

Critical oscillators as active elements in hearing

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1 Introduction

Active processes play a crucial role in the hearing organs of all vertebrates, where they amplify sound stimuli in a level-dependent and frequency-selective manner (Dallos 1992, Hudspeth 1997, Manley 2001). The most readily observable signature of active processes – oto-acoustic emissions – have been found in all classes of vertebrate (Kemp Chapter 1, Manley and van Dijk Chapter 6, Probst 1990, Manley and Köppl 1998, Manley 2000) and spontaneous movements have even been reported in the hearing apparatus of some insects (Göpfert Chapter 5, Göpfert et al. 2005) In different animal species, the physiology of the hearing organs and the molecular basis of active processes varies in significant ways. Despite this biological diversity, vertebrate ears share many features that characterize the active amplifier. These include oto-acoustic emissions (Probst 1990), a compressive nonlinearity (Robles and Ruggero 2001, Martin and Hudspeth 2001), high frequency selectivity and the physiological vulnerability of all these phenomena. The generality of this observed behavior suggests that a common physical principle may underlie active amplification in all auditory systems (Camalet et al. 2000, Eguiluz et al. 2000). We propose that the physics of dynamical systems provides an appropriate framework for identifying this principle and argue that the basic element of the active amplifier is a ‘critical oscillator’ – an active dynamical system that is on the verge of an oscillatory instability. In this Chapter, we discuss how the concept of critical oscillators provides a unifying description

of the general characteristics of the active process in hearing. Different physiological realizations of critical oscillators in different species, and the various ways in which these oscillators can be coupled together, can lead to diverse properties of certain aspects of auditory systems, while the generic features are conserved.

The importance of active processes in the ear was first noted by Gold (Gold 1948). He estimated the viscous damping of vibrating structures within the basilar membrane, which limits the sharpness of passive resonances, and concluded that a purely passive system could not provide the observed quality of resonance. He formulated his regenerative hypothesis: If active processes would overcome the viscous friction, resonances of high quality could be achieved. He thus proposed an amplifier based on a positive feedback. Because such an active system might become self-oscillatory, he realized that a mechanism of self-regulation would be required for it to operate reliably, and predicted the occurrence of oto-acoustic emissions. All these ideas are important in the framework of critical oscillators.

In order to cover a large dynamic range, it is important to amplify weak signals but not strong ones. This dependence of amplification on signal level corresponds to a compressive nonlinearity. Such a nonlinearity is well known to exist in the cochlear response, where it permits operation over a dynamic range of 120 dB of sound pressure levels (Rhode 1971, Ruggero et al. 1997, Robles and Ruggero 2001). Goldstein pointed out that this nonlinearity is ‘essential’: nonlinear effects do not disappear for small stimuli (Goldstein 1967). He also discussed the properties of combination tones that occur in the presence of two stimulus frequencies, which are an intrinsically nonlinear phenomenon. He argued that combination tones correspond to mechanical vibrations on the basilar membrane and suggested that they result from nonlinearities in the basilar membrane mechanics. Consequently, he suggested that the basilar membrane itself possesses an essential nonlinearity. These ideas are also closely related to the concept of critical oscillators. While nonlinearities can become important at large vibration amplitudes in a passive mechanical system, passive systems cannot be essentially nonlinear in response to periodic stimulation. Essential nonlinearities are thus a signature of active processes and can be directly linked to the cochlear amplifier.

This Chapter is organized as follows: In Section 2, we discuss general aspects of sound detection and amplification by nonlinear dynamic oscillators. This framework allows us to describe the characteristic properties of a broad class of active systems which respond to vibrations. We can formulate the ideas of Gold and Goldstein in a common framework which allows us to distinguish general properties from properties that are related to the specific architecture of a given auditory system. In Section 3, various different ways

to build active oscillators are discussed. We also show how a mechanism of self-regulation can maintain the active oscillators on the verge of an oscillatory instability. In Section 4, we weigh the evidence for the actual physical basis of critical oscillators in the auditory systems of insects, non-mammalian vertebrates and mammals. The mammalian cochlea is distinguished by the propagation of a traveling wave along the basilar membrane. In Section 5, we present a description of the cochlear traveling wave, based on the idea that critical oscillators with a range of characteristic frequencies drive the basilar membrane, and are coupled together through the cochlear fluid.

