCs (Kössl and Russell, 1992; Russell  
390 and Kössl, 1992; Levic et al., 2022) than when measured from the OoC fluid space  
391 (Fridberger et al., 2004) and close to the BM as a cochlear microphonic (Dong and Olson,  
392 2013), when it becomes increasingly broader and less distinct with increasing stimulation  
393 levels. We attribute this difference to two effects, namely, to the level-dependent increase in  
394 the damping as illustrated in Figure 4B and to the level-dependent increase in the numbers of  
395 generators (OHCs) contributing to the extracellular signal (Patuzzi et al., 1989) that smears  
396 the phase data, rather than to the single effect of fluid damping, as has been recently  
397 suggested and modelled based on cochlear microphonic measurements (Nankali et al., 2020).  
398 The same level-dependent summation of electrical signals from a gradually increasing  
399 number of generators leading to a partial phase cancellation might explain lack of an obvious  
400 low-frequency shift of the minimum in the gross OHC electrical responses (Fridberger et al.,  
401 2004; Dong and Olson, 2013), the shift was suggested to explain the level dependent  
402 behaviour of different indices of cochlear responses associated with the TM resonance  
403 (Lukashkin et al., 2007a) and the OHC RP data (green arrows in Figure 4C).

404 It was suggested that a low-frequency shift of  $\omega_{tm}$  and  $\omega_{bm}$  (green arrows in Figure 4C), and  
405 corresponding shift of the low-frequency minimum of OHC RP and its local maximum near  
406 the CF with increasing the sound intensity might occur due to the desynchronization of the  
407 nonlinear, level-dependent OHC force  $P_n$  contributing to the imaginary parts of the  
408 mechanical impedances of the components (insert in Figure 4A). There are two additional  
409 mechanisms which might contribute to the low-frequency shift. Vibration of an individual  
410 element within the cochlea generates a near field pressure, which increases the element's  
411 effective mass (Ni and Elliott, 2015). Increase in the TW wavelength with sound intensity  
412 might increase the fluid-loaded mass on the individual elements (Steele and Taber, 1979;  
413 Elliott et al., 2022; Nankali et al., 2022), thus, lowering their resonance frequencies (Equation  
414 3). Also, the TM material properties are frequency and, thus, velocity dependent and the TM



415 shear storage modulus increases with stimulation frequency/velocity, especially at the  
416 cochlear base (Jones et al., 2013). Increase in the TM velocity response with stimulus level  
417 and resultant TM stiffening might lead to larger regions of the TM and OoC being involved  
418 in local OHC excitation due to increased elastic coupling along the TM (Dewey et al., 2018).  
419 This would manifest in larger  $M_{tm}$  and  $M_{bm}$ , and corresponding decrease in  $\omega_{tm}$  and  $\omega_{bm}$ .  
420 It should be noted that the OHC RP data which are analysed in this study were obtained from  
421 the high-frequency cochlear base. Both the mechanical (Recio-Spinoso and Oghalai, 2017;  
422 Burwood et al., 2022) and neural (Liberman, 1978; Allen, 1980; Liberman and Dodds, 1984;  
423 Taberner and Liberman, 2005; Temchin et al., 2008) responses at the extreme low-frequency  
424 cochlear apex have much broader tuning and lack a low-frequency shoulder, and neural  
425 responses have no local sensitivity minimum below the CF. In fact, a large stretch of the  
426 cochlear partition at the extreme apex moves in phase, making phase-locking of neural  
427 responses (Rose et al., 1967; Kim and Molnar, 1979; Johnson, 1980; Palmer and Russell,  
428 1986) a preferable mechanism of frequency coding in this cochlear region. The difference in  
429 responses between the base and apex possibly reflects the relative difference in mechanical  
430 properties of cochlear structures. The dimensions of the TM vary along the length of the  
431 cochlea; its radial width and cross-sectional area and, hence, linear mass density increase  
432 from the basal to the apical end of the cochlea (Richardson et al., 2008). The lengths of the  
433 OHC hair bundles increase from the cochlear base to apex (Wright, 1984; Yarin et al., 2014),  
434 which results in a decrease of their rotational stiffness (Tobin et al., 2019; Miller et al., 2021)  
435 and, thus, reduction in elastic coupling between the TM and OoC.

