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Approaching the Hopf bifurcation largely increases the cochlear response

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This work investigates cochlear amplification in a transmission line model whose local elements are critical oscillators operating near a Hopf bifurcation. Here, starting from a physically based micromechanical description of the cochlea, the governing equations are reformulated into normal form, allowing the parameters of the reduced model to be directly related to measurable physical quantities. A transmission-line cochlear model including two-dimensional fluid coupling is solved in time domain with the state space technique and pressure Green's functions. The analysis further demonstrates the rapid growth of the cochlear response as the system approaches the Hopf instability. The distance from the bifurcation is expressed in terms of physiologically meaningful parameters, such as the strength of the active force and the cutoff frequency associated with the outer hair cell transmembrane potential. The proposed formulation therefore establishes a direct connection between abstract nonlinear oscillator theory and the physical processes governing cochlear mechanics. Preliminary results show how approaching the critical regime it is possible to get large gain dynamics in the peak region. Interestingly, although the nonlinear force is coupled to the relative mode only, both modes show the same nonlinear behavior, due to the back-action on the pressure associated with the focusing phenomenon.

Keywords: *Hopf bifurcation, cochlear micromechanics, traveling wave*

1. Introduction

The description of the cochlea as a system of critical oscillators operating near the Hopf bifurcation has long been proposed to explain its nonlinear response and remarkable amplification properties. In these models, the cochlear micromechanical system is typically represented using equations written in the normal form [1], [2]. This formulation is advantageous because of its generality, allowing it to describe a wide range of systems and dynamical behaviors within a unified framework.
Some skepticism remains regarding whether such an abstract representation can truly correspond to a physical system within the cochlea. To address this concern in [3], a physical model developed in [4] is proposed that presents physically grounded equations describing cochlear micromechanics and reformulates them into normal form. In doing so, the parameters of the normal form acquire a direct physical interpretation when examined in light of the underlying dynamical equations governing the oscillator. The work presented in [3] showed some limitations that have been overcome in this contribution in which the nonlinear cochlear model is solved in time domain.

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The transmission line model of the cochlea with two degrees of freedom micromechanics, incorporating two-dimensional fluid coupling, is solved in time domain using a state space formulation. The model is extensively shown in [5], [6], [7], and the active term is schematized as is [8], based on what had been proposed by [9], [10]. The eigenvalues of the system matrix were studied, and an analytical condition was found for the Hopf bifurcation.
This occurrence coincided with the annihilation of the real part of two complex conjugate critical eigenvalues of the system matrix.
Furthermore, the model illustrates how the cochlear response increases dramatically as the system approaches the Hopf bifurcation. The proximity to this critical regime is parameterized in terms of physically meaningful quantities, including the amplitude of the active force and the cutoff frequency of the low-pass filter representing the transmembrane potential of outer hair cells. This provides a direct link between theoretical predictions and measurable physiological parameters.

2. The Model

The cochlear micromechanics is represented by two coupled oscillators. The two oscillators may be identified with the basilar membrane (BM) and the Reticular Lamina (RL), the membrane at the top of the outer hair cells (OHCs). Only the BM is forced by the differential pressure. The coupling active force is an elastic force low-pass filtered at the aim of mimicking the effect of the OHCs transmembrane potential [8]. The mass, elastic and damping parameters m, K, and C, of the two oscillators are considered identical, and equal to those of the internal passive coupling.

The normal modes of the system are studied, which is particularly convenient considering that the internal active force is directly coupled only to the relative motion mode, while the same external force, i.e. the differential pressure, excites both normal modes, corresponding, respectively, to the center of mass and to the relative motion as in Eqs.(1).

$$(\ddot{x}_1 + \ddot{x}_2) = -\omega_0^2(x_1 + x_2) - \gamma(\dot{x}_1 + \dot{x}_2) - \frac{P_d}{m} \qquad (1)$$
$$(\ddot{x}_1 - \ddot{x}_2) = -3\omega_0^2(x_1 - x_2) - 3\gamma(\dot{x}_1 - \dot{x}_2) + \frac{p_{OHC}}{m} - \frac{P_d}{m}$$

