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Nonlinear Tuning from Coupled Critical Oscillators in a Travelling-Wave Model of The Cochlea

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Abstract. The nonlinear mechanical properties of the cochlea have been recognized as signatures of active amplification by critical oscillators—active dynamical systems that each operate at a Hopf bifurcation. A critical oscillator, however, evinces a maximal sensitivity that is inversely proportional to the bandwidth of its frequency tuning, resulting in a constant “gain-bandwidth” product. The cochlea does not work by this rule: the gain-bandwidth product increases with decreasing sound-pressure levels, so that sensitivity to low sound levels is high but tuning is relatively broad. The cochlea thus appears to violate a fundamental requirement for a principle of cochlear amplification based on critical oscillators. Here, we tackle this challenge by integrating tonotopically distributed critical oscillators in a traveling-wave model of the cochlea. Our nonlinear model accounts for two-dimensional hydrodynamics, longitudinal coupling between oscillators and energy pumping by the oscillators into the wave. The model produces, with a single set of parameters, a family of cochlear tuning curves over a broad range of input levels. We found that the gain-bandwidth product decreased at increasing levels, while preserving, but not precisely, the generic power-law behavior of critical oscillators. Marrying the physics of critical oscillators with traveling waves can thus account for the compressive nonlinearity underlying cochlear amplification, while ensuring that the bandwidth of the tuning curves remain relatively broad and varies little with sound level.

INTRODUCTION

The high sensitivity and sharp frequency selectivity of mammalian hearing are associated with a compressive nonlinearity in cochlear mechanics, which represents six orders of magnitude of sound-pressure levels in only two-to-three orders of magnitudes of basilar-membrane vibration [1]. At intermediate levels of the input, this level function has been described by a power law of exponent +1/3 [2–4]. Such power-law behavior is generic of active amplification by “critical oscillators”—active dynamical systems operating at the onset of an oscillatory instability called a Hopf bifurcation [5,6]. In return, criticality has been proposed as a fundamental principle to encapsulate in one concept the wide dynamical range of hearing, its sharp frequency selectivity, as well as oto-acoustic emissions. Within this framework, the different frequencies of sound are mechanically amplified by critical oscillators tuned to different frequencies and spatially distributed along the longitudinal axis of the cochlea according to its tonotopic map.

Two quantitative experimental observations, however, challenge the concept of critical oscillation as the physical basis of cochlear amplification. First, the “gain-bandwidth product”, i.e. the product of the maximal sensitivity and the bandwidth in a cochlear tuning curve, decreases with increasing sound-pressure levels. Sensitivity to low sound levels is high but tuning remains relatively broad. This behavior contrasts with that of a single critical oscillator. A critical oscillator driven at its natural frequency indeed shows an inverse relation between peak sensitivity ($\propto P^{-2/3}$) and bandwidth ($\propto P^{2/3}$) as a function of stimulus level (noted P here), so that the product of the two must remain constant. In other words, the cochlea appears to violate a fundamental requirement of sound detection by a critical oscillator. Second, a careful examination of the compressive nonlinearity across experimental datasets from the literature reveals that the exponent of a power-law fit to the data can deviate significantly from that expected for a critical oscillator. For instance, over an ensemble of mouse cochleae [7], a power-law fit of the compressive non-

linearity in experiments yields a power-law exponent 0.25 ± 0.06 ($n = 15$), thus below the $1/3$ value expected from a critical oscillator and with some variability across datasets (range: 0.15-0.43). Other published datasets in the gerbil [8] and the mouse [9] can show exponents very close to $1/3$, but one may still argue that the evidence for a universal power-law behavior in cochlear mechanics is debatable.

We show here that these two observations can be reconciled with the hypothesis of criticality as a fundamental principle for cochlear amplification. Our work is based on a pioneering model of the cochlea based on tonotopically distributed critical oscillators [4,10], which we developed in three directions to take 2D hydrodynamics into account, add mechanical coupling between oscillators, and consider active energy pumping by the oscillators into the traveling wave.

METHODS

We developed a box-model of the cochlea, in which the organ of Corti is represented by a string of tonotopically-tuned critical oscillators. The dynamic behavior of each oscillator is described by a generic equation of a complex variable, $z = h + iu$, called the normal form:

$$\partial_t z \simeq -(\varepsilon - i\omega_R(x))z - \beta|z|^2z + \kappa\partial_x^2 z + \frac{e^{-i\phi}}{\alpha} p_d. \quad (1)$$

Here the control parameter $\varepsilon = 0$ ensures that all the oscillators are critical, the variable $h = Re(z)$ describes the basilar-membrane displacement, the natural frequency of the oscillator $f_R(x) = \omega_R(x)/(2\pi) = f_0 \exp(-x/d)$ varies with position, x , along the longitudinal axis of the modeled cochlea according to an exponential tonotopic map of parameters $f_0 = 30 \text{ kHz}$ and $d = 2.9 \text{ mm}$, the coefficient β sets the strength of the oscillator's nonlinearity, the coefficient α is real and controls the response magnitude at low frequencies (i.e. stiffness), p_d is the driving pressure at position x , and the parameter ϕ is a phase shift that arises from the change of variable to bring the system's dynamics into normal form. The third term on the right-hand side of Equation 1 was added to the normal form to account for longitudinal coupling between neighboring oscillators, with a coupling strength set by κ . In practice, κ was real, corresponding to dissipative coupling. Note that the real part, A' , of the complex linear impedance $A(\omega) = \tilde{p}_d/(i\omega\tilde{h})$ obeys

$$A' \propto -(\omega_R^2 - \omega^2) \cos(\phi). \quad (2)$$

With our choice for the Fourier transform, $\tilde{z}(\omega) = \int z(t) \exp(-i\omega t) dt$, we see that a critical oscillator pumps energy into the environment, i.e. friction is negative, when driven below its characteristic frequency ($\omega < \omega_R$) but dissipates energy above. For the singular choice $\phi = \pi/2$, the oscillator neither pumps nor dissipates energy in the linear regime. The specific values of parameters α , β , κ , and ϕ are given in the figure legends.

