

A Wave Traveling over a Hopf Instability Shapes the Cochlear Tuning Curve

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The *tuning curve* of the cochlea measures how intense an input is required to elicit a given output level as a function of the frequency. It is a fundamental object of auditory theory, for it summarizes how to identify sounds on the basis of the cochlear output. A simple model is presented showing that only two elements are sufficient for establishing the cochlear tuning curve: a broadly tuned traveling wave, moving unidirectionally from high to low frequencies, and a set of mechanosensors poised at the threshold of an oscillatory (Hopf) instability. These two components generate the various frequency-response regimes needed for a cochlear tuning curve with a high slope.

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It is tempting to study sensory transduction systems as one would technological devices, characterizing the output as a function of the input. But the brain has the opposite task of identifying stimuli on the basis of the neural output of the senses. Hence, the relevant description of a sensory system is from the inside out, an *inverse* transfer function telling us what the most probable input was as a function of the observed output [1]. In auditory research this viewpoint was taken early on, in the form of *tuning curves* [2], which track the intensity a pure tone must have in order to elicit a given level of response, as a function of the pure tone's frequency. The response may be the electrical activity in an auditory nerve fiber (a *neural* tuning curve), the speed of motion somewhere in the cochlea (a *mechanical* tuning curve [3–5]), or any of several other observations. If the system were linear, it would be completely characterized by a frequency-dependent gain, and then the backward characterization would be the numerical inverse of the forward one. But the hearing organ is quite nonlinear and such simple relations do not hold. I present in this Letter an analysis of how some important features of the tuning curve arise, and a simple model that reproduces them and explains their physical origin.

The cochlea is an acoustical camera that focuses sound waves onto a sound-sensitive film, separating them along the film according to their frequency of oscillation. As acoustical vibrations enter the cochlea, they set into vibration the *cochlear partition* (CP), which divides the cochlea lengthwise into two chambers. The CP contains the organ of Corti, where the *hair cells*, the sound-sensitive cells, are located; and the *basilar membrane* (BM), the main compliance of the CP, whose stiffness changes lengthwise by 2 orders of magnitude (Fig. 1). But unlike other cameras, the cochlea's lens and its film are *the same*, for the hair cells are responsible for sharpness of frequency selectivity, amplification of the signal, and its detection. If they are damaged, the cochlea is unable to detect sound, frequency selectivity is abolished, and even the size of the mechanical vibrations in the BM is dimin-

ished by orders of magnitude. These multiple roles might be due to the detection technology. In 1948, Gold hypothesized [6] that, in order for the cochlea to provide tuning in the presence of high viscous damping, it would have to have an active process similar to regenerative receivers, in which positive feedback can generate at the same time high amplification and sharp frequency selectivity. This *regenerative hypothesis* predicted (and was bolstered by) the discovery of *spontaneous otoacoustic emissions*, the generation of sound by the cochlea. At the microscopic scale, a model of the transduction channel recently predicted [7] that hair bundles operate near a Hopf bifurcation, the oscillatory instability underlying regeneration, and experiments on single hair cells appear to agree [8,9]. Theoretical considerations provide further evidence: The Hopf bifurcation displays nonlinearities which agree with otherwise bizarre nonlinear characteristics of the ear [7–13]. Gold had already noted that a feedback loop would be required to keep the system tuned to the threshold of instability, as in superregenerative

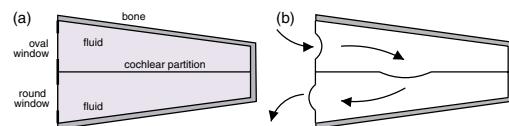


FIG. 1 (color online). (a) The cochlea is a fluid cavity encased in bone, divided into two acoustically distinct chambers by the cochlear partition, which contains the basilar membrane and the active sound-sensing elements, the hair cells. (b) Sound waves enter the cochlea through the oval window (to which the last ossicle, the stapes, is connected). Since the fluid within the cochlea is incompressible and the cochlea is encased in bone, a fluid displacement caused by a displacement of the oval window will be forced to travel along the cochlea until it reaches a region where the compliance of the BM allows it to be displaced vertically. At this point the displacement crosses over into the lower cavity, travels back, displaces the round window, and is dissipated. The location of the crossing over is frequency dependent, with higher frequencies peaking near the windows.

receivers; a molecular implementation of self-tuning was proposed in [11].