### 436 **Limitations of the study**

437 The objective of this work is to find a minimal model which still can qualitatively explain the  
438 complex behaviour of the OHC RP for different levels and frequencies of stimulation below  
439 and around the CF at the high frequency cochlear base. For this purpose, the model does not  
440 include global phenomena, e.g. TW along the BM and elastic coupling along the cochlear  
441 partition, and it cannot be used to fit experimental data. Only the qualitative behaviour of the  
442 OHC RP amplitude and phase responses is considered. The model assumes uniform negative  
443 damping/cochlear amplification over the entire frequency range, which, however, does not  
444 affect the conclusions because the conclusions are based on the OHC RP behaviour around  
445 the frequency range of  $[\omega_{tm}, \omega_{bm}]$  where nonlinear cochlear amplification is observed. Also,

446 the model explains OHC RPs recorded at the high-frequency cochlear region and responses at  
447 the extreme low-frequency cochlear apex might not be well explained.

## 448 **METHODS**

449 MATLAB (The MathWorks. Inc. 2022a) was used to find solutions for the linear (Figure 3)  
450 and nonlinear (Figure 4) models in the time domain for a harmonic stimulation  $P(t) =$   
451  $P_a \sin(\omega t)$  and the fast Fourier transform was applied to the solutions to extract the  
452 component at frequency  $\omega$ .

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## 456 **AUTHOR CONTRIBUTIONS**

457 IR and ANL conceived and designed the study. OR completed the analytical analysis of the  
458 mechanical systems. ANL performed computational simulations. All authors wrote the  
459 manuscript.

## 460 **DECLARATION OF INTERESTS**

461 The authors declare that they have no known competing financial interests or personal  
462 relationships that could have appeared to influence the work reported in this paper.

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## 621 **Supplemental information**

622 We would like to analyse the system of equations (4, 5) to answer the following questions:

- 623 1. What is the condition for a minimum of  $\Delta X$  at  $\omega_{tm}$  to occur?
- 624 2. What is contribution of the normal modes into the response?
- 625 3. Does the  $\Delta X$  minimum occur when  $K_{tm}$  is absent, i.e. when there is no limbal  
626 attachment of the TM to the spiral limbus?

627 To answer the question 1, and using the complex-exponential method, the equations (4, 5)  
628 can be rewritten

629 
$$\frac{d^2 Z_{bm}}{dt^2} + \zeta_{bm} \frac{dZ_{bm}}{dt} + \omega_{bm}^2 Z_{bm} - \omega_c^2 (Z_{tm} - Z_{bm}) \left( \frac{M_{tm}}{M_{bm}} \right) = -i \frac{P_a}{M_{bm}} e^{i\omega t}, \quad (S1)$$

630 and



$$631 \quad \frac{d^2 Z_{tm}}{dt^2} + \zeta_{tm} \frac{dZ_{tm}}{dt} + \omega_{tm}^2 Z_{tm} + \omega_c^2 (Z_{tm} - Z_{bm}) = 0. \quad (S2)$$

632 Let us assume the steady state solution in the following form:

$$633 \quad Z_{bm} = A_{bm} e^{i(\omega t - \delta_{bm})},$$

$$634 \quad Z_{tm} = A_{tm} e^{i(\omega t - \delta_{tm})}, \quad (S3)$$

635 with  $X_{bm} = \text{Re}(Z_{bm})$  and  $X_{tm} = \text{Re}(Z_{tm})$ .