We assumed that the oscillators are immersed in an incompressible and inviscid fluid. The string of oscillators divides the box, of length $L = 19 \text{ mm}$, into two identical compartments, each of height $H = 1 \text{ mm}$. Because of fluid incompressibility, the pressure difference, $p(x, y, t)$, between the two compartments obeys Laplace equation, $\Delta p(x, y, t) = 0$, at any point within the domain corresponding to $L \geq x \geq 0$ and $H \geq y \geq 0$. The Laplace equation was solved using the Green-function formalism [11] to obtain a relation between p_d and h with the following four boundary conditions: $p(0, y, t) = G_{ME} P_{EC}(t)$, where $G_{ME} = 10$ and P_{EC} is the sound pressure in the ear canal, $p(L, y, t) = 0$, $\partial_y p(x, H, t) = 0$, and $\partial_y p(x, 0, t) = -2\rho \partial_t^2 h$. When we applied the simplifying assumption that the pressure field is one-dimensional (Fig. 1), corresponding to $p(x, y, t) = p(x, t)$, we instead solved $(2\rho/H) \partial_t^2 h = \partial_x^2 p$, in which the driving pressure $p_d(x, t)$ equates the bulk pressure $p(x, t)$, with two boundary conditions: $p(0, t) = G_{ME} P_{EC}(t)$, and $p(L, t) = 0$. Together with Equation 1, using in addition $\partial_x z(0) = \partial_x^2 z(0) = \partial_x z(L) = \partial_x^2 z(L) = 0$ if $\kappa \neq 0$, we could then compute numerically $p_d(x, t)$ and $z(x, t)$ in response to a single tone, $P_{EC}(t) = P_0 \sin(2\pi f t)$, of amplitude P_0 and frequency $f = 1 \text{ kHz}$. We discretized space by considering a string of 1000 oscillators and time by using 500 time points per cycle of the stimulus. Equation 1 was integrated in time using the second-order Adams-Bashforth method.

To simplify notations in the following, we call $h(x)$ the phase-locked amplitude of the time-dependent vibration $h(x, t)$ as a function of position and at a fixed stimulus frequency. Experimental data instead correspond to measurements of basilar-membrane vibration at a fixed position and varying sound frequencies. To allow for comparison between simulations and experimental data, the modeled response $h(x)$ to a single tone is plotted as $h(f_R(x_{CF})/f_R(x))$, in which $x_{CF}(f)$ is the position of maximal vibration at frequency f for a low-level stimulus, typically 10 dB. Because local scaling invariance applies near the peak of $h(x)$, we have $h(f_R(x_{CF})/f_R(x)) \simeq h(f/CF(x))$, in which $CF(x)$ is the characteristic frequency at which the response h is maximal at position x .

RESULTS

1D Model with No Coupling and No Energy Pumping

We start with the simplest implementation of a cochlear model based on tonotopically distributed critical oscillators [4]. The model considers a singular implementation of a critical oscillator, corresponding to parameter $\phi = \pi/2$, for which the oscillators cannot provide net energy pumping into the traveling wave (Eq. 2). In addition, the model ignores longitudinal mechanical coupling and, importantly, is solved by assuming 1D hydrodynamics. In this case, the tuning curves display properties that match the generic behavior of a critical oscillator (Fig. 1a): the characteristic frequency (noted CF below) matches the natural frequency, f_R , of the local oscillator, the sensitivity at CF evinces a power-law behavior of exponent $-2/3$ (Fig. 1b) and the bandwidth is inversely related to the sensitivity (Fig. 1c), corresponding to a gain-bandwidth product that does not depend on stimulus level (Fig. 1d). As a consequence, the model can describe the nonlinear level function relating sensitivity at CF to the sound-pressure level as observed in cochlear mechanics, but the tuning curves are then way too sharp at low sound-pressure levels. The model also fails to produce a linear regime of responsiveness at low levels.

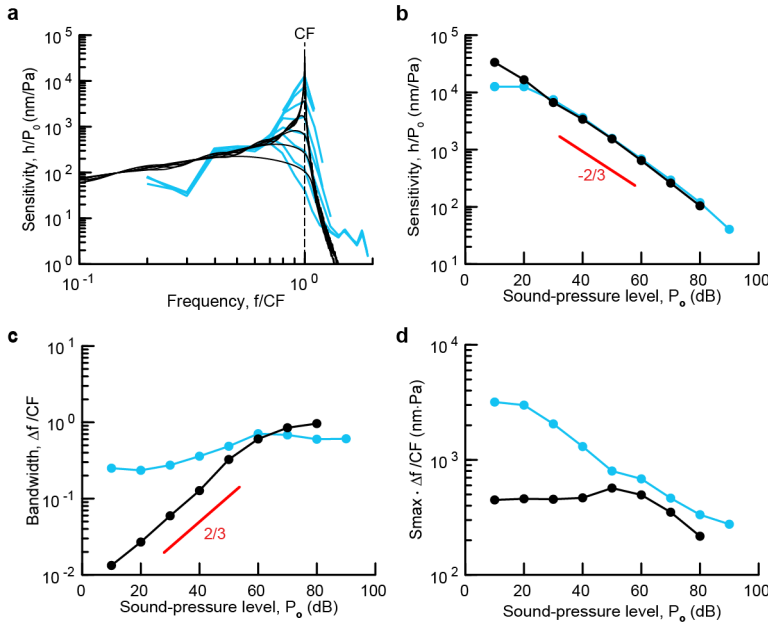


FIGURE 1. Behavior of the 1D cochlear model with no mechanical coupling and no energy pumping (black). (a) Sensitivity, h/P_0 , as a function of the sound frequency, f/CF , normalized by the characteristic frequency (CF; dashed line) at sound-pressure levels, P_0 , that increase from 10 dB (highest sensitivity) to 80 dB (lowest sensitivity) in 10-dB increments. Here, $CF = f_R$, the natural frequency of the local oscillator at the position of measurement. (b) Sensitivity, h/P_0 , as a function of P_0 at CF. (c) Normalized bandwidth, $\Delta f/CF$, of the tuning curves shown in (a) as a function of P_0 . (d) Gain-bandwidth product, $S_{max} \cdot \Delta f/CF$, as a function of P_0 , in which S_{max} is the maximal sensitivity at a given value of P_0 . In (a-d), we show experimental data (cyan) adapted from [12]: the basilar-membrane vibrations at the 10-kHz position of the chinchilla cochlea are used for a qualitative comparison to the model at the 1-kHz position. Parameters: $\alpha = 1.7 \text{ kPa s m}^{-1}$, $\beta = 2 \cdot 10^{18} \text{ m}^{-2} \text{ s}^{-1}$, $\kappa = 0$, and $\phi = \pi/2$.