2 Generic response of critical oscillators

2.1 Active and passive oscillators

It is important to distinguish active oscillators from passive harmonic or anharmonic oscillators. Active oscillators are dynamical systems that are powered by a source of energy. Consequently, they can generate spontaneous oscillations that persist even in the presence of damping; they settle to a steady state of oscillation in which the heat dissipated by the damping is compensated by energy input from the source (Strogatz 2001). This contrasts with passive oscillators, for which the amplitude of oscillation always eventually decays. The amplitude of spontaneous oscillation of an active oscillator evidently depends on the internal state of the dynamical system, which can usually be summarized by a parameter C known as the ‘control parameter’. For one range of values of the control parameter, oscillations are absent and the system remains quiescent; in another region of parameter space, the system oscillates with a particular amplitude and a particular frequency, both of which vary smoothly as C varies. There is one particular value of the control parameter – the critical value C_c – which marks the boundary between these two regions (see Fig. 6). This is the precise point at which the system becomes unstable and spontaneous oscillations of vanishing amplitude, but with a well-defined characteristic frequency ω_c are generated. It corresponds mathematically to a ‘supercritical Hopf bifurcation’ of the dynamical system: i.e. the bifurcation of a fixed point to a limit cycle (Strogatz 2001). We call a dynamical system that is poised exactly at this critical point a ‘critical oscillator’.

In practice, spontaneous oscillations usually occur in complex systems consisting of many components. In this case, the variations of a large number of rapidly changing degrees of freedom result in fluctuations, which can be described as background noise acting on the more slowly oscillating dis-

placement of the system (van Kampen 1992). The oscillation frequency is then not perfectly fixed, because the noise causes the phase of the oscillation to wander over time. Indeed, there is typically a finite coherence time, after which the phase of oscillations is randomized (Stratonovich 1981). But in the limit where the number of interacting degrees of freedom is very large, the coherence time can become infinite. Then the system has a persistent, perfectly periodic output. Such coherent oscillations are characterized by a power spectrum that exhibits delta peaks, due to the coherent periodic motion, together with a broader spectrum reflecting fluctuations and noise. Note that coherent oscillations cannot occur in a passive system, but only in active systems. The occurrence of phase coherence in a multi-component dynamical system is related to the appearance of order in large thermodynamic systems, where collective effects give rise to abrupt transitions in behavior. The Hopf bifurcation of a complex dynamical system is thus a generalization of the concept of equilibrium phase transitions, applied in this case to an active, non-equilibrium system (Risler et al. 2004 and 2005).

Extensive studies of thermodynamic phase transitions have revealed one remarkable feature: When a system is close to a critical point, the way that it responds to external influences is universal and independent of the many microscopic details of the system (Ma 2000). How a liquid turns into a gas with rising temperature is the same for all materials, for example, and the mathematics that describes this transition also accounts for the onset of magnetism in ferromagnetic substances. The same universality of behavior applies to complex dynamical systems close to a Hopf bifurcation. Thus many of the characteristic properties of critical oscillators are generic. In particular, their response to an oscillatory stimulus can be discussed quite generally, irrespective of the specific components from which they are built.

2.2 Nonlinear response function

In the context of hearing, we are interested in knowing the displacement $x(t)$ of an active oscillator in response to a stimulus which is periodic in time, with angular frequency ω . The external force acting on the system may then be written as a Fourier series, $f(t) = \sum f_n e^{in\omega t}$, where f_n denote complex Fourier coefficients with $f_n = f_{-n}^*$.