But the picture is more complex at the level of the whole cochlea. Tuning curves have a minimum at the frequency for which the system is most sensitive, the center frequency (CF) of the nerve fiber, or the spot on the cochlea being observed. For frequencies up to the CF, the cochlear velocity response is qualitatively similar to a Hopf resonance [10,11]. Sufficiently close to a Hopf bifurcation, systems respond in a universal way [10,11], which is locally symmetric around the resonant frequency. The “tuning curve” of a single Hopf bifurcation [10] is of the form

$$F^2 = R^6 + \Delta\omega^2 R^2, \quad (1)$$

where R is the output, F the input, and $\Delta\omega$ the difference between the input frequency and the resonance. It behaves linearly away from the CF, and approaches a cubic root at the resonance. The cubic root mapping is referred to as a nonlinear compression and is visible in Fig. 2(a) in the *spacing* between adjacent curves. But while Eq. (1) is symmetric in $\Delta\omega$, around the CF there is a universal asymmetry, with an extremely steep right flank. The slope of the right flank is a fundamental measure of auditory acuity, up to 300 dB per octave [14] in lower vertebrates [15] and even greater in mammals. Note the maximal slope of Fig. 2(b) is achieved not where the curves in Fig. 2(a) are steepest, but where they are most packed: They are nonlinearly compressed at the CF and *all higher frequencies*. So above 10 kHz all the curves drop with the same high slope, compressed together in a tight bundle. The high slope in Fig. 2(b) therefore results, not from any sharp tuning in Fig. 2(a) but from the enveloping of the curves in Fig. 2(a) above the CF. The fundamental problem is understanding this enveloping.

This enveloping does not occur at all for a single Hopf oscillator, since the response Eq. (1) is symmetric in $\Delta\omega$ and compressive only near CF. So at the theoretical level a single Hopf instability is insufficient to explain the tuning curves of the cochlea; we need more ingredients. I shall argue that the missing ingredient is the *traveling wave* (TW), the transverse wave observed in the organ of Corti as sound propagates. The cochlea has quite a complex geometry and is made of materials with exponentially varying properties, so it is surprising that impedances are so well matched that the TW propagates at all; but it does, and observation suggests that there virtually are no reflections, so the TW propagates *unidirectionally*. This suggests a simple picture. BM vibrations start at the base of the cochlea, where high frequencies are mapped, and move along the BM, gaining amplitude as the local CF decreases. At some point, the vibrations traverse the locus of their own CF and are strongly amplified and nonlinearly compressed by the active process. As they keep progressing down the BM, they will eventually be strongly damped by the passive portion of the response, but *beyond* the CF locus the vibrations have *already* been

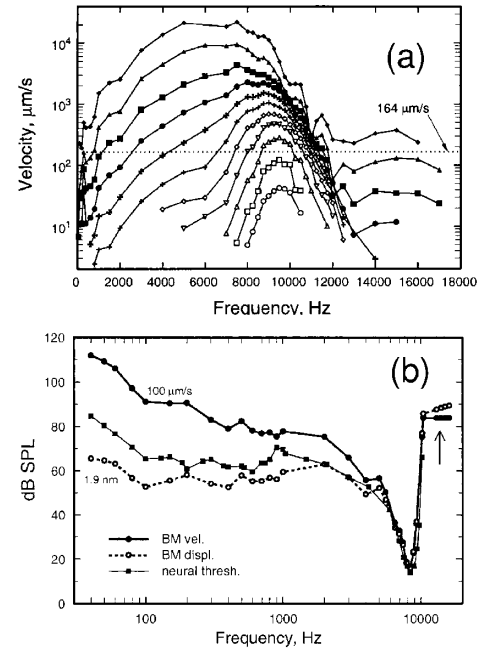


FIG. 2. Cochlear velocimetry data, taken by laser interferometry at a spot in the BM of a chinchilla, from [4]. (a) “Forward” measurement: BM speed vs frequency for varying intensity. Adjacent curves are separated by 10 dB. If the system were linear, these would be equally spaced vertically throughout. (b) “Reverse” measurement: the tuning curves, for various responses: BM velocity, displacement, and threshold of neural activity.

nonlinearly compressed. The unidirectionality of the traveling wave moving through an *array* of Hopf oscillators generates asymmetry between lower and higher frequencies; the direction of propagation from high to low frequencies then dictates that nonlinear saturation occurs to the *right* of the resonance [Fig. 2(a)].

I shall now build a simple model for this picture. Models can be built as continuum mechanics descriptions in the form of a partial differential equation (PDE) for BM motion coupled to active elements [16–19]. Although an advantage of PDE formulations is they relate to mechanically measurable parameters [20], they are hard to solve and so it is hard to determine whether they contain Hopf resonances, or from where some feature such as enveloping arises. I will make a much simpler model, by using *a priori* the unidirectionality of the TW. This allows us to split the wave portion of a wave equation $\partial_x^2 - \partial_t^2 = 0$ into a forward cone $\partial_x - \partial_t = 0$ and a backward equation, and then to completely neglect the latter due to low backscatter. The first order PDE then describes a unidirectional wave, and being eikonal becomes an ordinary differential equation (ODE). We shall model the passive mechanical part of the cochlea as an array of very weakly tuned low-pass filters, organized in a unidirectional series, and the active elements as an array of Hopf oscillators of changing central frequencies, all arranged in parallel [21] and then collected together by a mechanical system identical to the first, as shown in Fig. 3.