2D Model with No Coupling and No Energy Pumping

Because the wavevector, q , of the traveling wave diverges at vanishing stimulation levels, there must be a transition between 1D-hydrodynamics when $qH \ll 1$, for which the pressure $p(x, y) \simeq p(x)$ in the fluid is uniform in the transverse direction (y axis), to 2D hydrodynamics when $qH \gg 1$, for which $p(x, y) \simeq p_d(x) e^{-qy}$. This transition affected qualitatively how the pressure, $p_d(x) = p(x, y = 0)$, driving the oscillators (Eq. 1) varies with position. At low sound-pressure levels, the driving pressure decreased monotonically toward zero in 1D but remained nearly constant in 2D (Fig. 2a). In addition, the driving-pressure profile varied more dramatically with sound level in 2D than in 1D. Remarkably, the peak sensitivity at low-to-intermediate stimulus levels was nearly the same in 1D and 2D (Fig. 2b), but tuning was broader, and the bandwidth was less sensitive to stimulus levels in 2D (Fig. 2d). This results in a gain-bandwidth product that decreased with level (Fig. 2e). This finding already demonstrates that cochlear models based on critical oscillators are not doomed to obey the constraint imposed on single oscillators: tuning in the cochlea can be “tall and broad” even if that of its functional units—the critical oscillators—is “tall and thin”.

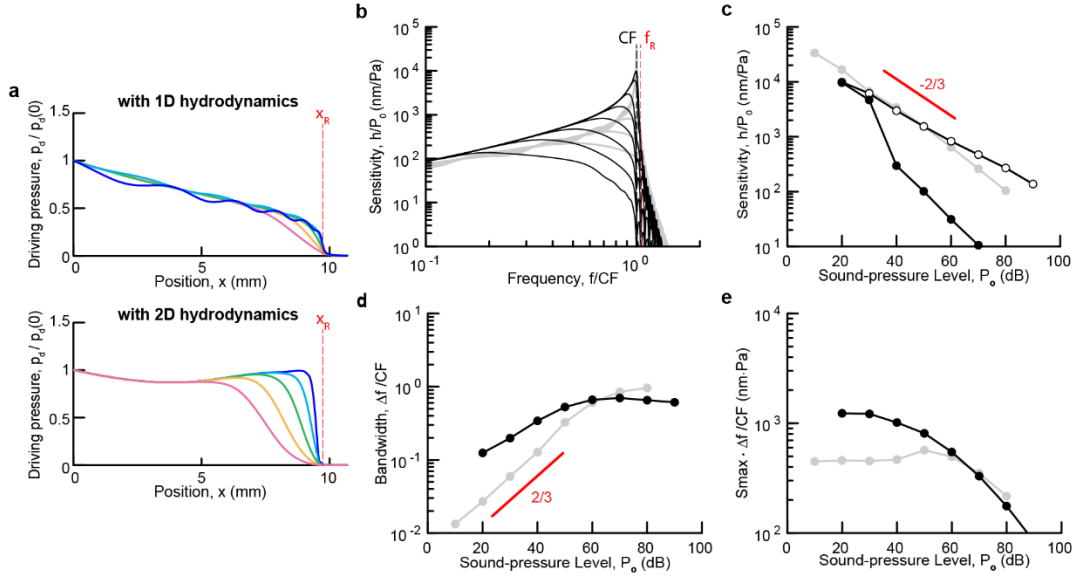


FIGURE 2. Behavior of the 2D cochlear model with no mechanical coupling and no energy pumping. (a) Normalized driving-pressure profiles, $p_d/p_d(x=0)$ at increasing sound-pressure levels, P_0 (blue to magenta; 10 dB increments) for 1D (top) and 2D (bottom) hydrodynamics. The position, x_R , at which the local oscillator is driven at resonance is indicated by dashed lines. (b) Sensitivity, h/P_0 , as a function of the normalized sound frequency, f/CF , at sound-pressure levels, P_0 , that increase from 10 dB (highest sensitivity) to 80 dB (lowest sensitivity) in 10-dB increments. Here, $f_R/CF = 1.05$. (c) Sensitivity, h/P_0 , as a function of P_0 at CF (closed circles) and following the peak sensitivity (open circles). (d) Normalized bandwidth, $\Delta f/CF$, of the tuning curves shown in (b) as a function of P_0 . (e) Gain-bandwidth product, $S_{max} \cdot \Delta f/CF$, as a function of P_0 , in which S_{max} is the maximal sensitivity at a given value of P_0 . In (b-e), the gray curves replicate the results of the 1D model shown in Fig. 1, allowing for a direct comparison with the 2D model (black). Same parameter values as in Fig. 1.

Going from 1D to 2D, however, also resulted in a large increase in the high-frequency slopes of the tuning curves (Fig. 2b). As a consequence, the $-2/3$ power law observed in 1D at CF was lost in 2D: the sensitivity plummets to low values beyond 30 dB (Fig. 2c, closed disks). Remarkably, the power-law behavior that is generic of the underlying critical oscillators could be retrieved (open disks in Fig. 2c) by following the leftward shift in frequency of the sensitivity peak at increasing stimulus levels (Fig. 2a).