636 Substituting expressions (S3) for  $Z_{bm}$  and  $Z_{tm}$  into equations (S1, S2) yields

$$637 \quad A_{bm} e^{i(\omega t - \delta_{bm})} \left( -\omega^2 + i\zeta_{bm}\omega + \left( \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}} \right) \right) - \omega_c^2 \frac{M_{tm}}{M_{bm}} A_{tm} e^{i(\omega t - \delta_{tm})} = -i \frac{P_a}{M_{bm}} e^{i\omega t} \quad (S4)$$

$$638 \quad A_{tm} e^{i(\omega t - \delta_{tm})} \left( -\omega^2 + i\zeta_{tm}\omega + (\omega_{tm}^2 + \omega_c^2) \right) - \omega_c^2 A_{bm} e^{i(\omega t - \delta_{bm})} = 0, \quad (S5)$$

639 and after re-arranging

$$640 \quad A_{bm} e^{-i\delta_{bm}} \left( -\omega^2 + i\zeta_{bm}\omega + \left( \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}} \right) \right) - \omega_c^2 \frac{M_{tm}}{M_{bm}} A_{tm} e^{-i\delta_{tm}} = -i \frac{P_a}{M_{bm}}, \quad (S6)$$

$$641 \quad A_{tm} e^{-i\delta_{tm}} \left( -\omega^2 + i\zeta_{tm}\omega + (\omega_{tm}^2 + \omega_c^2) \right) - \omega_c^2 A_{bm} e^{-i\delta_{bm}} = 0. \quad (S7)$$

642 From equation (S7), we have

$$643 \quad A_{tm} e^{-i\delta_{tm}} \left( -\omega^2 + i\zeta_{tm}\omega + (\omega_{tm}^2 + \omega_c^2) \right) = \omega_c^2 A_{bm} e^{-i\delta_{bm}} \quad (S8)$$

644 or

$$645 \quad A_{tm} e^{-i\delta_{tm}} \left( -\omega^2 + i\zeta_{tm}\omega + (\omega_{tm}^2 + \omega_c^2) \right) = \omega_c^2 A_{bm} e^{-i\delta_{bm}}. \quad (S9)$$

646 Denote  $r e^{-i\theta} = -\omega^2 + i\zeta_{tm}\omega + (\omega_{tm}^2 + \omega_c^2)$ , where  $r^2 = (-\omega^2 + \omega_{tm}^2 + \omega_c^2)^2 + \zeta_{tm}^2 \omega^2$

647 and

$$648 \quad -\theta = \text{atan2}(\zeta_{tm}\omega, -\omega^2 + \omega_{tm}^2 + \omega_c^2), \quad (S10)$$

649 where  $\text{atan2}$  is a four-quadrant inverse tangent, then

$$650 \quad A_{tm} e^{-i\delta_{tm}} r e^{-i\theta} = \omega_c^2 A_{bm} e^{-i\delta_{bm}}, \text{ or} \quad (S11)$$

$$651 \quad A_{tm} r e^{-i(\delta_{tm} + \theta)} = \omega_c^2 A_{bm} e^{-i\delta_{bm}}, \text{ or} \quad (S12)$$

$$652 \quad A_{tm} = \omega_c^2 \frac{A_{bm}}{r}, \text{ and} \quad (S13)$$



$$653 \quad \delta_{\text{tm}} = \delta_{\text{bm}} - \theta. \quad (\text{S14})$$

654 Local minimum of  $\Delta X$  is observed when the amplitudes and phases of  $Z_{\text{bm}}$  and  $Z_{\text{tm}}$  are close.  
 655 Let us compare pairs  $A_{\text{tm}}$  and  $A_{\text{bm}}$ ,  $\delta_{\text{tm}}$  and  $\delta_{\text{bm}}$  in (S13, S14). In case of light damping,  
 656  $\zeta_{\text{bm}}, \zeta_{\text{tm}} \ll \omega_{\text{bm}}, \omega_{\text{tm}}, \omega_{\text{c}}$ . Therefore, from the definitions (S10) of  $r$ , when  $\omega = \omega_{\text{tm}}$ ,  $r$  is  
 657 close to  $\omega_{\text{c}}^2$  (the difference  $r - \omega_{\text{c}}^2$  is proportional to  $\zeta_{\text{tm}} \ll 1$ ) and from (S13)  $A_{\text{tm}} \cong A_{\text{bm}}$ .  
 658 Also, since  $\zeta_{\text{tm}} \ll 1$ , from the definition (S10) of  $\theta$ , when  $\omega = \omega_{\text{tm}}$ ,  $-\theta$  is proportional to  
 659  $\zeta_{\text{tm}}\omega_{\text{tm}}/\omega_{\text{c}}^2$ , which is a small value as well, and  $\delta_{\text{tm}} \cong \delta_{\text{bm}}$ . To summarise, when  $\omega = \omega_{\text{tm}}$ ,  
 660 amplitudes  $A_{\text{tm}}$  and  $A_{\text{bm}}$ , and phases  $\delta_{\text{tm}}$  and  $\delta_{\text{bm}}$  of  $X_{\text{tm}}$  and  $X_{\text{bm}}$  are close, and their  
 661 difference  $\Delta X \rightarrow 0$  when  $\zeta_{\text{tm}} \rightarrow 0$ .