The active force, being an internal one, only acts on the equation of the relative motion whilst the center of gravity remains unaffected. One can assume that the normal mode associated with the relative motion,

$$X_- = x_1 - x_2\,, \qquad (2)$$

represents a resonant oscillator forced by an active force p_{OHC}. The active force is modeled as a low-pass filtered linear (elastic) function of the relative displacement [8], [9]:

$$\dot{p}_{\mathrm{OHC}} + \frac{1}{\tau(x)} p_{\mathrm{OHC}} = -\frac{C_{\mathrm{nl}}\,\omega(x)}{\tau(x)} X_- - \frac{K_{\mathrm{nl}}}{\omega(x)\tau(x)} \dot{X}_- \qquad (3)$$

where τ(x) is a position-dependent characteristic time, ω(x) defines the tonotopic map and C_{nl} and K_{nl} are nonlinear function modelling the saturation of the response.

$$C_{nl} = C4(x)\left[1 - tanh\left[\frac{(X_-)^2}{X_{\mathrm{sat}}^2}\right]\right] \qquad (4)$$

$$K_{nl} = K4(x)\left[1 - tanh\left[\frac{(\dot{X}_-)^2}{X_{\mathrm{sat}}^2}\right]\right] \qquad (5)$$

In the classical transmission-line approximation, the pressure satisfies a local relation. Here, instead, we introduce a nonlocal fluid coupling derived from a two-dimensional incompressible and inviscid fluid model.

The differential pressure field is expressed through Green's functions, yielding:

$$P_d(x,t) = -\int_0^L G(x,\tilde{x})\left(\ddot{X}_-(\tilde{x},t) + \ddot{X}_+(\tilde{x},t)\right) d\tilde{x} + G_s(x)\,\ddot{\sigma}_{\mathrm{ow}}(t), \qquad (6)$$

where $\ddot{X}_{\mp}$ is the acceleration of each normal mode,

The cochlea is discretized into N elements, yielding a set of coupled oscillators. Additional degrees of freedom account for boundary conditions at the oval window and helicotrema.

We define the state vector

$$\mathbf{U}(t) = [\dot{X}_+^{(i)}, X_+^{(i)}, \dot{X}_-^{(i)}, X_-^{(i)}, Q^{(i)}]_{i=1}^N, \qquad (7)$$

where $Q \equiv p_{\mathrm{OHC}}$, and

$$X_+ = x_1 + x_2 \qquad (8)$$

The system can then be written in compact form as

$$\boldsymbol{M}_x\dot{\boldsymbol{U}} = \boldsymbol{A}\boldsymbol{U} + \boldsymbol{F}_{nl}(\boldsymbol{U}) + \boldsymbol{B}G_s\,\ddot{\sigma}_{ow}(t) \qquad (9)$$

A is the linear dynamical matrix, containing the linear part of the active force

$\mathbf{M}_x = \mathbf{I} + \mathbf{BGC}$ is the nonlocal mass matrix,

G is the discretized Green's function,

$\mathbf{F}_{\mathrm{nl}}$ nldescribes the nonlinear active feedback.

$$\mathbf{F}_{\mathrm{nl}}(\mathbf{U}) = \mathbf{B}_3\,\mathbf{N}(\mathbf{U})\,\mathbf{D}_{\mathrm{nl}}\mathbf{U} \qquad (10)$$

Nonlinearity is introduced through a saturating damping function:

$$N = \left[1 - tanh\left[\frac{(X_-)^2}{X_{\mathrm{sat}}^2}\right]\right] \qquad (11)$$

where N is a diagonal matrix containing *N* elements as that in Eq.(11).

The mass matrix was inverted, and the system was solved in time domain using the Matlab solver `ode23`.

$$\dot{\mathbf{U}} = \mathbf{M}_x^{-1}[\mathbf{A}_{\mathrm{tot}}\mathbf{U} + \mathbf{F}_{\mathrm{nl}}(\mathbf{U}) + \mathbf{B}G_s\,\ddot{\sigma}_{\mathrm{ow}}(t)]. \qquad (12)$$

The cochlear length L was discretized in N = 600 partitions. Different frequencies were used as stimulus.