2D Model with Dissipative Coupling but No Energy Pumping

We reasoned that mechanical coupling between the oscillators could help shaping the drop in sensitivity beyond the characteristic frequency. We focused on the effects of pure dissipative coupling, i.e. parameter κ was real (Eq. 1 in Methods). Introducing coupling resulted in a linear regime of responsiveness at low sound-pressure levels, and in turn in a drop of sensitivity (Fig. 3a and b). This makes sense because dissipative coupling effectively generates a non-zero value of the control parameter $\varepsilon = \varepsilon_{EFF} \sim -\kappa_r q^2$ (q is the local wavevector) in the normal form (Eq. 1) and thus detunes the oscillators from criticality. We note that a linear regime of responsiveness is also generally observed in experiments (e.g see Fig. 1b, cyan). In addition, coupling yielded tuning curves with a larger apical extent from the position of peak sensitivity than without coupling (Fig. 3a). Correspondingly, coupling resulted in a decrease of the characteristic frequency at position x , which then became noticeably lower than the natural frequency, $f_R(x)$, of the local critical oscillator (Fig. 3a, dashed lines). In addition, coupling also led to broader tuning at low stimulus levels (Fig. 3c). However, due to the linearization of the mechanics at low stimulus levels, the maximal sensitivity computed in response to weak stimuli was now significantly lower (Fig. 3b).

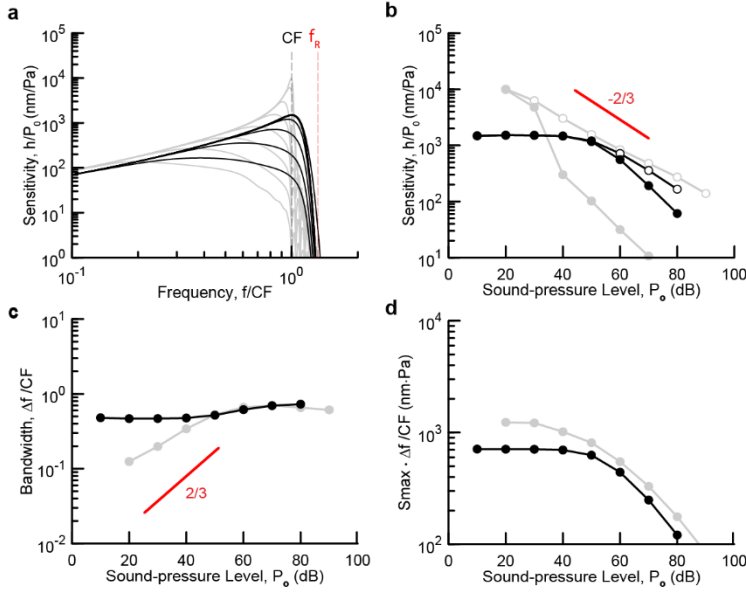


FIGURE 3. Behavior of the 2D cochlear model with dissipative coupling but still no energy pumping. (a) Sensitivity, h/P_0 , as a function of the normalized sound frequency, f/CF , at sound-pressure levels, P_0 , that increase from 10 dB (highest sensitivity) to 80 dB (lowest sensitivity) in 10-dB increments. Here, $f_R/CF = 1.32$. (b) Sensitivity, h/P_0 , as a function of sound-pressure level at CF (closed circles) and following the peak sensitivity (open circles). (c) Normalized bandwidth, $\Delta f/CF$, of the tuning curves shown in (a) as a function of P_0 . (d) Gain-bandwidth product, $S_{max} \cdot \Delta f/CF$, as a function of P_0 , in which S_{max} is the maximal sensitivity at a given value of P_0 . In the linear regime ($P_0 \leq 50$ dB), the gain-bandwidth product is constant. In (b-e), the gray curves replicate the results of the 2D model with no coupling shown in Fig. 2, allowing for a direct comparison with the 2D model with coupling (black). Same parameter values as in Fig. 1, but for $\kappa = 8 \cdot 10^{-7} \text{ m}^2 \text{ s}^{-1}$.

2D Model with Dissipative Coupling and Energy Pumping

We now recall that, because of our singular choice of parameter $\phi = \pi/2$ (Eq. 1), we have so far considered critical oscillators that cannot pump energy into the travelling wave. Here we consider the case where $0 < \phi < \pi/2$, for which the oscillators automatically pump energy into the wave (Eq. 2) as it travels from the base toward the apex. This is because, at each position x , the driving frequency f is smaller than the natural frequency $f_R(x)$ of the local oscillator [2,13]. Energy pumping results in the spatial accumulation of energy gain during wave propagation, evoking broader tuning curves at given maximal sensitivity than in the singular case $\phi = \pi/2$ (Fig. 4a and c). In contrast to 1D or 2D models with no energy pumping ($\phi = \pi/2$; Fig. 4b), energy gain produced prominent peaks in the driving pressure profiles at low sound-pressure levels (Fig. 4d).

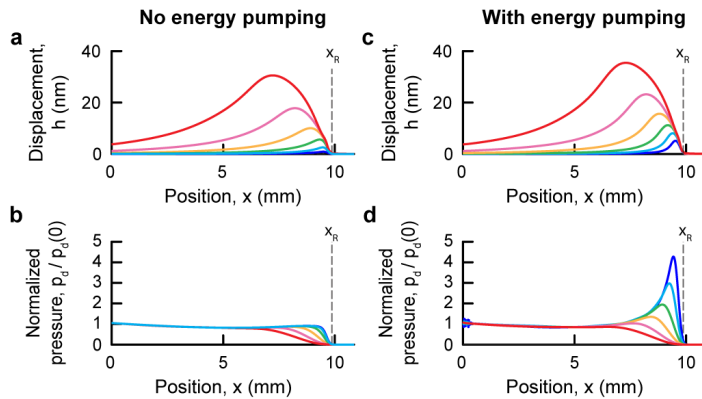


FIGURE 4. 2D model with dissipative coupling, without ($\phi = 0$; a-b) or with ($\phi = \pi/2 - 0.3$; c-d) energy pumping by the critical oscillators into the traveling wave. The displacement profile $h(x)$ ((a) and (c)), and the normalized driving pressure profile $p_d(x)/p_d(0)$ ((b) and (d)) are plotted at various sound-pressure levels, from 30 dB (blue) to 80 dB (red). With energy pumping, the driving-pressure profiles show striking peaks as the wave approaches the characteristic place, x_R , where the local oscillator is driven at resonance. Parameters: $\alpha = 3 \text{ kPa s m}^{-1}$, $\beta = 6 \cdot 10^{18} \text{ m}^{-2} \text{ s}^{-1}$ and $\kappa = \kappa_0 \exp(-x/d)$, with $\kappa_0 = 10^{-5} \text{ m}^2 \text{ s}^{-1}$.

