WAVE PROPAGATION BY CRITICAL OSCILLATORS

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Waves propagating along the basilar membrane are amplified by an active nonlinear process. The general aspects of the active amplification of periodic signals can be discussed in the framework of critical oscillators. Here, we show how the concepts of a traveling wave and of critical oscillators can be combined to describe the main features of nonlinear wave propagation, energy flow and reflections in the cochlea.

1 Introduction

The cochlea acts as a spatial frequency analyzer which exhibits resonant vibrations at characteristic frequencies that vary with position along the basilar membrane (BM) [1]. These vibrations are monitored by sensory hair cells [2]. This feature of the cochlea can be represented by a transmission line of resonant elements which naturally accounts for the propagation of waves along the basilar membrane which reach a peak amplitude near a position where the characteristic frequency matches the stimulus frequency [3,4,5,6,7]. Active processes in the cochlea play a role in the amplification of weak signals [8,2]. The signatures of these active processes are an increased sharpness of frequency filtering, the occurrence of oto-acoustic emissions and nonlinearities [9,10,11,12,13]. All these signatures are physiologically vulnerable, pointing to an origin of these phenomena in dynamic cellular processes. The compressive nonlinear nature of the active process permits the ear to operate over a large dynamic range of 120 dB, by amplifying weak signals more than strong ones. This nonlinear response of the basilar membrane is thus relevant even for weak stimuli and is connected with interference effects between different frequencies in complex sounds, leading to the generation of distortion products and combination tones [14].

The active nature of the cochlear response has been addressed in previous theoretical work [15,16,17,18,19]. The nonlinear amplification of weak periodic stimuli by active processes can be described generically in the framework of critical oscillators [20,21]. A resonant system generally operates linearly at small stimulus intensities. If a nonlinear response is required in order to amplify weak signals, the system must approach an oscillating instability. Active dynamic systems often exhibit such instabilities or Hopf bifurcations where spontaneous oscillations appear. In the vicinity of this critical point, compressive nonlinearities become important and are unavoidable. Their properties are generic, i.e. they appear robustly in a way which is independent of many details of the molecular and cellular processes which underly the oscillating instability. Operation of the system at the oscillating side of the instability, however, compromises signal amplification and detection since spontaneous oscillatory behaviors of the active system interfere with the incoming signal. The ideal point of operation is therefore the critical point itself, where weak signals are most strongly amplified while strong stimuli only induce a behavior which resembles a passive response. The observation of active nonlinear processes even for weak stimulus amplitudes thus indicates that the cochlea contains dynamical systems which operate in the vicinity of a Hopf bifurcation [22,20,21]. Self-regulation mechanisms could play a role to ensure operation of oscillators sufficiently close to the critical point that nonlinearities can become beneficial for the detection of weak signals [20].

The strength of the concept of critical oscillators is that it can capture many important features of hearing. In particular the nonlinear response, the generation of distortion products and the active process are taken into account in a concise and general way which is robust and applicable despite the complexity and the diversity of underlying cellular processes. It thus provides a physical scenario which can clarify general principles that underly signal amplification. In order to discuss the cochlear response and the associated wave propagation, it is therefore useful to combine the concept of critical oscillators with the wave physics in the cochlea. This leads to a simplified description of cochlear vibrations as nonlinear waves which result from the coupling of critical oscillators with varying characteristic frequencies as a function of position and which are coupled hydrodynamically. Here, we briefly outline the features of these nonlinear waves and argue that this framework is ideally suited to discuss nonlinear effects, energy flow and pumping of these waves as well as nonlinear wave reflections in the cochlea.

2 Cochlear waves

The basic physics of cochlear waves may be described most succinctly by a one-dimensional model [3,4,5,6,7]. The BM separates the cochlear duct into two channels which are connected at the apex by a small aperture, the helicotrema. A sound stimulus impinging on the oval window, at the base of the cochlea, causes changes in the pressures $P_1(x,t)$ and $P_2(x,t)$ in both channels. Here t is the time and x is the position along the cochlea, with the oval window at $x = 0$ and the helicotrema at $x = L$. The pressure gradients induce longitudinal currents

$J_1(x,t)$ and $J_2(x,t)$, which flow in opposite directions in the two channels. We define the relative current $j \equiv J_1 - J_2$ and the pressure difference $p \equiv P_1 - P_2$. The balance of pressure gradients and inertial forces in the fluid together with the fluid incompressibility and viscosity leads to a relation for the BM motion and the pressure gradients

$$2\rho b \partial_t^2 h + \eta \partial_t h = \partial_x \left[b l \partial_x p \right] \quad . \tag{1}$$

Here, $h(x,t)$ is the height profile of the BM, characterizing local displacements; b and l denote the width and height of the cochlear channels, respectively. The damping coefficient η is proportional to the fluid viscosity. The pressure difference p acts to deform the BM. If the response is passive (e.g. in the dead cochlea), close to the basal end, it takes the simple form $p = Kh$.