The matrix A has five eigenvectors, the first two, associated with the motion of the center of mass, are complex conjugate, the third and fourth are also cc and associated with the oscillatory relative motion. The last eigenvector is real and represents pure damping. The oscillator associated with the relative motion plus the low passed active force can be put into the normal form of a critical oscillator as in Eq.(13):

$$\partial_t z = (\varepsilon + j\omega_r)z - (\alpha_{nl} + j\beta_{nl})z|z|^2 + fP_d \qquad (13)$$

where $\lambda_i = (\varepsilon + j\omega_r)$ is one of the eigenvectors of the matrix A associated to the relative motion. fP_d represents the stimulus pressure in the space in which A is diagonal. If V is the matrix made by the eigenvectors as columns, such as

$$V^{-1}AV = \Lambda \qquad (14)$$

The vector z, representing the dynamical variables in the new space, is related to the old basis by the linear transformation

$$z = V^{-1}x \qquad (15)$$

where x is the state space vector of the original basis.

The oscillator becomes critical when the real part of the eigenvalue λ is zero. A Hopf bifurcation occurs when the real part of the eigenvalue associated with the oscillatory motion crosses the imaginary axis. For $\varepsilon < 0$ the oscillatory motion is stable, for $\varepsilon = 0$ a limit cycle oscillation occurs, and finally for $\varepsilon > 0$ the motion is linearly unstable, and the response would diverge in absence of a nonlinear saturation term.

The critical condition for the system under consideration can be found analytically, by requiring the coefficient of the quadratic term in the characteristic polynomial associated with Eqs.(1,3) to vanish. This condition is verified if:

$$d = bc, \tag{16}$$

where

$$b(x) = \left(\frac{C(x)}{m} + \frac{1}{\tau(x)}\right),$$

$$c(x) = \left(\frac{C(x)}{m\tau(x)} + \frac{3K(x)}{m}\right), \tag{17}$$

$$d(x) = \frac{\left(3K(x) + lpa(x)C_4(x)\omega(x)\right)}{m\tau(x)},$$

where $\omega(x)$ is the tonotopic frequency and $\omega_1 = 2\pi f_1$ Is the frequency of the probe. If one defines the quantity:

$$r(x) = \frac{bc}{d} \tag{18}$$

The bifurcation occurs when $r(x) = 1$. The approach to the critical regime can be better expressed in a quantitative way by the local value of the dimensionless parameter:

$$\delta(x) = \sqrt[3]{r(x)} - 1 \tag{19}$$

An expression can be derived also for the critical value of the coefficient C_4:

$$C_{4\_crit} = \frac{m\tau bc - 3K}{lpa(x)\omega(x)} \tag{20}$$

lpa(x) is a function of the tonotopic map and of the cutoff frequency associated with the low pass filtering associated with the slow build-up of the transmembrane voltage.

The parameters of the close-to-critical cochlear model summarized in Table I are not tuned to represent a specific animal species and may be considered as just an example for the reader to play with.

Table 1. List of the parameters used in the model.

L	32 [mm]
k_ω	200 [m^{-1}]
ρ	1000 [$kg \cdot m^{-3}$]
k_0	8500 [m^{-1}]
H	$\frac{2\rho}{(mk_0^2)}$
m	0.05 [kgm^{-2}]
$K(x)$	$1.1 \cdot 10^{10} \cdot exp(-2k_\omega x)$
$\omega(x)$	$\sqrt{\frac{3K(x)}{m}}$
$K_4(x)$	0
$C(x)$	$1500 \cdot exp(-k_\omega x)$
$C_4(x)$	14 C(x)
$\tau(x)$	10^{-3} [s]
f_{cut}	$\frac{1}{\tau(x)}$
X_{sat}	$1.4 \cdot 10^{-7}$[m]
$lpa(x)$	$\left(\frac{\omega(x)}{2\pi f_{cut}}\right)^{0.75}$

3. Results and Discussion

The center of mass (CM) and the relative motion (RM) response levels normalized to the stimulus level (gain) are shown in Figure 1 for the close-to-critical parameter choice of Table 1.