By boosting the driving pressure, energy pumping increased the peak sensitivities to weak stimuli (Figs. 4a and c, blue). The way the shape of the tuning curves varied with the sound-pressure level (Fig. 5a), as well as the weak dependence of the phase profiles on level (Fig. 5b), compared favorably with experiments. This led to level functions of sensitivity (Fig. 5c), bandwidth (Fig. 5e), and gain-bandwidth product (Fig. 5f) with similar functional dependences on P_0 as in experiments. We note that the level functions at CF displayed a compressive behavior that was too strong compared to experiments (Fig. 5c and d, closed circles). Again, as in Figures. 2 and 3, the generic power-law behavior of critical oscillators revealed itself by following the peak sensitivity (Fig. 5c and d, open circles) at intermediate sound-pressure levels. Note that the response of the model was tested at a stimulus frequency of 1 kHz, whereas

basilar-membrane vibrations were measured at the 10-kHz position along the tonotopic axis of the cochlea. Although we can still confront functional dependencies, i.e. the shape of the curves, in the model to those observed in experiments, we refrain here from comparing absolute values of the observables.

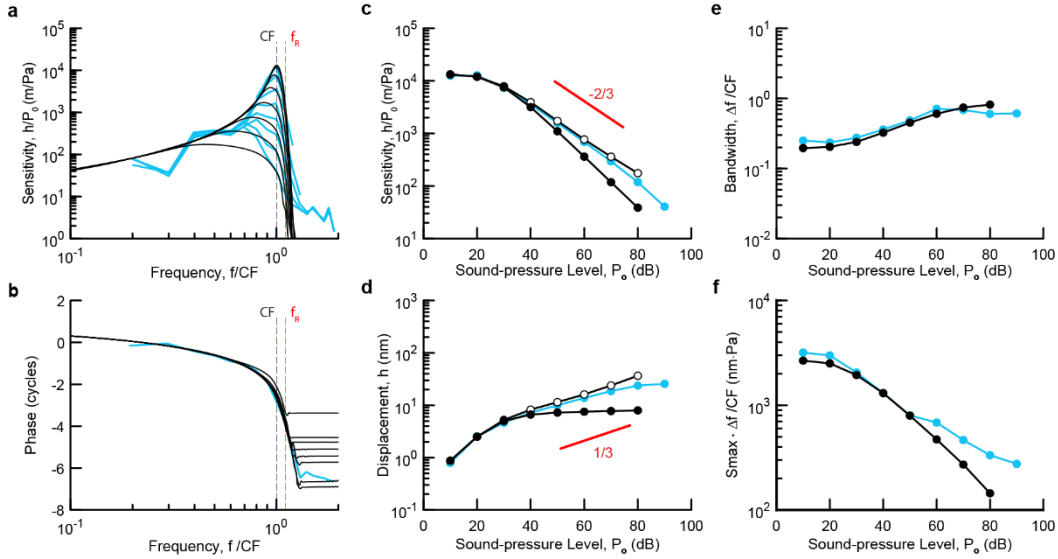


FIGURE 5. Behavior of the 2D cochlear model with dissipative coupling and energy pumping (black). (a) Sensitivity, h/P_0 , as a function of the normalized sound frequency, f/CF , at sound-pressure levels, P_0 , that increase from 10 dB (highest sensitivity) to 80 dB (lowest sensitivity) in 10-dB increments. Here, $f_R/CF = 1.10$. (b) Phase of the displacement relative to that at position $x = 0$ as a function of the normalized frequency, at varying values of P_0 . (c) Sensitivity, h/P_0 , as a function of P_0 at CF (closed circles) and following the peak sensitivity (open circles). (d) Displacement, h , as a function of P_0 at CF (closed circles) and following the peak sensitivity (open circles). (e) Normalized bandwidth, $\Delta f/CF$, of the tuning curves shown in (a) as a function of P_0 . (f) Gain-bandwidth product, $S_{max} \cdot \Delta f/CF$, as a function of P_0 , in which S_{max} is the maximal sensitivity at a given value of P_0 . In (a-f), we show experimental data (cyan) adapted from [12]: the basilar-membrane vibrations at the 10-kHz position of the chinchilla cochlea are used for a qualitative comparison to the model at the 1-kHz position. Parameters: $\alpha = 3 \text{ kPa s m}^{-1}$, $\beta = 6 \cdot 10^{18} \text{ m}^{-2} \text{ s}^{-1}$, $\kappa = \kappa_0 \exp(-x/d)$, with $\kappa_0 = 10^{-5} \text{ m}^2 \text{ s}$, and $\phi = \pi/2 - 0.2$.

CONCLUSION

Our work demonstrates that the interplay between critical oscillators and the traveling wave can produce high sensitivity with relatively broad and level-independent tuning, i.e. “tall and broad” tuning curves (Fig. 5). This finding alleviates a major criticism addressed to criticality as the fundamental basis of cochlear amplification (see e.g. [14,15]). In addition, a power-law fit to the level function that relates the magnitude of the response displacement to the sound-pressure level leads to exponents that are consistently smaller than $1/3$ —the generic value expected from a single critical oscillator driven at its natural frequency, as often observed in experiments. The $1/3$ power law instead betrayed itself when following the peak of sensitivity, not at the characteristic frequency.

Overall, our analysis emphasizes the importance of 2D hydrodynamics, longitudinal coupling between the oscillators and active energy pumping into the wave to shape tuning curves, as recognized earlier. Importantly, the hypothesis of critical oscillation heavily constrains the nonlinear local response of the system, for it is dictated by the normal form (Eq. 1) from first principles. With a small number of adjustable parameters, the model produces, all at once, a set of tuning curves that qualitatively matched key characteristics of cochlear tuning curves and level functions over a broad range of sound-pressure levels.