We first consider a simpler, passive system that does not generate spontaneous motion, so that $x = 0$ in the absence of external forcing. The response contains the same Fourier modes as the stimulus and is expressed as $x(t) = \sum x_n e^{in\omega t}$, where the $x_n = x_{-n}^*$ are the complex Fourier components of the displacements. If fluctuations are present, $x(t)$ is defined as the average displacement observed after time t when the stimulus is repeated

many times. For sufficiently small stimulus amplitudes we can express the response to a periodic stimulus as an expansion:

$$x_n = G_n^{(1)} f_n + \sum_k G_{nk}^{(2)} f_{n-k} f_k + \sum_{kl} G_{nkl}^{(3)} f_{n-k-l} f_k f_l + O(f^4). \quad (1)$$

This expression is the most general form of the nonlinear response that satisfies time-translation invariance, ensuring that the properties of the system are independent of its history. Note that in the absence of a stimulus ($f_n = 0, \forall n$), the response vanishes, $x_n = 0$, as expected for a passive system. In Eq. (1), the complex quantity $G_n^{(1)}(\omega)$ is the frequency-dependent linear response function. The effects of nonlinearities are captured by the higher order coefficients $G^{(k)}$ with $k > 1$, which are also complex numbers.

Consider now an active system that is capable of generating spontaneous oscillations. In the region of phase-space where the system is quiescent, Eq. (1) remains valid. But what happens if the control parameter C is varied so that the system moves towards the Hopf bifurcation? As the oscillating instability is approached, the linear response function $G_1^{(1)}(\omega)$ increases. Right at the critical point, $C = C_c$, where the system becomes unstable, $G_1^{(1)}(\omega)$ formally diverges for the specific frequency $\omega = \omega_c$. Here, ω_c is the characteristic frequency of the spontaneous oscillations that emerge in the absence of a stimulus. As a consequence of this divergence, the validity of Eq. (1) is restricted to smaller and smaller amplitudes of force as the Hopf bifurcation is approached: it can be used only as long as $|G_1^{(1)} f_1|$ remains finite.

There is however a related description of the response which is valid near the instability. Before reaching the bifurcation point, we can formally invert Eq. (1) for small $|f_k|$ within the radius of convergence of the expansion, and re-express it as an expansion of f_n in terms of x_n

$$f_n = F_n^{(1)} x_n + \sum_k F_{nk}^{(2)} x_{n-k} x_k + \sum_{kl} F_{nkl}^{(3)} x_{n-k-l} x_k x_l + O(x^4), \quad (2)$$

where x_n are assumed to be small. All coefficients $F^{(n)}$ can be related to the coefficients $G^{(n)}$ of Eq. (1). In particular, $F_n^{(1)} = 1/G_n^{(1)}$ is simply the inverse of the linear response function, while the nonlinear terms are related in a more complicated way. As the Hopf bifurcation is approached from the quiescent side, $G_1^{(1)}(\omega)$ diverges for the characteristic frequency, $\omega = \omega_c$, which implies that $F_1^{(1)}(\omega)$ becomes zero at this frequency. Therefore Eq. (2) is the appropriate expansion, valid for small amplitudes, in the vicinity of the instability and can even be used once the instability has been traversed and spontaneous oscillations occur. Note that all expansion coefficients $F^{(n)}$ are, in general, functions of frequency ω .

2.3 Hopf bifurcation

We shall now examine the response of a critical oscillator to a simple sinusoidal stimulus of small amplitude f_1 , with $f_k = 0$ for $k > 1$. The response is principally at the same frequency, but higher harmonics x_k with $k > 1$ are also present and have amplitudes $x_k \sim O(x_1^k)$. Focussing on x_1 and x_2 , we find (Jülicher et al. 1997, Camalet et al. 2000)

$$f_1 \simeq F_1^{(1)} x_1 + (F_{1,2}^{(2)} + F_{1,-1}^{(2)}) x_{-1} x_2 + (F_{1,1,1}^{(3)} + 2F_{1,-1,1}^{(3)}) x_1^2 x_{-1}, \quad (3)$$

$$0 \simeq F_2^{(1)} x_2 + F_{2,1}^{(2)} x_1^2, \quad (4)$$

where we have assumed, without loss of generality, that $F_{nkl}^{(3)} = F_{nlk}^{(3)}$. Equation (4) determines $x_2 \simeq -(F_{2,1}^{(2)}/F_2^{(1)}) x_1^2$ as a function of x_1 . Inserting this relation in Eq. (3), we obtain a simple expression for the response amplitude x_1 in the presence of a sinusoidal stimulus:

$$f_1 \simeq \mathcal{A} x_1 + \mathcal{B} |x_1|^2 x_1. \quad (5)$$

Here, we have defined the effective linear and cubic response functions $\mathcal{A} \equiv F_1^{(1)}$ and $\mathcal{B} \equiv -(F_{2,1}^{(2)}/F_2^{(1)})(F_{1,2}^{(2)} + F_{1,-1}^{(2)}) + (F_{1,1,1}^{(3)} + 2F_{1,-1,1}^{(3)})$. Note that while the linear coefficient \mathcal{A} is directly given by the linear response function, the structure of nonlinearities is more subtle. Significantly, Eq. (5) does not contain quadratic terms; the dominant nonlinearity is cubic. However, the coefficient \mathcal{B} of the cubic term contains linear, quadratic and cubic coefficients of the expansion (2). This derivation is valid for any complex system near a Hopf bifurcation, so Eq. (5) is the generic form of the response of a critical oscillator, independent of the physical details of the system.

The above description also accounts for spontaneous oscillations in the absence of a stimulus. In this case, Eq. (5) with $f_1 = 0$ has a nontrivial solution with amplitude

$$|x_1|^2 \simeq -\frac{\mathcal{A}}{\mathcal{B}}. \quad (6)$$

The frequency ω_c of these oscillations is determined by the criterion that $-\mathcal{A}/\mathcal{B}$ is real and positive. The critical point occurs for the particular case where $\mathcal{A}(\omega_c) = 0$ for the critical frequency. As discussed above, the distance of the system from the critical point is controlled by the parameter C . We can therefore express the linear coefficient \mathcal{A} for small frequency difference $\omega - \omega_c$ and small deviation of the control parameter from its critical value $C - C_c$ as

$$\mathcal{A}(\omega, C) \simeq \alpha(\omega - \omega_c) + \beta(C - C_c), \quad (7)$$

where α and β are complex coefficients, the values of which depend on the particular system. Equations (5) and (7) together characterize the generic

behavior of a critical oscillator, describing both how oscillations are generated, and how the system responds to a stimulus.

2.4 Generic mechanical response

Although the frequency dependence of the coefficients \mathcal{A} and \mathcal{B} in Eq. (5) varies from one system to another, Eq. (7) holds for any system that is close to a Hopf bifurcation (Camalet et al. 2000). Consequently the response of a critical oscillator exhibits some very general features. Most importantly, if the oscillator is poised exactly at the critical point with $C = C_c$, and is stimulated at its characteristic frequency, $\omega = \omega_c$, the linear coefficient \mathcal{A} vanishes and the amplitude of the response varies as

$$|x_1| \simeq |\mathcal{B}|^{-1/3} |f_1|^{1/3} \quad (8)$$

This power law is formally satisfied for arbitrarily small f_1 , so the response displays an ‘essential nonlinearity’.

It is easy to see why an active oscillator is ideally suited to act as a mechanosensor in the auditory system. First, the compressive nonlinearity permits the detection of a wide range of signals. Forces that vary by a factor of one million cause displacements of the detection apparatus that vary by a factor of only one hundred – a physically reasonable range. Second, the critical oscillator acts as an active amplifier that boosts faint signals. Defining the signal gain as the ratio $|x_1|/|f_1|$ of output and stimulus amplitudes, Eq. (8) implies that this gain diverges with a power law

$$\frac{|x_1|}{|f_1|} \sim |f_1|^{-2/3}, \quad (9)$$

so the weakest stimuli are infinitely amplified. Third, the response is highly frequency selective. If the critical oscillator is stimulated at a frequency that differs from the characteristic frequency, $\omega \neq \omega_c$, the nonlinear response can be lost: Equations (5) and (7) indicate that the response becomes linear if $|\omega - \omega_c| \gg \Delta\omega_a$ where

$$\Delta\omega_a = \frac{|\mathcal{B}^{1/3}|}{|\alpha|} |f_1^{2/3}|. \quad (10)$$

This therefore defines an ‘active bandwidth’, $\Delta\omega_a$, within which active amplification occurs. Note that the bandwidth depends on the stimulus amplitude, and the tuning becomes very sharp at low levels.