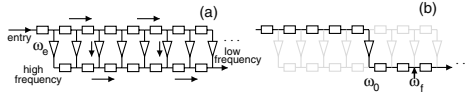


FIG. 3. Scheme of the model. (a) The mechanical equivalent circuit. Rectangles are passive, linear, weakly tuned elements; triangles are active elements poised at the Hopf bifurcation. Sound enters at the top left of the diagram, where high frequencies are mapped, proceeds through the top track of linear elements, filters down through the active elements, and is collected through the bottom track of linear elements. The entire structure is parametrized by local resonant frequency; highest frequency is ω_e at the entry point, and diminishes exponentially as the wave travels. (b) The response at any given point in the BM ω_f is a sum over all paths of the form shown, parametrized by ω_0 , obeying $\omega_0 > \omega_f$: Sound moves left and is not allowed to return.

The gain function of each linear filter is

$$g(\omega, \omega_0) = \frac{2}{(2\frac{\omega^2}{\omega_0^2} - 1)^2 + 1},$$

where ω is the input frequency and ω_0 the local resonant frequency. The overall gain G is obtained by cascading these filters; if they are distributed on an exponential scale (a usual assumption), we get in the limit

$$\log G(\omega, \omega_0) = \int_{\omega_0}^{\omega_e} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i},$$

where ω_e is the entry frequency of the cochlea, e.g., 20 kHz. This integral can be expressed analytically in terms of the second-order polylogarithms Li_2 . The amplitude X at the top portion of the path at a position labeled ω_0 (i.e., CF = ω_0) as a function of an input with amplitude F and frequency ω is $X_{\omega_0}(F, \omega) = FG(\omega, \omega_0)$. The response R of a Hopf oscillator forced by amplitude X at frequency ω given an internal frequency ω_0 is given by the root of Eq. (1) which is analytically solvable. Then the rest of the path to the observation point ω_f achieves a gain of

$$Y_{\omega_0}(\omega, \omega_0) = R \exp \int_{\omega_f}^{\omega_0} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i}.$$

The total response is the sum over all paths (labeled by their ω_0), keeping track of the relative phases of different paths; the phase lags for the linear filter portion and the Hopf elements are additive. The entire model is solvable in quadratures of a complex function.

We first examine the path with highest amplitude. For input frequencies $\omega < \omega_f$, this path will go through the top line and then shift down on the last Hopf oscillator. Thus, all lower frequencies than the CF respond exactly like a single Hopf oscillator composed with a linear filter. For frequencies higher than the CF, the dominant path is the one which goes through the Hopf oscillator whose resonance frequency ω_0 equals that of the input, ω . For

all frequencies *higher* than the CF the response looks approximately similar to the response at the position whose CF equals the input frequency, composed with the bottom part of the path. Thus, to the right of the CF, all curves stay nonlinearly saturated and drop down together, as shown in Fig. 4. Because the response of a Hopf element at $\omega = \omega_0$ is simply a cubic root, we have a particularly simple expression for the shape of the response to the right of the resonance: $Y = F^{1/3} \exp(\Gamma)$ with

$$\Gamma = \left[\int_{\omega_f}^{\omega} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i} + \frac{1}{3} \int_{\omega}^{\omega_e} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i} \right],$$

where we can see explicitly that the response goes as the cubic root of the input times a filter. Note that if the Hopf elements and the TW have coincident resonances, a sharp tuning curve will not obtain, as shown in Fig. 4(a). The active process has to be tuned to higher frequencies than the linear part, as shown in Fig. 4(b) [compare also Fig. 2(a)].