ACKNOWLEDGEMENTS

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REFERENCES

1. Robles L, Ruggero MA (2001) Mechanics of the Mammalian Cochlea. *Physiol Rev* 81: 1305–1352.
2. Hudspeth AJ, Jülicher F, Martin P (2010) A Critique of the Critical Cochlea: Hopf—a Bifurcation—Is Better Than None. *J Neurophysiol* 104: 1219–1229.
3. Eguíluz VM, Ospeck M, Choe Y, et al. (2000) Essential Nonlinearities in Hearing. *Phys Rev Lett* 84: 5232–5235.
4. Duke T, Jülicher F (2003) Active Traveling Wave in the Cochlea. *Phys Rev Lett* 90: 158101.
5. Strogatz ST (1997) *Nonlinear Dynamics and Chaos*, Reading, MA, Addison-Wesley.
6. Crawford JD (1991) Introduction to bifurcation theory. *Rev Mod Phys* 63: 991–1037.
7. Dewey JB, Shera CA (2023) Bandpass Shape of Distortion-Product Otoacoustic Emission Ratio Functions Reflects Cochlear Frequency Tuning in Normal-Hearing Mice. *J Assoc Res Otolaryngol* 24: 305–324.
8. Versteegh CPC, van der Heijden M (2012) Basilar Membrane Responses to Tones and Tone Complexes: Nonlinear Effects of Stimulus Intensity. *J Assoc Res Otolaryngol* 13: 785–798.
9. Ren T, He W, Kemp D (2016) Reticular lamina and basilar membrane vibrations in living mouse cochlea. *Proc Natl Acad Sci* 113: 9910–9915.
10. Fruth F, Jülicher F, Lindner B (2014) An Active Oscillator Model Describes the Statistics of Spontaneous Otoacoustic Emissions. *Biophys J* 107: 815–824.
11. Allen JB (1977) Two-dimensional cochlear fluid model: New results. *J Acoust Soc Am* 61: 110–119.
12. Ruggero MA, Rich NC, Recio A, et al. (1997) Basilar-membrane responses to tones at the base of the chinchilla cochlea. *J Acoust Soc Am* 101: 2151–2163.
13. Martin P, Hudspeth AJ (2021) Mechanical Frequency Tuning by Sensory Hair Cells, the Receptors and Amplifiers of the Inner Ear. *Annu Rev Condens Matter Phys* 12: 29–49.
14. Lyon RF (2017) *Human and machine hearing: extracting meaning from sound*, Cambridge University Press.
15. Shera CA (2022) Whistling While it Works: Spontaneous Otoacoustic Emissions and the Cochlear Amplifier. *J Assoc Res Otolaryngol* 23: 17–25.

COMMENTS & QUESTIONS

[Online Forum]

Renata Sisto: I read your interesting paper. I found very similar results: the tall and broad activity pattern of the cochlea is explained by an active mechanism and a short wave fluid effect that I named "fluid focusing". The hydrodynamics contribution to the gain produces this decoupling between the gain and the tuning, this last remaining quite unchanged with the stimulus level. In my work (see for example Sisto R, et al. *JASA* (2021) and Sisto R, et al. *JASA* (2023)) I studied the competition between the viscous dissipation and the active power injected in the system. This competition makes the cochlear admittance quite flat in the peak region, as it is observed in the Olson's data.

- (1) In your paper the stabilizing force, proportional, in your model, to the wavevector squared comes from the longitudinal coupling between the nonlinear oscillators. Did you have any chance of studying instead the effect of viscous forces in the fluid? These forces could be a proxy of the viscous damping coming from the interaction with structures of the OcO with a visco-elastic behavior.
- (2) Did you solve your model in time or frequency domain? In principle, you should have solved your nonlinear equations in time domain but you cite the wavenumber. How did you estimate the wavenumber?
- (3) Did you calculate the pressure as in Allen 1977, as the integral over the longitudinal direction of the acceleration multiplied by the 2D pressure Green function?

Authors: We are well aware of your work and we take this opportunity to acknowledge the discussion we had on this topic at MoH2022. It prompted us to take 2D hydrodynamics into account.

- (1) The response of our model is stable even in the absence of mechanical coupling between the oscillators. In this case, stability is ensured by the cubic nonlinear term in the normal form ($\text{Re}(\beta) > 0$), for it provides level-dependent dissipation that controls the response magnitude at all sound-pressure levels. Dissipative coupling introduces a linear regime of responsiveness at low levels, where the response magnitude is then indeed limited by this stabilizing term. We have not yet studied the effects of fluid viscosity.
- (2) Yes, we solved the model in the time domain. We cite the wavevector, noted q , to provide some intuition about (i) the validity of the 1D approximation and (ii) the effect of dissipative coupling on the behavior of the oscillators. For the latter, the argument is that critical oscillators with dissipative coupling are equivalent to uncoupled, but non-critical, oscillators. This is because coupling is expected to effectively produce a negative control parameter proportional to the square of the local wavevector, moving the oscillators away from criticality. This is a handwaving argument based on the WKB approximation.
- (3) Yes, we calculated the pressure using the Green-function formalism as described in Allen, J. JASA (1977).

Bastian Epp: Thanks for the nice manuscript - which I really enjoyed reading! It nicely ties a number of things together that are partially mentioned in the literature. I have hardly any specific comments on the manuscript but would like to bring up some suggestion and questions that might be interesting to think about/put into context.