To profit best from the active response, the system should be poised exactly at the Hopf bifurcation. As we discuss later, adjustment of mechanosensors to the proximity of the critical point is likely to be automatically achieved

by a feedback control mechanism. The adjustment cannot be perfect, however. When the system is close to, but not exactly at the critical point, $C \neq C_c$, the linear term \mathcal{A} is non-zero for all frequencies. Therefore, the power-law response is only apparent for $|f_1| \gg |\mathcal{A}/\mathcal{B}|^{1/2}$ when the nonlinearity dominates; for smaller $|f_1|$, the response is linear. The generic response of a dynamic oscillator to periodic stimulation is displayed in Fig. 6

The concept of critical oscillators provides a natural explanation for the mechanical responses observed in auditory systems, where there is considerable evidence of an essential compressive nonlinearity. The above analysis shows that an essential nonlinearity is only possible in an active system. Indeed, the vanishing of $\mathcal{A}(\omega_c)$ for non-zero ω_c is impossible in a passive system, because the unavoidable damping necessarily leads to a non-zero imaginary part of \mathcal{A} . Conversely, the vanishing of \mathcal{A} , which leads to an essential singularity, is necessarily linked to the existence of spontaneously oscillating solutions at neighboring parameter values, since the functions \mathcal{A} and \mathcal{B} are continuous and differentiable on general physical grounds. Thus an essential nonlinearity in the response of a complex system to a periodic stimulus provides direct evidence that the system is on the verge of an oscillating instability.

2.5 Normal form

The preceding generic description of a critical oscillator is closely related to the so-called ‘normal form’ of a dynamical system in the proximity of a Hopf bifurcation (Strogatz 2001, Wiggins 2003). The normal form describes the long time relaxation of an active oscillator to its limit cycle. Usually, the normal form is defined in the absence of an external stimulus and in the absence of fluctuations. A nonlinear variable transformation is used to define a complex variable Z . Expressed in this variable, the limit cycle corresponds to motion along a circle on the complex plane. The normal form can be linked to the generic expansion (5) together with the expression (7). We define the complex variable $Z(t) = x_1(t)e^{i\omega t}$ and describe the relaxation to the limit cycle as a slow variation of the amplitude x_1 of the unstable mode with time. This implies that near the bifurcation $x(t) \simeq x_1(t)e^{i\omega t} + x_{-1}(t)e^{-i\omega t}$ and that $dZ/dt = (dx_1/dt + i\omega x_1)e^{i\omega t} \simeq i\omega x_1 e^{i\omega t}$. Here, we assume that relaxation is slow compared to the oscillation frequency. Rapid variations of $x(t)$ due to the presence of higher harmonics are ignored; they simply lead to nonlinear corrections to the linear relation $x \simeq 2\text{Re}(Z)$. Eq. (5) together with Eq. (7), in the time domain, can be expressed by the dynamic equation

$$\frac{dZ}{dt} = -(r + i\omega_0)Z + B|Z|^2Z + \frac{e^{i\theta}}{\Lambda}f(t). \quad (11)$$

This is the normal form of a system close to a Hopf bifurcation, in the presence of a force $f(t)$. The real parameter $r = (C - C_c)\text{Im}(\beta/\alpha)$ characterizes the proximity to the bifurcation, which is situated at $r = 0$. For $r < 0$ there is a limit-cycle solution, representing spontaneous oscillations at frequency $\omega_0 = \omega_c + (C - C_c)\text{Re}(\beta/\alpha)$, whose amplitude is governed by the complex nonlinear coefficient $B = -\mathcal{B}/\alpha$. The external force is multiplied by a complex factor $e^{i\theta}/\Lambda = i/\alpha$. The real coefficient Λ is an effective friction, and the phase θ characterizes the phase shift at which the external force acts on the variable Z .