662 Note that from the definition of  $\theta$  (S10), it follows that at  $\omega = \sqrt{\omega_{\text{tm}}^2 + \omega_{\text{c}}^2}$ ,  $\theta$  changes its  
 663 value from 0 to  $-\pi$ . In other words, and if neglecting small terms, this can be rewritten as

$$664 \quad \delta_{\text{tm}} = \delta_{\text{bm}}, \text{ when } \omega^2 < \omega_{\text{tm}}^2 + \omega_{\text{c}}^2; \text{ and } \delta_{\text{tm}} = \delta_{\text{bm}} + \pi, \text{ when } \omega^2 > \omega_{\text{tm}}^2 + \omega_{\text{c}}^2.$$

665 The modelling results support this outcome, see Figure 3E, where the phases of TM and BM  
 666 responses coincide until  $\omega = \sqrt{\omega_{\text{tm}}^2 + \omega_{\text{c}}^2}$ , after which there is a jump in the value between  
 667 the phases by  $\pi$ .

668 After substituting notations introduced in (S13) and (S14), to (S6), we have

$$669 \quad A_{\text{bm}} e^{-i\delta_{\text{bm}}} \left( -\omega^2 + i\zeta_{\text{bm}}\omega + \left( \omega_{\text{bm}}^2 + \omega_{\text{c}}^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \right) \right) - \omega_{\text{c}}^4 \frac{M_{\text{tm}}}{M_{\text{bm}}} \frac{A_{\text{bm}}}{r} e^{-i(\delta_{\text{bm}} - \theta)} = -i \frac{P_{\text{a}}}{M_{\text{bm}}}, \quad (\text{S15})$$

670 As in the analysis above, let us introduce new variables as follows

$$671 \quad r_1 e^{-i\theta_1} = -\omega^2 + i\zeta_{\text{bm}}\omega + \left( \omega_{\text{bm}}^2 + \omega_{\text{c}}^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \right). \quad (\text{S16})$$

672 Then (S15) takes form

$$673 \quad A_{\text{bm}} e^{-i\delta_{\text{bm}}} r_1 e^{-i\theta_1} - \omega_{\text{c}}^4 \frac{M_{\text{tm}}}{M_{\text{bm}}} \frac{A_{\text{bm}}}{r} e^{-i(\delta_{\text{bm}} - \theta)} = -i \frac{P_{\text{a}}}{M_{\text{bm}}}, \text{ or} \quad (\text{S17})$$

$$674 \quad A_{\text{bm}} e^{-i\delta_{\text{bm}}} \left( r_1 e^{-i\theta_1} - \frac{\omega_{\text{c}}^4}{r} \frac{M_{\text{tm}}}{M_{\text{bm}}} e^{i\theta} \right) = \frac{P_{\text{a}}}{M_{\text{bm}}} e^{-i\pi/2}. \quad (\text{S18})$$

675 Denote

$$676 \quad r_2 e^{i\theta_2} = r_1 e^{-i\theta_1} - \frac{\omega_{\text{c}}^4}{r} \frac{M_{\text{tm}}}{M_{\text{bm}}} e^{i\theta}. \quad (\text{S19})$$

677 Then (S18) takes form

$$678 \quad A_{\text{bm}} r_2 e^{-i(\delta_{\text{bm}} - \theta_2)} = \frac{P_a}{M_{\text{bm}}} e^{-i\pi/2}, \quad (\text{S20})$$