- (1) I very much enjoyed the statement that you are looking into a "fundamental requirement for a principle of cochlear amplification based on...". This is very nice frame for your arguments. It might be an idea to differentiate your contribution a bit more - having active and nonlinear oscillators in a tonotopic arrangement is not novel (as you are aware of). And maybe some models were (accidentally?) implementing critical oscillators in a less accessible and precise form as you do (normal form). All this might be relevant to also come to the conclusions that "Assuming that critical oscillators are....then ...". It is not impossible that other solutions exist.
- (2) You write in the introduction that compressive growth/power-law is an intrinsic property of such oscillators. Yes - and this is tempting! But it might actually coincidence. And as you state later in the study - things change when going into a system of oscillators rather than single oscillators.
- (3) It might be worth considering that the experimental observations relative to the "gain-bandwidth product" are all derived from individual oscillators. I know that you are regularly facing this argument - but why not be explicit here? Same for "...requirement of sound detection by a critical oscillator". The latter is not really relevant as it seems hard to imagine that the cochlea is modeled by a (single) oscillator.
- (4) "Our work is based on a pioneering..." - it might be worth laying out in which respect Florian's model [10] actually was "pioneering". It had some shortcomings and arbitrary choices as well, and other models (more empirically derived) can account for the same (and more).
- (5) Relative to coupling, I am curious if you have any idea what would happen if you change the coupling coefficient to be complex-valued? The work by Vilfan/Duke, Hero Wit, ... show that coupling changes clustering behaviour (and we looked into this as well - see our MS). Will this critically change the overall findings?
- (6) In the Results, you mention that there exists a "linear regime" in BM I/O measures. Any thoughts if that "really" exists or if it is a consequence of noise?

Authors: Thank you very much for your positive and constructive comments. We respond below point by point.

- (1) You are raising an important point, which can help clarifying the nature of our contribution. We are indeed aware that there are other models based on a tonotopic arrangement of nonlinear oscillators, including in your own work. In our physical description of the cochlea, we start with a principle: all the oscillators are "critical", i.e. operate precisely at a point of an oscillatory instability—a Hopf bifurcation. This premise heavily constrains the nonlinear behavior of the model. This is because any critical oscillator must evince a nonlinear dynamical behavior that is dictated by an effective equation of motion given by the normal form, irrespective of the detailed mechanisms that brings the oscillator at the critical point. Importantly, the dominant nonlinearity is cubic (no quadratic term) and phase invariant. Unlike a passive system, the nonlinearity manifests itself at very low stimulation levels because of cancellation of the linear term near the natural frequency: the system is nonlinear at stimulation levels where a passive system would be linear. There is no need to introduce any phenomenological "knob" to vary the value of some parameter, e.g. damping, as a function of level to fit the nonlinear behavior of the cochlea. The nonlinearity emerges as a mathematical

consequence of criticality; we have no choice. We can in turn evaluate the GENERIC consequences of our principle by integrating the critical oscillators in an otherwise standard traveling-wave model of the cochlea. Because these properties are generic, observing them does not provide support for a particular implementation of criticality; different models will evince the same properties as long as the underlying oscillators are critical. Conversely, it is tempting to conjecture, as you suggest, that any detailed or phenomenological model that successfully describes the cochlear nonlinearity might have found a way to ensure that the underlying oscillators operate near a Hopf bifurcation, even if it is not apparent at the onset.

- (2) As you indicate, and as we know, the cochlea is not a single oscillator and the response at any given position must be shaped by the traveling wave riding on multiple, tonotopically organized oscillators before reaching the characteristic place. This feature is common to all cochlear models: the local response is shaped by nonlocal effects. This is clarified even further by our work. It is precisely the interplay between critical oscillators and the traveling wave that produces “tall and broad” tuning curves and tuning bandwidth that increases only weakly with level. This effect alleviates a fundamental impediment of single critical oscillators, known as “critical slowdown”, for which the weaker the stimulus, the sharper the tuning, and thus the slower the response. In addition, although the local oscillators are here all critical, the compressive nonlinearity that emerges at CF in the model is more compressive than the $1/3$ power law expected from a single critical oscillator driven in isolation. The exact value of the exponent of a power-law fit at CF appears to depend on details is thus not generic. There is thus no *a priori* reason that the compressive nonlinearity in the cochlea be precisely a $1/3$ power law, even if the underlying oscillators individually show such a power law. So, coincidence? It is still remarkable that the cochlea shows a compressive nonlinearity so close to a $1/3$ power law, even if it is not precisely with an exponent of $1/3$ and that the exponent shows some variability between samples. The principle of criticality offers an economical way to account for the nonlinear behavior of the cochlea.
- (3) Contrasting the response of the cochlea at a fixed position to the expected behavior of a single oscillator helps conveying this message: the cochlea cannot be modeled by a single oscillator. Its nonlinear behavior is nevertheless strongly shaped by the properties of the underlying oscillators. From the perspective of physics, it is also striking that the cochlea works as a detector that manages to show both high sensitivity and relatively broad tuning, resulting in relatively fast responsiveness. A single resonator, and a critical oscillator is no exception, does not do that.
- (4) We refer here to models based on a tonotopic organization of critical oscillators using a normal form to describe their dynamic behavior, instead of using specific phenomenological equations of motion (e.g. van der Pol or the oscillator equation inferred by Zweig) or detailed descriptions of the impedance of the organ of Corti (e.g. Meaud and Grosh). Yes, other models can account for the same, but then we would argue that they must contain or mimic the nonlinear behavior afforded by criticality to reproduce the nonlinear behavior of the cochlea. Our contribution, and that of the “pioneers”, is precisely to reveal what is generic of any model operating locally near a Hopf bifurcation. This allows to better distinguish what is generic from what is specific of a given model’s assumptions. Note also that these approaches are not in opposition; they complement each other.
- (5) We have performed simulations using a complex value of the coupling parameter, with nearly equal real and imaginary parts. It does not change our general conclusions but affects slightly the shape of the peak in tuning curves (thus the exponent of a power-law fit to the response function at CF). Elastic coupling also allows vibrations to extend beyond the position where the local oscillator is driven at resonance.
- (6) This is an interesting question. Noise added to the normal form indeed results in a linear regime of responsiveness, effectively moving away the oscillators from criticality. We would argue that both noise and mechanical coupling contribute to the linear regime observed in experiments. There could also be an intrinsic linear regime if the oscillators are not precisely critical. This is OK because the signatures of criticality will remain as long as the control parameter (noted epsilon) remain much smaller than the natural frequency of the oscillator (noted ω_R).