The essential nonlinearity of a critical oscillator is clear from Eq. (11). When the system is precisely at the bifurcation, $r = 0$, and $f(t)$ is a sinusoidal force at the characteristic frequency $\omega = \omega_c$, the solution is $Z = x_1 e^{i\omega t}$ with $|x_1| \sim |f|^{1/3}/|\Lambda B|^{1/3}$. The normal form is also convenient for characterizing the linear response that occurs at small forces in the case where the active oscillator is not exactly critical. For a real stimulus force with $f_{-1} = f_1^*$, and for small $\omega - \omega_0$, the response is $x_1 \simeq \chi(\omega)f_1$, where the linear response function $\chi = \mathcal{A}^{-1}$ is

$$\chi \simeq \frac{1}{\Lambda} \left[\frac{e^{i\theta}}{i(\omega_0 - \omega) + r} + \frac{e^{-i\theta}}{-i(\omega_0 + \omega) + r} \right]. \quad (12)$$

2.6 Effects of fluctuations

From the point of view of complex systems, a Hopf bifurcation is an idealization that can only strictly be realized in the thermodynamic limit: only an infinite number of interacting degrees of freedom can generate spontaneous oscillations which are truly coherent (Risler et al. 2004 and 2005). In small systems, such as single cells, an oscillatory state is subject to fluctuations caused by the irregular movements of many molecular or microscopic components. These fluctuations destroy the precision of the oscillation period. As a result, the phase coherence of the oscillations is limited to a coherence time τ (Stratonovich 1981). Fluctuations therefore conceal the Hopf bifurcation that occurs in the equivalent deterministic system.

Even so, a noisy active oscillator can function effectively as a detector of periodic mechanical stimuli. Suppose that an active dynamical system is close to the point where a Hopf bifurcation would occur in the absence of fluctuations. It would then spontaneously oscillate at low amplitude and in an irregular fashion, with a short coherence time. If the system is then stimulated by a sinusoidal force $f(t) = f_1 e^{i\omega t} + c.c.$ at its characteristic frequency $\omega = \omega_c$, the response at that frequency x_1 varies with the level of the stimulus according to Eq. 5. The augmentation of this Fourier component of the

displacement is equivalent to an increase of phase coherence in the response (see Fig. 6), even though the overall amplitude of the noisy oscillations does not necessarily increase (Camalet et al. 2000). This entrainment, or ‘phase-locking’ of the dynamical system can be detected, to infer the presence of the stimulus. In the case of hearing, low-level sounds could be detected by analysing the timings of spike trains elicited in the auditory nerve.

The effect of noise on a dynamical system that is close to a Hopf bifurcation is most readily discussed using the normal form. Fluctuations can be modelled by adding to Eq. (11) a stochastic force $\eta(t)$ with zero average $\langle \eta \rangle = 0$. Assuming for simplicity Gaussian white noise we use $\langle \eta(t)\eta(0) \rangle = 2D(t)$ and $\langle \eta(t)\eta^*(0) \rangle = 0$. The spectral density $\tilde{C}(\omega)$, which is the Fourier transform of the auto-correlation function $C(t) = \langle x(\tau+t)x(\tau) \rangle$, is of the form (Martin et al. 2001)

$$C(\omega) \simeq \frac{1}{\Lambda^2} \left[\frac{\tilde{D}(\omega)}{r^2 + (\omega - \omega_0)^2} + \frac{\tilde{D}(-\omega)}{r^2 + (\omega + \omega_0)^2} \right], \quad (13)$$

where the effect of nonlinearities has been neglected. This spectrum, which exhibits a peak at the characteristic frequency ω_0 , is characteristic of noisy active oscillators. The coherence time $\tau \simeq r^{-1}$ characterizes the width of the peak.

The observation of noisy oscillations with a finite coherence time τ is insufficient to determine whether a given system is a passive damped oscillator subject to thermal fluctuations, or whether it is an active nonlinear system that oscillates spontaneously. Comparison of the spectral density with the response to mechanical stimuli, however, provides key information about the passive or active nature of the system. In the case of a passive system in thermodynamic equilibrium at temperature T , fluctuations result from Brownian motion and satisfy a fluctuation-dissipation theorem. This relates the auto-correlation function to the linear response function $\tilde{\chi}(\omega) = \tilde{\chi}'(\omega) + i\tilde{\chi}''(\omega)$, where $\tilde{\chi}'$ and $\tilde{\chi}''$ denote the real and the imaginary part, respectively. It can be written as (Forster 1990):

$$\tilde{C}(\omega) = \frac{2k_B T}{\omega} \tilde{\chi}(\omega)'' . \quad (14)$$

Therefore, for a passive system the linear response function is completely determined by a knowledge of the auto-correlation function $C(t)$. For an active oscillator, on the other hand, the fluctuation-dissipation theorem does not apply and the linear response function is not so constrained. So by measuring both the auto-correlation function and the linear response function of a noisy oscillator, and seeing whether the fluctuation-dissipation theorem

is obeyed or violated, it is possible to determine whether a system is passive or active (Martin et al. 2001).

