The Cochlear Tuning Curve

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Abstract

The tuning curve of the cochlea measures how large 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 infer what a sound was 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 suffice to generate the various frequency-response regimes which are needed for a cochlear tuning curve with a high slope.

Our senses are understood to very different degrees. For example, a fair amount is known and understood about visual transduction: the eye is like a camera, with a lens that focuses light onto the sensitive film of the retina. The lens is solely responsible for the sharpness of imaging, while the rod cells of the retina are solely responsible for the high sensitivity of the eye; both have attained fundamental physical limits, diffraction-limited focusing and single-photon sensitivity. Furthermore we know the molecular players involved in phototransduction and quite a bit about how these players play together to generate a neural response to a single photon. By contrast, we know many facts about the ear, but we do not yet fully understand how to put them together into a coherent picture. We do know that the ear is nothing like a microphone; if anything, we could say that the ear is like a camera, with a “lens” that sharply focuses sound (according to frequency) onto a sound-sensitive film. We know that the sharpness and sensitivity of this process have achieved fundamental physical limitations. But the intriguing twist of the plot is that, in the cochlea, the lens and the film are one and the same: the hair cells are both the active sound-sensing elements, as well as the source of the active mechanical feedback of sound that results in the cochlea’s frequency selectivity. If the active mechanisms in the hair cells are turned off, the cochlea can neither sharply “focus” sound nor amplify faint sounds. This dual role of the hair cells as both lens and film has made it difficult to unravel various pieces of the puzzle. Furthermore, the picture is similarly difficult at the molecular level: the transduction channels which are ultimately responsible for generating an electrical
impulse in response to sound have long eluded identification. First because they are so few, about tens per hair cell, as opposed to $>10^9$ rhodopsin molecules per rod cell. Secondly because the high-frequency nature of the detection has thrust upon these channels dual roles which preclude their direct interaction with other molecular players which might help in identifying them. Five different molecules mediate the information cascade between photon detection and the closing of ion channels that generates an electrical impulse; there is no evidence yet of any intermediates in hair cells, where the (still hypothetical) tip link-gating channel complex seems to have simultaneous roles in sound detection, electrical impulse generation and mechanical feedback.

The dual roles of the cochlea in amplification and frequency tuning appear to be two aspects of the same phenomenon. In 1948, T. Gold hypothesized [1] that in order for the cochlea to provide tuning in view of high viscous damping, it would have to follow a mechanism similar to regenerative receivers, where positive feedback can generate at the same time high amplification and sharp frequency selectivity. This regenerative hypothesis lay dormant for many years, due to what appeared as evidence against it. It slowly surfaced because one of its fundamental implications, that misadjusted feedback would result in sound emission, is to date the only explanation we have for spontaneous otoacoustic emissions, the universally occurring phenomenon of sound being emitted by the cochlea. A second line of microscopic experimental evidence for Gold’s hypothesis has been slowly surfacing recently. It was noted in [2], based on modeling of the transduction channel, that hair bundles appear to be operating near a Hopf bifurcation, the oscillatory instability behind regeneration, and experimental confirmation soon followed [3, 8]. Finally, purely theoretical considerations provide backing circumstantial evidence: the Hopf bifurcation possesses intrinsic essential nonlinear characteristics which agree with otherwise unexplainable nonlinear characteristics of the ear [4, 9]. It had already been noted by Gold that a feedback loop to keep the system tuned to the threshold of instability would be required, in the manner of superregenerative receivers; a plausible molecular implementation of self-tuning has been shown in [5]; though the exact players are debatable, the mechanism is generic.

The problem is that the Hopf instability alone does not seem to explain, by itself, the mechanical and neural tuning curves of the cochlea. A fundamental property of sensory systems is that they are “built” to be “used” by the brain; i.e., the most illuminating characterization of such systems is not the “forward” transfer responses which tell us how the system reacts to stimuli, but the “reverse” characteristics, in which we try to know what stimulus caused a given reaction. This is the viewpoint of the brain, which tries to infer what is out there in the world based on the information coming out of the sensory systems; an extremely clear example in the H1 neuron of the fly is given in [10], as well as the theoretical infrastructure to relate these ideas to Bayesian approaches and info theory. In the case of hearing, this viewpoint was taken very early on; because of the inaccessibility of the cochlea, first characterizations were of the neural output present in the auditory nerve rather than mechanical responses, and took the following form. A single frequency is presented, and its intensity is varied until the output reaches a specified level—be it spikes per second in the case of the nerve, or a given amplitude of vibration in the basilar membrane. As the frequency is swept, one reconstructs a curve telling how much input is necessary to elicit a given response as a function of the frequency, which is called the tuning curve [2]; in the case of auditory nerve
measurements, this is called the neural tuning curve. The shape of these curve is close to universal: the tuning curve has one minimum, one specific frequency for which the intensity required to elicit a given response is minimal, the central frequency (CF) of the nerve fiber or spot on the cochlea being observed. Around that minimum there is marked and universal asymmetry: a very shallow left flank, and an extremely steep right flank, and then saturation. The slope of the right flank is a fundamental measure of auditory acuity, reaching the 120 dB per octave in mammals, and a non-negligible 90-100 dB/oct in lower vertebrates such as *Gekko gekko*. Contrarily, sufficiently close to a Hopf bifurcation systems respond in a universal way [4, 5], which is symmetric around the resonant frequency, at least locally. In [4] a closed form solution shows the “tuning curve” of a single Hopf bifurcation to be locally symmetric; this is computed to be $F^2 = R^6 + \Delta \omega^2 R^2$ which is (a) symmetric, and (b) shallowly increasing near the critical frequency. Thus Gold’s hypothesis *by itself* does not fully generate a theory of cochlear function.