3 Critical oscillators

In the active cochlea, the passive response is amplified by a force-generating system. This system comprises a set of mechanical oscillators which are supported on the BM, and which are positioned in such a way that they can drive its motion. The characteristic frequency $\omega_r(x)$ of the oscillators is a function of position along the membrane. We assume here, that active elements do not oscillate spontaneously but that they operate in the vicinity of a critical point. If the BM contains such critical oscillators, its deformation h in response to pressure differences across the membrane p has characteristic properties as a function of frequency and amplitude, and nonlinear amplification occurs. This can be discussed most easily for a single, isolated oscillator. Its characteristic response to a periodic stimulus pressure $p(t) = \tilde{p} e^{-i\omega t} + c.c.$ at frequency ω with Fourier amplitude $\tilde{p}$ can be expressed in a general form as [20]

$$\tilde{p} = A(\omega)\tilde{h} + B|\tilde{h}|^2 \tilde{h} + O(\tilde{h}^5) \quad . \tag{2}$$

Here, $\tilde{h}$ is the Fourier amplitude of the resulting periodic vibration $h(x,t) \simeq \tilde{h}(x) e^{-i\omega t} + c.c.$ and A and B are complex coefficients.

This expression follows from a systematic expansion in the oscillation amplitude $\tilde{h}$ (comparable to a Landau expansion of the free energy of thermodynamic systems near a critical point) and is valid near a Hopf bifurcation. Further away from the bifurcation on the non-oscillating side, the nonlinearities become unimportant while away from the bifurcation on the oscillating side higher order terms can become relevant. Proximity to an oscillatory instability thus automatically provides for nonlinearities which are inherently linked to the active process and thus are not related to the passive nonlinearities properties of the material which appear for large deformations. Note, that for critical oscillators, the dominant nonlinearity is cubic.

The linear response function $A(\omega) = A'(\omega) + iA''(\omega)$ is a complex coefficient with real part A' and imaginary part A''. For a critical oscillator, it vanishes at the characteristic frequency, $A(\omega_r) = 0$. Thus, at this particular frequency, the response becomes essentially nonlinear for small amplitudes. The shape of the resonance, for nearby frequencies, is described by $A(\omega) \simeq \alpha(\omega - \omega_r)$ close to the characteristic frequency ω_r, where α is a complex number. Furthermore, by its definition as a linear response function, A obeys $A(\omega) = A^*(-\omega)$. As a consequence, $A'(0) = K$ is the passive stiffness of the system and $A''(0) = 0$. The real and imaginary parts of $A(\omega)$ thus have the general form as displayed in Fig. 1.

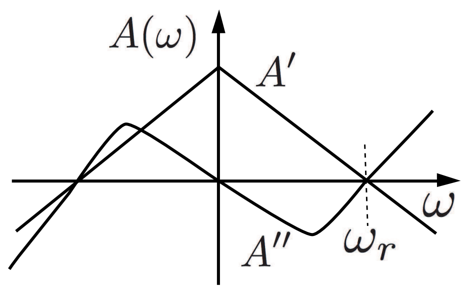

Figure 1. Schematic representation of the real and imaginary parts of the linear response function $A(\omega) = A' + iA''$ of a critical oscillator with frequency ω_r.

4 Active nonlinear traveling waves

We describe the basilar membrane by Eq. (1) using Eq. (2) for the local mechanical response properties. Motivated by the observed variation of the characteristic frequency along the BM, we assume that the position dependence of characteristic frequencies is given by $\omega_r(x) = \omega_0 e^{-x/d}$.We thus obtain a nonlinear wave equation for the BM deformation. In frequency representation, it reads [19]

$$-2\rho b\omega^2\tilde{h} - i\omega\eta\tilde{h} = \partial_x \left[bl\partial_x \left(A(x,\omega)\tilde{h} + B|\tilde{h}|^2\tilde{h} \right) \right] \quad . \tag{3}$$