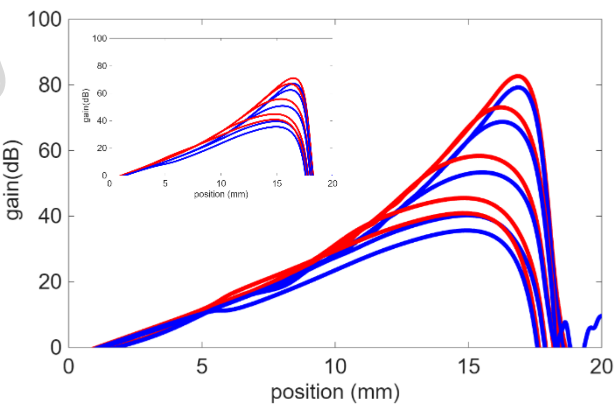

Figure 1. Basilar Membrane (red) and Reticular Lamina (bue) gain, varying the stimulus level from 0 to 80 dB with 20 dB steps. In the insert, the response of a subcritical model with C_4 equal to 50% of the critical model value.

The spatial variation of the critical parameter condition may also be represented, as in Fig.2, by showing the curve representing the local value of the active mechanism parameter C_4(x) and its critical value, which would locally yield $\delta = 0$. With the parameters choice yielding the tall and broad response of Fig.1, the system is close to critical in a wide region basal to the peak. The approach to the critical regime in the peak region increases the maximum gain and its dynamical range.

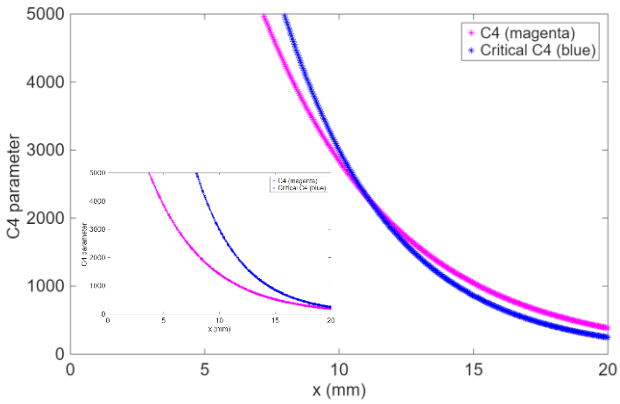

Figure 2. Function $C_4(x)$ used in Fig.1 compared to the local critical value. In the insert, the same plot for the subcritical model.

4. Conclusions

A 2DOF transmission line cochlear model was presented in which the 2d fluid effect in the short-wave region was kept into account by means of the fluid's Green's functions of the pressure. The model is nonlinear and was solved in time domain in terms of the normal models of two coupled oscillators with same mass, stiffness and damping. One mode describes the center of mass and the other the oscillators' relative motion. Whilst the pressure acts on both the oscillator, the active force being internal only acts on the relative motion. Another equation was added to modeling the active force treated as an elastic low pass filtered force coupling the two oscillators. The consequence of the low pass integration is the phase rotation transforming the elastic force into an anti-damping one. The system constituted by the motion equations for the relative motion and the active force can be put in the normal form of a critical Hopf oscillator. The critical conditions were studied, and it was demonstrated that the cochlear response increases dramatically when the bifurcation is approached. At the bifurcation the real part of the eigenvalues representing the relative motion and the active force vanishes, causing a linear instability, which is eventually kept under control by the compressive nonlinearity.

This work suggests that the mechanics of the OoC can be locally schematized by a system of two oscillators and that the dynamics of the relative motion mode may be represented as that of a critical oscillator. The condition for the bifurcation and the strength of the stabilizing nonlinearity may be defined in terms of meaningful physiological quantities.

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