679 from which it follows that

$$680 \quad A_{\text{bm}} r_2 = \frac{P_a}{M_{\text{bm}}}, \text{ and } \delta_{\text{bm}} = \theta_2 + \frac{\pi}{2}. \quad (\text{S21})$$

681 Recall from (S19),

$$682 \quad \theta_2 = \text{atan2} \left( -r_1 \sin \theta_1 - \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \sin \theta, r_1 \cos \theta_1 - \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \cos \theta \right).$$

683 In order to understand behaviour of the phase  $\theta_2$ , let's consider the arguments of the atan2  
684 function. After substituting all the notations used in the derivation, we have

$$\begin{aligned} 685 \quad & -r_1 \sin \theta_1 - \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \sin \theta \\ 686 \quad & = -r_1 \sin \left( -\text{atan2} \left( \zeta_{\text{bm}} \omega, -\omega^2 + \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \right) \right) \\ 687 \quad & - \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \sin \left( -\text{atan2} \left( \zeta_{\text{tm}} \omega, -\omega^2 + \omega_{\text{tm}}^2 + \omega_c^2 \right) \right) \\ 688 \quad & = r_1 \sin \left( \text{atan2} \left( \zeta_{\text{bm}} \omega, -\omega^2 + \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \right) \right) \\ 689 \quad & + \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \sin \left( \text{atan2} \left( \zeta_{\text{tm}} \omega, -\omega^2 + \omega_{\text{tm}}^2 + \omega_c^2 \right) \right) = r_1 \frac{\zeta_{\text{bm}} \omega}{r_1} + \frac{\omega_c^4 M_{\text{tm}}}{r M_{\text{bm}}} \frac{\zeta_{\text{tm}} \omega}{r} \\ 690 \quad & = \zeta_{\text{bm}} \omega + \frac{\omega_c^4 M_{\text{tm}}}{r^2 M_{\text{bm}}} \zeta_{\text{tm}} \omega. \end{aligned}$$

691 The expression above is positive since  $\omega$  is positive. Note a singularity when  $r = 0$  or  $\omega =$   
692  $\sqrt{\omega_{\text{tm}}^2 + \omega_c^2}$ , which is where  $\theta$  changes its value from 0 to  $-\pi$ .

$$\begin{aligned}
 693 \quad r_1 \cos \theta_1 - \frac{\omega_c^4 M_{tm}}{r M_{bm}} \cos \theta \\
 694 \quad &= r_1 \cos \left( -\operatorname{atan2} \left( \zeta_{bm} \omega, -\omega^2 + \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}} \right) \right) \\
 695 \quad &- \frac{\omega_c^4 M_{tm}}{r M_{bm}} \cos \left( -\operatorname{atan2} \left( \zeta_{tm} \omega, -\omega^2 + \omega_{tm}^2 + \omega_c^2 \right) \right) \\
 696 \quad &= r_1 \cos \left( \operatorname{atan2} \left( \zeta_{bm} \omega, -\omega^2 + \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}} \right) \right) \\
 697 \quad &- \frac{\omega_c^4 M_{tm}}{r M_{bm}} \cos \left( \operatorname{atan2} \left( \zeta_{tm} \omega, -\omega^2 + \omega_{tm}^2 + \omega_c^2 \right) \right) \\
 698 \quad &= r_1 \frac{-\omega^2 + \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}}}{r_1} - \frac{\omega_c^4 M_{tm}}{r M_{bm}} \frac{-\omega^2 + \omega_{tm}^2 + \omega_c^2}{r} \\
 699 \quad &= -\omega^2 + \omega_{bm}^2 + \omega_c^2 \frac{M_{tm}}{M_{bm}} - \frac{\omega_c^4 M_{tm}}{r^2 M_{bm}} (-\omega^2 + \omega_{tm}^2 + \omega_c^2).
 \end{aligned}$$