Care must be exercised to take into account all paths, because we need to keep track of relative phases, and the broadening of the Hopf response at higher intensities means that the number of paths that contribute changes with intensity. If phases are neglected, the width over ω_0 for which the contribution is significant cancels the nonlinear compression because it increases as a $\frac{2}{3}$ power law [10]. To obtain a lowest-order approximation to a summation involving changing phases, we remember the classic ‘‘Cornu’s spiral’’ construction for diffraction through a slit: If the paths have rapidly varying phases, then only

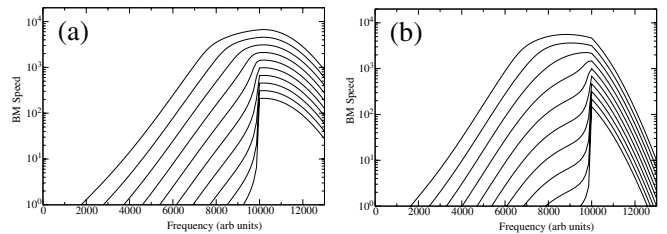


FIG. 4. Maximal path contribution to the final result. In (a) the linear TW response and the Hopf active elements are ‘‘aligned,’’ meaning their resonant frequencies coincide; in (b) they are displaced by a factor of 1.3. CF at the observation point is 1000 Hz. Please note that the response divides into two clear regimes. For $\omega < \omega_f$, to the left of the CF, it looks similar to the Hopf resonance described in [10,11]. To the right of the CF, when $\omega > \omega_f$, all curves are nonlinearly compressed through a cubic-root law. Evidently (a) may not have a sharp tuning curve, for even though the high-frequency regime is nonlinearly compressed, it impinges on the maximum with zero slope. (b) has a sharp tuning curve. The implication is that the Hopf elements *need* to be tuned at higher frequencies than the maximum of the passive TW component. The discontinuity in slope and the high left-flank slope occur because the model does not have a longitudinal BM stiffness, this is only the main path, and the Hopf bifurcation is exactly poised.

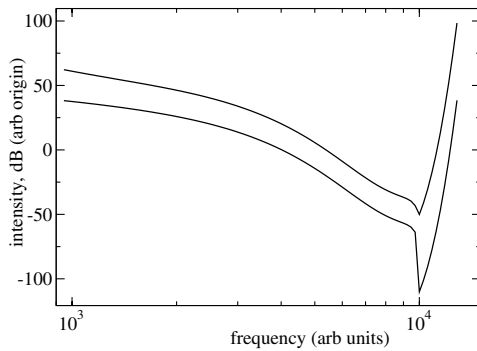


FIG. 5. Tuning curves obtained by intersecting Fig. 4(b) with speed levels 100 and 1000.

the maxima and the stationary points of phases can contribute. Because the arguments presented here do not fix the phase behavior of the filter cascade (which could be arbitrary), we cannot compute this object explicitly; thus we shall stay with the maximal path contribution only.

The tuning curve of the model is the inverse of the function computed above, and is shown in Fig. 5. The slope of this curve can be intuitively understood as how many lines of the response graph we do intersect as we move horizontally per unit of frequency change. This number is the slope of the lines in the graph times how many lines we do intersect as we move *vertically*: the more vertically bunched the lines are, the more bunched they are horizontally. Thus, the immediate effect of the nonlinear saturation is to triple [21] the number of decibels per octave supplied by the asymptotic front of the traveling wave on the steep right-hand flank of the tuning curve. Furthermore, the bunching and enveloping on the lines on the right-hand side do not just result in a steep right side flank, but also in some invariance of the tuning curve to the level of response required.

We have presented a simple picture of the physical origin of the asymmetry of the tuning curve, in terms of a unidirectional traveling wave moving over a field of Hopf elements. We drew additional conclusions related to the need to tune the active elements at higher frequencies than the passive mechanical components, and to have rapid phase gradients to prevent summation over many w_0 . Limitations to the accuracy with which the system is poised at the oscillatory threshold cause a linear regime for low amplitudes [10,11] agreeing with the behavior below the dashed line in Fig. 2(a), while saturation of the active process could be used to model the top of that figure [22]; we have, however, forsaken the urge to fit every nook of Fig. 2 in favor of a qualitative approach with the least freedom possible. Hopefully this picture may guide us in interpreting more detailed and complex models.

I owe to Victor Martinez-Eguiluz the observation that saturation in Fig. 2 agrees with the direction of the TW. I am deeply indebted to Jim Hudspeth, Boris Shraiman, Oreste Piro, Mario Ruggero, and Bruce Knight for many discussions on tuning curves, and to Yong Choe, Mark Ospeck, Pascal Martin, Dolores Bozovic, and Frank Jülicher for discussions on the role of Hopf bifurcations in auditory detection.

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 - [21] If the elements are put even partly in series, stronger nonlinear compression ensues, because the iteration of a cubic root leads to a fixed point. In principle, even infinitely steep tuning curves could ensue. Such a model is probably more adequate but it is a lot harder to treat analytically and will be examined elsewhere.
 - [22] Also from this model follows the known asymmetry between the two cubic combination tones (i.e., when $f_1 < f_2$ the combination tone $2f_1 - f_2$ is stronger than $2f_2 - f_1$).