2.7 Response to multiple frequencies

While a critical oscillator provides the benefit of active amplification, the nonlinearity of its response means that different frequencies interfere with one another, so that the spectrum of the response differs from the spectrum of the stimulus. The nonlinearities naturally lead to the generation of new frequencies or ‘distortion products’, and also to ‘two-tone suppression’.

To illustrate the basic interference phenomena that arise from nonlinearities, we consider how a critical oscillator responds to a signal containing two frequency components ω_1 and ω_2 ,

$$f(t) = f_{10}e^{i\omega_1 t} + f_{01}e^{i\omega_2 t} + c.c. , \quad (15)$$

where *c.c.* denotes the complex conjugate and f_{10} and f_{01} are the Fourier amplitudes of frequency component ω_1 and ω_2 , respectively. For a dynamical system in the vicinity of a Hopf bifurcation, we can generalize the arguments which lead to Eq. (2) (Jülicher et al. 2001, Stoop and Kern 2004). The nonlinearities in the system lead to many more frequency components in the response, which can be generally written as

$$x(t) = \sum_{kl} x_{kl} e^{i(k\omega_1 + l\omega_2)t} . \quad (16)$$

In the vicinity of a Hopf bifurcation, we can generalize Eq. (5) and write

$$f_{10} \simeq \mathcal{A}(\omega_1)x_{10} + \mathcal{B}|x_{10}|^2x_{10} + \bar{\mathcal{B}}|x_{01}|^2x_{10} \quad (17)$$

$$f_{01} \simeq \mathcal{A}(\omega_2)x_{01} + \mathcal{B}|x_{01}|^2x_{01} + \bar{\mathcal{B}}|x_{10}|^2x_{01} \quad (18)$$

This expression reveals the basic features of the response to two tones. We assume that ω_1 is the critical frequency of the oscillator. If a stimulus component at this frequency is present, $f_{10} \neq 0$, but the second frequency component is absent, $f_{01} = 0$, then $x_{01} = 0$ and we recover the general response to a single stimulus, Eq. (5). But if the second frequency component is introduced, $f_{01} \neq 0$, a corresponding frequency component is generated in the response, $x_{01} \neq 0$. This frequency component x_{01} changes the response to the first stimulus, which now satisfies

$$f_{10} \simeq \mathcal{A}'x_{10} + \mathcal{B}|x_{10}|x_{10} , \quad (19)$$

where $\mathcal{A}' = \mathcal{A} + \bar{\mathcal{B}}|x_{01}|^2$. The presence of the second frequency component thus changes the linear response. The critical oscillator consequently responds to the stimulus at the characteristic frequency as if it were not at the

critical point. This implies that the nonlinear amplification is reduced in the presence of a second frequency, and the threshold of detection is increased (Ruggero et al. 1992). This feature is thus similar to the general phenomenon of two-tone suppression in hearing – reduced sensitivity to a sound stimulus when a second nearby frequency is simultaneously present (Zwicker 1999). This two-tone suppression is most important when the frequency difference $\Delta\omega = \omega_1 - \omega_2$ is small, because $x_{01} \sim f_{01}/\Delta\omega$ then becomes large.