700 For the purpose of understanding of  $\theta_2$ , we are interested in the intervals where the  
 701 expression above is positive or negative intervals. On the positive  $\omega$  semi-axis, there are three  
 702 points, defining such intervals. Two of them coincide with the system resonances  $\varphi_1$  and  $\varphi_2$   
 703 (see the derivation of the normal modes in the simplified case, when dampers are neglected  
 704 below, in the solution to question 2) and  $\omega = \sqrt{\omega_{tm}^2 + \omega_c^2}$ . The expression is positive at  $\omega =$   
 705 0. With increasing  $\omega$ , it changes its sign after the first resonance to negative, then becomes  
 706 positive after  $\omega = \sqrt{\omega_{tm}^2 + \omega_c^2}$  and negative again after the second resonance frequency. If  
 707 neglecting small terms,

$$708 \quad \theta_2 = \begin{cases} 0, & 0 < \omega < \varphi_1, \\ \pi, & \varphi_1 < \omega < \sqrt{\omega_{tm}^2 + \omega_c^2}, \\ 0, & \sqrt{\omega_{tm}^2 + \omega_c^2} < \omega < \varphi_2, \\ \pi, & \omega > \varphi_2. \end{cases} \quad (S22)$$

709

710 Therefore,

$$711 \quad \delta_{\text{bm}} = \begin{cases} \frac{\pi}{2}, & 0 < \omega < \varphi_1, \\ \frac{3\pi}{2}, & \varphi_1 < \omega < \sqrt{\omega_{\text{tm}}^2 + \omega_c^2}, \\ \frac{\pi}{2}, & \sqrt{\omega_{\text{tm}}^2 + \omega_c^2} < \omega < \varphi_2, \\ \frac{3\pi}{2}, & \omega > \varphi_2. \end{cases} \quad (S23)$$

712

713 This result is fully replicated in numerical modelling, see Figure 3E, note that  $\delta_{\text{bm}}$  has an  
714 opposite sign from the BM phase.

715 Finally, let us consider the difference  $Z_{\text{bm}} - Z_{\text{tm}}$ .

$$716 \quad Z_{\text{bm}} - Z_{\text{tm}} = A_{\text{bm}} e^{i(\omega t - \delta_{\text{bm}})} - A_{\text{tm}} e^{i(\omega t - \delta_{\text{tm}})} = A_{\text{bm}} e^{i(\omega t - \delta_{\text{bm}})} \left( 1 - \frac{\omega_c^2}{r} e^{i\theta} \right).$$

717 The relative phase of the difference is  $\Delta_{\text{ph}} = \theta_3 - \delta_{\text{bm}}$ , where  $r_3 e^{-i\theta_3} = 1 - \omega_c^2 e^{i\theta} / r$ .

718 Imaginary part of the latter expression is  $-\omega_c^2 \sin\theta / r$ . Recall that  $\theta$  is small since it is  
719 proportional to  $\zeta_{\text{tm}} \omega / \omega_c^2$ . Therefore,  $\theta_3$  is close to 0 or  $\pi$ , if the real part is positive or  
720 negative, correspondingly.

$$721 \quad \text{Re} \left( 1 - \frac{\omega_c^2}{r} e^{i\theta} \right) = 1 - \frac{\omega_c^2}{r} \cos\theta = 1 - \frac{\omega_c^2}{r^2} (-\omega^2 + \omega_{\text{tm}}^2 + \omega_c^2).$$

722 Omitting the details of derivation, there are two points, which divide the positive  $\omega$  semi-axis  
723 into three intervals. The first point is close to  $\omega_{\text{tm}}$  and the second one is close to the  
724 singularity  $\sqrt{\omega_{\text{tm}}^2 + \omega_c^2}$ . The real part is positive in the first interval between 0 and  $\omega_{\text{tm}}$ , then  
725 changes the sign to negative between  $\omega_{\text{tm}}$  and  $\sqrt{\omega_{\text{tm}}^2 + \omega_c^2}$ , then changes the sign again to  
726 positive on  $\omega > \sqrt{\omega_{\text{tm}}^2 + \omega_c^2}$ . After combining everything together and if neglecting small  
727 terms, the phase of the difference takes the following values

$$728 \quad \Delta_{\text{ph}} = \theta_3 - \delta_{\text{bm}} = \begin{cases} -\frac{\pi}{2}, & 0 < \omega < \omega_{\text{tm}}, \\ \frac{\pi}{2}, & \omega_{\text{tm}} < \omega < \varphi_1, \\ -\frac{\pi}{2}, & \varphi_1 < \omega < \varphi_2, \\ -\frac{3\pi}{2}, & \omega > \varphi_2 \end{cases} \quad (S24)$$