![Generic shape of a tuning curve.](image1)

![Cochlear velocimetry data, and its tuning curve, from [11].](image2)

Figure 1: Generic shape of a tuning curve.

Figure 2: Cochlear velocimetry data, and its tuning curve, from [11].

I shall now supply the missing ingredient, the *traveling wave* (TW). In order to understand tuning curves, one should study the forward quantitative measurements carefully. Careful examination of cochlear velocimetry data, for instance from [11, 12], show the following. The response curves to the left of the resonance look quite similar to a
Hopf response. However, the Hopf bifurcation is nonlinearly compressive only in the vicinity of the resonance frequency, while the cochlear velocimetry data is nonlinearly compressive at the resonant frequency and all higher frequencies. The amplitudes at higher frequencies fall extremely fast, but the responses are still bunched together at close to $\frac{1}{3}$ dB per dB. Since the tuning curve is obtained by intersecting the response curves horizontally and checking which amplitude intersects the horizontal line at a given frequency, we get immediate insight: the steepness of the right flank is not generated as a result of high order poles or any such filtering: it is the result of the nonlinear compression acting only on frequencies greater than or equal to the CF. This suggests that as sound travels the cochlea, entering at the base, where high frequencies are mapped, it propagates until reaching the location for its frequency, where it is nonlinearly amplified. As it continues into the cochlea its amplitude diminishes rapidly, but it has already been nonlinearly saturated. The unidirectionality of the traveling wave, together with the fact we have an array of Hopf oscillators rather than only one, give us a strong asymmetry between lower and higher frequencies; the fact that the traveling wave propagates from high to low frequencies then dictates that nonlinear saturation occurs in Fig 2 on the right of the resonance.

Figure 3: Scheme of the model. (a) The mechanical equivalent circuit. Rectangles are passive, linear, weakly tuned elements, while the triangles represent active elements poised at the Hopf bifurcation. Sound enters through 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 may be parametrized by local resonant frequency; highest frequency is $\omega_e$ at the entry point, and diminishes exponentially as the wave travels. (b) The response at any given point in the basilar membrane $\omega_f$ is a sum over all paths of the form shown, which are parametrized by $\omega_0$, and where $\omega_0 > \omega_f$: sound moves unidirectionally through this structure and is not allowed to return back.

Are these two elements, Hopf plus traveling wave, enough to explain the tuning curve? Let us build a simple model of the mechanics of the cochlea. Let’s say that the passive
mechanical part of the cochlea is set up as a series of very weakly tuned low pass filters, organized in a unidirectional series. Let us use a $Q = 1$ Lorentzian response for simplicity. Let us say that there are an array of Hopf oscillators, whose central frequencies track the central frequencies of the passive part of the system, all arranged in parallel, and then collected together by a mechanical system identical to the first. (This arrangement has been selected for analytical tractability; other more complex topologies show similar results). The response is a sum over all paths through this graph; since the top and lower portion of the paths are linear they can be explicitly summed.

In what follows, I shall use specific functions chosen to (a) be reasonable and (b) be analytically tractable. The qualitative features of the model do not depend in the least upon this choice. Linear filtering shall be achieved through a local gain function where $\omega$ is the input frequency and $\omega_0$ the local resonant frequency

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

which is equivalent to asserting that locally the filtering being done has a $Q$ of 1 at $1/\sqrt{2}$ of the local resonant frequency. Then the overall gain $G$ is obtained by cascading these filters; we replace the product of the gains with an exponential of the sum of the logarithms of the gains, and replace the sum by an integral, to get