Alessandro Altoè: The model you are proposing looks not too dissimilar to existing theories that do not rely on critical oscillator: you have 2D hydrodynamic coupling and power injection into the traveling wave basal the peak, which have been considered the strictly necessary ingredients to explain the data for a long time (see Kolston 2000 Hear Res in addition to the suggestions of Bastian). And you also have a cubic nonlinearity to explain compression. I wonder where the “criticality” of the oscillators comes into play and to what extent helps explaining the data. In particular, when you add dissipative coupling the oscillators are “critical” only in their mathematical definition, but

perhaps not in practice as they are effectively damped ("detuned from criticality" as you stated). Could you comment on this aspect?

Authors: Thank you for your comments. The specificity of the model, compared to other models, lies in the normal form for the equation of motion of the oscillators. The normal form is NOT a model but the mathematical consequence of a principle: criticality, i.e. operation of the oscillators precisely at a Hopf bifurcation. Its properties are remarkable: the linear term goes to zero when the oscillator is driven at its natural frequency, i.e. the linear response diverges, so that the dominant nonlinearity takes control. We have no choice for the dominant nonlinear term: it is cubic (no quadratic term) and phase invariant. This allows, from first principles, to generate a set of tuning curves all at once, i.e. without having to turn a knob to adjust the value of some parameter of the model with level.

The signature of criticality is the frequency dependent compressive nonlinearity. Criticality explains how to get a compressive nonlinearity over a large range of stimulus magnitudes: by canceling both the elastic and frictional components of the linear response, the nonlinear response extends to low levels of stimulation, i.e. the response is nonlinear at levels where a passive system would be linear.

We find that mechanical coupling effectively detunes the oscillators. However, this effect is weak enough that the signature of criticality—the compressive nonlinearity—still manifests itself over a broad range of levels. Note that the local experimental response of the organ of Corti does not only reflect the impedance of the local oscillator but also how its driving pressure has been shaped by the traveling wave. Our work allows to discuss this interplay and see what properties emerge from it. We find that, even if the emerging nonlinearity at CF deviates slightly from the generic nonlinearity of a critical oscillator driven in isolation, it is still dominated by the generic nonlinear behaviors of the critical oscillators.

Finally, we agree that 2D hydrodynamics, mechanical coupling and energy pumping have already been identified as key features to obtain “tall and broad” tuning curves. As also stated in response to Bastian Epp’s comments, a model based on criticality as underlying principle for the behavior of the local oscillators (in isolation) does not say anything about its detailed implementation, for the oscillators’ nonlinear properties are generic. There are many ways to bring an active dynamical system to a Hopf bifurcation. In return, we conjecture that any detailed or phenomenological model that successfully describes the cochlear nonlinearity might have found a way to ensure that the underlying oscillators operate near a Hopf bifurcation, even if it is not apparent in the formulation of the model.

[Post-Talk Q&A]

Paul Kolston: You showed a clear difference between the 1D and the 2D models, but it is actually 3D because the wavelength contracts radially as well, and the basilar membrane does not span the full width of cochlear compartments. Did you look at what effects having a 3D fluid dynamics finite element model would have on your response?

Author (Henri Ver Hulst): We did not, but that would be an interesting way to extend the model.

Renata Sisto: Things are not very different in 3D. 2D hydrodynamics is sufficient to capture the fluid focusing effect, so the main features of the short wave effect can be captured in 2D.

Paul Kolston: But in 2D, you are assuming that the basilar membrane spans the full width and moves up and down.

Renata Sisto: There are also other modes, and there are higher modes.

Paul Kolston: All right, thank you.

Julien Meaud: Very nice work. I have a question about how critical it is to be critical. When taking the full model with coupling, what happens if you are on the stable side of the bifurcation? Do you recover the same properties or is it fundamentally different?

Author (Henri Ver Hulst): If we are on the stable side of the bifurcation, it means that we need a threshold sound-pressure level to see the compressive nonlinearity that is characteristic of criticality (the system is linear below). At some point, it will kick in, but if you stimulate it with small stimulation, it won’t. So, there will be a threshold stimulation at which you will be starting to see the compressive nonlinearity. *Offline addition: the system is said to*

remain “critical” if the power-law behavior extends over a broad range of stimulus magnitudes. There is no need to operate precisely at the critical point to generate this signature of criticality.

Julien Meaud: Isn't it what you see in the full model anyway? You have a linear growth initially, right?

Author (Henri Ver Hulst): Yes. It means that it can be a bit detuned from criticality. The signature of criticality is really in the $1/3$ power law exponent that is seen over a broad range of sound-pressure levels. In any real system, criticality cannot be observed at all stimulus levels, as it should be in the model, so there are cutoffs. For example here, mechanical coupling produces a low-level cutoff where the critical power law is lost.

Dáibhid Ó Maoiléidigh: At some point, you followed the peak of the response to calculate the compression, but that is not what is done experimentally. So, are you suggesting that somehow in experiments, they accidentally followed the peak? It was not clear to me why you were comparing that to experiments.

Author (Henri Ver Hulst): Thank you for asking the question. Actually, your question is related to the variability of the power law exponent in experiments, and the fact that it is usually lower than $1/3$ if the response is measured at a fixed position. Because the position at which the sensitivity peaks shifts basally with sound level, we expect—this is what I showed at the end of my talk with this very compressive behavior of the displacement curve in our model—that the power law relation will generally change, but that the signature of criticality should remain by following the peak sensitivity. *Offline addition: In experiments, we would argue that the power-law exponent remains close to $1/3$ power law because the shift of the peaks is small.*

Alessandro Altoè: Very nice talk, I have one question. I don't understand why your model is fundamentally different from models that are not based on Hopf bifurcation because you have a traveling wave, power injection before the peak, and 2D hydrodynamics, which are considered to be the essential ingredients to fit the data. What does the Hopf add to it?

Author (Henri Ver Hulst): That's what I think is really amazing about the Hopf, it's not different. We believe that the wide diversity of nonlinear models that actually work in the time domain work precisely because they work near a Hopf bifurcation. The fact that you can have a diversity of models that all work is for us a signature that they all work near a Hopf bifurcation, and therefore they obtain similar level functions as the one that we observe. *Offline addition: We bring a fundamental understanding to the nature of the cochlear nonlinearity, which emerges from the principle of criticality. See a more precise and detailed answer in response to a similar question above (Forum discussion).*