729 Note that at  $\omega = \sqrt{\omega_{\text{tm}}^2 + \omega_c^2}$ , both  $\delta_{\text{bm}}$  and  $\theta_3$  change their values by  $-\pi$ , thus this jump is  
 730 cancelled out and the value of  $\Delta_{\text{ph}}$  remains.

731 The amplitude of the difference is

$$732 \quad |Z_{\text{bm}} - Z_{\text{tm}}| = A_{\text{bm}} r_3 = \frac{P_a}{M_{\text{bm}}} \frac{r_3}{r_2} = \frac{P_a}{M_{\text{bm}}} \frac{r_3}{r_2}.$$

733 This expression has singularities, which correspond to resonance frequencies (see discussion  
 734 above regarding  $\theta_2$ ). For the sake of the space, instead of substituting all terms in the above  
 735 expression, we can focus on the expression for  $r_3$ .

$$736 \quad r_3^2 = \left(1 - \frac{\omega_c^2}{r} \cos\theta\right)^2 + \left(\frac{\omega_c^2}{r} \sin\theta\right)^2 = \frac{1}{r^2} (\omega^4 + \omega^2(-2\omega_{\text{tm}}^2 + \zeta_{\text{tm}}^2) + \omega_{\text{tm}}^4)$$

737 The above shows that since the damping coefficient  $0 < \zeta_{\text{tm}} \ll \omega_{\text{tm}}$ , the minimal value of  
 738 the amplitude of the difference is when  $\omega = \sqrt{\omega_{\text{tm}}^2 - 0.5\zeta_{\text{tm}}^2} \approx \omega_{\text{tm}} - 0.25\zeta_{\text{tm}}^2/\omega_{\text{tm}} \approx \omega_{\text{tm}}$ ,  
 739 which corrects the previous finding. Note, that at this frequency,  $r_3^2$  is of the same order of  
 740 magnitude as  $\zeta_{\text{tm}}^2 \ll 1$ .

741 **Answer to question 1:** Minimum of the relative displacement  $\Delta X$  between the TM and BM  
 742 always occurs at the TM resonance frequency  $\omega_{\text{tm}}$  (see also Figure 10 in Nankali et al.,  
 743 2020). Its frequency position does not depend on the properties of the driven oscillator, i.e.  
 744 the BM/OoC. The  $\Delta X$  minimum becomes more pronounced with decreasing the TM  
 745 damping.

746 To answer question 2, let us consider the original system of equations (4, 5) without dampers  
 747 and external force to find frequencies of the normal modes:

$$748 \quad \frac{d^2 X_{\text{bm}}}{dt^2} + \omega_{\text{bm}}^2 X_{\text{bm}} - \omega_c^2 (X_{\text{tm}} - X_{\text{bm}}) \left(\frac{M_{\text{tm}}}{M_{\text{bm}}}\right) = 0, \quad (\text{S25})$$

$$749 \quad \frac{d^2 X_{\text{tm}}}{dt^2} + \omega_{\text{tm}}^2 X_{\text{tm}} + \omega_c^2 (X_{\text{tm}} - X_{\text{bm}}) = 0. \quad (\text{S26})$$

750 We look for a solution in the form of a cosine function

$$751 \quad \begin{pmatrix} X_{\text{bm}} \\ X_{\text{tm}} \end{pmatrix} = \begin{pmatrix} x_{\text{bm}} \\ x_{\text{tm}} \end{pmatrix} \cos(\varphi t), \quad (\text{S27})$$