The complex solutions of this equation $\tilde{h}(x) = H(x)e^{i\phi(x)}$ describe the amplitude H and the phase ϕ of the BM displacement elicited by a periodic stimulus with incoming sound pressure $p(x = 0, t) = \tilde{p}(0)e^{i\omega t}$. For simplicity, we take the coefficient B, describing the nonlinearity close to resonance, to be a purely imaginary constant, $B = i\beta$. This simple choice ensures that Eq. (2) has no spontaneously oscillating solution for $\tilde{p} = 0$. Examples for solutions to the wave equation are displayed in Fig. 2

The wave equation Eq. (3) describes traveling waves which are linear for small vibration amplitudes $\tilde{h}$ at locations far from the resonance point x_r where $\omega = \omega_r(x_r)$. As the wave enters at $x = 0$, it encounters oscillators which locally have a high characteristic frequency as compared to the wave frequency $\omega < \omega_r$. Consequently, the imaginary part $A''(\omega) < 0$ and energy is pumped into the wave by the active process (see Fig. 1). This pumping of the wave can cancel or even overcome the effects of viscous friction and thus enhance wave propagation and energy flow, but is not related to any unstable behavior of the wave.

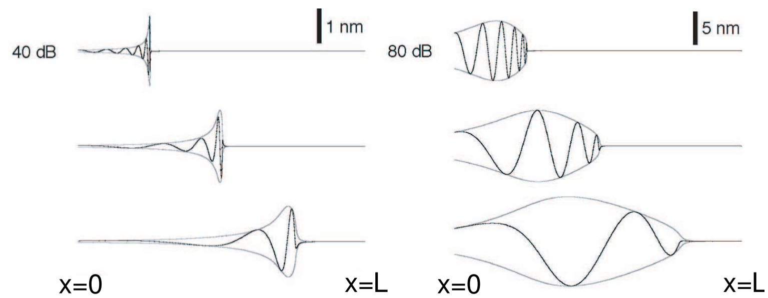

Figure 2. Nonlinear active traveling waves for three different stimulus frequencies (f = 370 Hz, 1.3 kHz and 4.6 kHz) and two different sound pressure levels (40 dB and 80 dB). Note that the waveform depends on stimulus intensity.

As the wave propagates towards the apex, its wavelength diminishes and its amplitude builds up, until it approaches the place of resonance. In the immediate vicinity of the characteristic place, $|A|$ becomes small while $\tilde{h}$ increases. Thus the cubic term in Eq. (3) rapidly becomes more important than the linear term. This leads to a strongly nonlinear BM response. The wave peaks at $x = x_p < x_r$, where the response displays the characteristic nonlinearity of critical oscillators, $\tilde{h}(x_p) \sim \tilde{p}(x_p)^{1/3}$. However, the vibration amplitude as a function of sound pressure level at a fixed position can exhibit responses which are not simple power laws. At positions beyond the characteristic place, $x > x_r$, A' becomes negative and consequently the wave number $q \sim \omega/\sqrt{A'}$ becomes imaginary, indicating the breakdown of wave propagation. The wave is thus reflected from the characteristic place and the BM displacement decays very sharply for $x > x_r$.

5 Discussion

Critical oscillators provide a general framework for the description of active amplification of sounds by cellular processes. While this description does not provide insights into the specific active processes which underly mechanical amplification on the cellular and molecular levels, it captures the general features in a simple and physically consistent way. The nonlinear wave equation which we present here provides a simple theoretical description of the nonlinear and active nature of the cochlear amplifier [19]. This framework can be extended to describe the BM motion elicited by stimuli containing multiple frequencies, by considering the generic nonlinear coupling of frequency components by critical oscillators [14]. The suppression of the response to one tone by the presence of a second tone, and the generation and wave-like propagation of distortion products, are natural consequences of this description. Furthermore, the flow of energy in the wave, as well as the pumping of the wave by active processes, can be clearly defined in this framework, taking into account nonlinear effects and energy supply by the active systems. The nonlinear wave described here has similarities to a laser cavity [23]; wave reflections along the basilar membrane and especially at the characteristic place lead to interesting and nonlinear reflection phenomena which will be discussed elsewhere. It has been suggested that oto-acoustic emissions are related to modes in the cochlea which result from constructive interference of forward and backward traveling waves. Such modes also occur naturally in our nonlinear active wave description. Therefore, the framework of critical oscillators coupled hydrodynamically on the basilar membrane is consistent with the interpretation of oto-acoustic emissions as active wave resonances in the cochlea discussed in Ref. [23].

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