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

if we think the filters are distributed on an exponential scale (usual model for the middle portion of the basilar membrane, since there is an approximately exponential stiffness); here $\omega_e$ is the entry frequency of the cochlea, e.g., 20 kHz. Thus, the amplitude $X$ at the top portion of the path at a position labelled $\omega_0$ (i.e., $\text{CF} = \omega_0$) as a result of an input with amplitude $F$ and frequency $\omega$ is

$$X_{\omega_0}(F, \omega) = FG(\omega, \omega_0)$$

and since the integrals can be computed analytically there is a closed form expression for $X$; the expression involves second-order polylogs $Li_2$ and is not particularly illuminating, so we skip it here. Please notice that the form of $g$ is arranged so that $G$ has indeed a maximum at $\omega_0$ because $\log g(\omega, \omega_0)$ changes sign at $\omega_0$. The response $R$ of a Hopf oscillator forced by amplitude $X$ at frequency $\omega$ given an internal frequency $\omega_0$ is given by the root of the cubic

$$X^2 = R^6 + (\omega - \omega_0)^2 R^2$$

which is annoyingly solvable: $A^3 + dA = B \rightarrow$

$$A = \frac{3\sqrt{27B + \sqrt{729B^2 + 108d^5}}}{3^{2/3}} = \frac{2^{1/3}d}{3\sqrt{27B + \sqrt{729B^2 + 108d^5}}}$$
Then the rest of the path to the observation point $\omega_f$ achieves a gain of

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

and so the entire contribution of any one path can be analytically computed. The final response shall be the sum over all paths through intermediate points $\omega_0$, which obviously depends upon how we weight the density of local $\omega_0$s. For simplicity, I shall keep compatibility with the reasoning above and keep the $\omega_0$ exponentially distributed, thus the density will equal $d \log w_0 = d\omega_0/w_0$. In addition, we need to keep track of the relative phases of different paths; the phase lag for both the linear filter portion and the Hopf elements are all computable in closed form. Therefore the entire model is

![Figure 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 observation point is 1000 Hz. Please note that the response divides into two clear regimes: $\omega < \omega_f$, to the left of the CF, looks like the Hopf resonance described in [4, 5], while 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.](image)

A first, qualitative examination of this model can be achieved by remarking that the response is going to be dominated by a single path through this graph, the one with the highest amplitude. For frequencies $\omega$ lower than the CF $\omega_f$ this path will go through the top line and then shift down on the last Hopf oscillator, the one corresponding to the current position. Thus all lower frequencies than the CF respond exactly like a single Hopf oscillator composed with a weak linear filter. For frequencies higher than the CF, to lowest order the dominant path is the one which goes through the Hopf oscillator whose resonance frequency $\omega_0$ equals that of the input, $\omega$; thus the response, for all
frequencies higher than the CF, look approximately like the response at the position whose CF equals the input frequency, composed with the bottom part of the path, which is a linear attenuation. Thus, to the right of the CF, all curves stay nonlinearly saturated and just drop down together. The plot is on Figure 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:

$$Y = F^{1/3} \exp \left[ \int_{\omega_f}^{\omega} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i} + \frac{1}{3} \int_{\omega}^{w_*} \log g(\omega, \omega_i) \frac{d\omega_i}{\omega_i} \right]$$

where we can see explicitly that the response goes like the cubic root of the input times a filter. While the formula looks right on paper, a plot of the response quickly shows not all is well: if the Hopf elements and the TW have coincident resonances a sharp tuning curve does not obtain, see Figure 4b.

![Figure 5. Tuning curves obtained by intersecting Fig 4b with speed levels 100 and 1000.](image)

This picture changes if we take into account all paths, because the broadening of the Hopf response at higher intensities means that the number of paths that contribute significantly to the final result changes with intensity. However, we also need to keep track of relative phases. If phases are not taken into account at all we obtain a “wrong” result: because the width over $\omega_0$ for which the contribution is significant increases as a $2^{1/3}$ power law, the nonlinear compression would be utterly obliterated in the high-frequency regime. There is a trivial solution to this problem (following the classic “Cornu spiral” construction): if the paths have rapidly varying phases, then only the maxima and the stationary points of phases can contribute. For simplicity we shall stay with the maximal path contribution only.

The tuning curve is the inverse of the function computed above with respect to input and output amplitudes. The slope of this curve can be intuitively understood as how many lines of the response graph do we intersect as we move horizontally per unit of frequency change. This number clearly relates to what the slope of the lines is in the graph, times how many lines do we 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 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: as we change our horizontal line up and down, the tuning curve does not substantially change shape.

At this point a detailed discussion of the relationship between this (trivial) model and various well established models in the literature, like Chadwick or Mammano and Nobile, should ensue, but I feel it’s better left for a later occasion. Also from this model one can verify the asymmetry between the two cubic combination tones (i.e., when \( f_1 > f_2 \) the combination tone \( 2f_1 - f_2 \) is stronger than \( 2f_2 - f_1 \)). Etc.

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