752 then after substituting (S27) into (S25) and (S26) and using matrix notations we have

$$753 \quad \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x_{\text{bm}} \\ x_{\text{tm}} \end{pmatrix} (-\varphi^2) \cos(\varphi t) + \begin{pmatrix} \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} & -\omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \\ -\omega_c^2 & \omega_{\text{tm}}^2 + \omega_c^2 \end{pmatrix} \begin{pmatrix} x_{\text{bm}} \\ x_{\text{tm}} \end{pmatrix} \cos(\varphi t) = 0. \quad (\text{S28})$$

754 Rearranging yields

$$755 \quad \begin{pmatrix} \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} - \varphi^2 & -\omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \\ -\omega_c^2 & \omega_{\text{tm}}^2 + \omega_c^2 - \varphi^2 \end{pmatrix} \begin{pmatrix} x_{\text{bm}} \\ x_{\text{tm}} \end{pmatrix} \cos(\varphi t) = 0. \quad (\text{S29})$$

756 A trivial solution is  $\begin{pmatrix} x_{\text{bm}} \\ x_{\text{tm}} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ . To find non-trivial solutions the determinant of the matrix  
757 should be equal to zero, which leads to the following equation with respect to  $\varphi$ :

$$758 \quad \det \begin{pmatrix} \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} - \varphi^2 & -\omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \\ -\omega_c^2 & \omega_{\text{tm}}^2 + \omega_c^2 - \varphi^2 \end{pmatrix} \\ = \left( \omega_{\text{bm}}^2 + \omega_c^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} - \varphi^2 \right) (\omega_{\text{tm}}^2 + \omega_c^2 - \varphi^2) - \omega_c^4 \frac{M_{\text{tm}}}{M_{\text{bm}}} = 0. \quad (\text{S30})$$

759 After collecting coefficients of the powers of  $\varphi$ , we have

$$760 \quad \varphi^4 - \left( \omega_{\text{bm}}^2 + \omega_{\text{tm}}^2 + \omega_c^2 \left( \frac{M_{\text{tm}}}{M_{\text{bm}}} + 1 \right) \right) \varphi^2 + \omega_{\text{bm}}^2 \omega_{\text{tm}}^2 + \omega_c^2 \left( \omega_{\text{bm}}^2 + \omega_{\text{tm}}^2 \frac{M_{\text{tm}}}{M_{\text{bm}}} \right) = 0. \quad (\text{S31})$$

761 After substituting  $\Phi = \varphi^2$ , the equation (S31) is reduced to a quadratic equation

$$762 \quad \Phi_{1,2} = \frac{1}{2} \left( \begin{pmatrix} \omega_{\text{bm}}^2 + \omega_{\text{tm}}^2 + \omega_c^2 \left( \frac{M_{\text{tm}}}{M_{\text{bm}}} + 1 \right) \\ \pm \sqrt{(\omega_{\text{bm}}^2 - \omega_{\text{tm}}^2)^2 + \omega_c^4 \left( \frac{M_{\text{tm}}}{M_{\text{bm}}} + 1 \right)^2 + 2\omega_c^2 \left( \frac{M_{\text{tm}}}{M_{\text{bm}}} - 1 \right) (\omega_{\text{bm}}^2 - \omega_{\text{tm}}^2)} \end{pmatrix} \right). \quad (\text{S32})$$

763 Note that both  $\Phi_1$  and  $\Phi_2$  are positive and we can find frequencies of the normal modes

764  $\varphi_{1,2} = \sqrt{\Phi_{1,2}}$ . For the chosen model parameters  $\varphi_1 = 1.37$  and  $\varphi_2 = 5.35$ .

765 **Answer to question 2:** The second normal mode of the system is shifted towards high  
766 frequencies due to strong coupling  $K_c$  between the TM and OoC, and its contribution for  
767 frequencies below  $\omega_{\text{bm}}$  is minimal.

768 **Answer to question 3:** The local minimum of  $\Delta X$  is always observed at  $\omega_{\text{tm}}$  (see answer to  
769 question 1). Therefore, it is not observed when  $K_{\text{tm}} = 0$ , the TM limbal attachment is absent  
770 and  $\omega_{\text{tm}} = 0$ . Two normal modes of the system (equation (S32)) exist.