In addition to two-tone suppression, new frequencies are generated by nonlinearities in the response (see Fig. 6). In general, and according to Eq. (16), these frequency components are given by

$$\omega_{kl} = k\omega_1 + l\omega_2 , \quad (20)$$

where k and l are integers. Particular examples are the frequencies $\omega_{2,-1} = 2\omega_1 - \omega_2$ and $\omega_{-1,2} = 2\omega_2 - \omega_1$ which are the most prominent frequencies of distortion products in hearing. For small $\Delta\omega$ there is a particularly strong response at these frequencies, because they are directly generated by the two frequency components in the stimulus. These new frequencies mix with the original ones to create further distortion products, so a whole hierarchy of frequencies is generated:

$$\omega_{k+1,-k} = \omega_1 + (k - 1)\Delta\omega . \quad (21)$$

The amplitude of these distortion products decays exponentially as

$$x_{k+1,-k} \sim e^{-\lambda|k-3/2|} . \quad (22)$$

The number of strongly excited distortion products is given by $\lambda^{-1} \sim \Delta\omega^{-1}$, and so the response contains many components when the two stimuli are close in frequency.

This exponential decay of the spectrum of distortion products is characteristic of dynamical oscillators that are close to a Hopf bifurcation. A general nonlinear system (or a system far from a Hopf bifurcation) does not generate this response (Jülicher et al. 2001). The observation of an exponential spectrum in the two-tone response of the basilar membrane (Robles et al. 1997) therefore indicates that critical oscillators might be an important part of the active process in the mammalian cochlea.

3 Building critical oscillators

3.1 Physical realizations of active mechanical oscillators

Any active mechanical system that is close to a supercritical Hopf bifurcation behaves in the general way described in the previous section. Because the supercritical Hopf bifurcation is the simplest type of transition from a quiescent to an oscillatory regime, such dynamical systems are easy to manufacture. Here, we consider a variety of physical realizations of critical oscillators which might be relevant in hearing.

Inertial oscillator with negative damping. One of the simplest active oscillators to envisage is a damped inertial oscillator, supplemented by an internal driving force that counteracts the friction. The equation of motion, when the system is under the influence of an external force f , is

$$m\ddot{x} = -\lambda\dot{x} - kx + f_a + f, \quad (23)$$

where m is a mass, λ is a coefficient of damping, k is the modulus of an elastic spring, and f_a is the internally generated active force. If the active force is in phase with the velocity of the oscillator, it acts as a negative friction and, if it overcomes the damping, spontaneous oscillations are generated. Some kind of nonlinearity is essential to stabilize the oscillations. One way of doing this is for the active force to diminish with amplitude, $f_a = (C - Bx^2)\dot{x}$, so that the total friction becomes positive for large oscillations. The system is then known as a van der Pol oscillator (van der Pol 1926, Strogatz 2001), and obeys

$$m\ddot{x} = -(\lambda - C + Bx^2)\dot{x} - kx + f. \quad (24)$$

If the driving force is periodic with frequency ω , the response at the same frequency satisfies Eq. (5) with

$$\mathcal{A} = k - m\omega^2 + i\omega(\lambda - C), \quad (25)$$

$$\mathcal{B} = i\omega B. \quad (26)$$

The coefficient C plays the role of a control parameter, and the Hopf bifurcation occurs at $C = C_c = \lambda$. The system then generates spontaneous oscillations with characteristic frequency $\omega_c = (k/m)^{1/2}$. Note that it is necessary for \mathcal{B} to be purely imaginary to stabilize the system. It is also important that the nonlinearity is in the damping; the combination of an active force that is simply proportional to the velocity, and a nonlinear spring $k(x) = k'x + B'x^3$, for example, would not create a stable oscillator. Alternative stabilizing nonlinearities in the damping are possible, however, such as

an active force which decreases with velocity $f_a = (C - B\dot{x})\dot{x}$. In this case \mathcal{A} is unchanged but $\mathcal{B} = 3i\omega^3 B$. This oscillator thus has the same critical point and characteristic frequency, but the frequency-dependence of the oscillation amplitude is different.

Time-delayed feedback. It is easy to understand how the above kind of active undamping works, but it is less obvious how a feedback mechanism could be constructed to ensure that the active force is precisely in phase with the velocity. An alternative is to use a feedback proportional to the displacement, but with a time delay τ , so that $f_a = Cx(t - \tau)$ (Boukas and Liu 2002). In the case where the mechanical system has a simple nonlinear drag and a nonlinear elasticity, its equation of motion is then

$$m\ddot{x} = -(\lambda + Bx^2)\dot{x} + (k + B'x^2)x + Cx(t - \tau) + f \quad (27)$$

The coefficients of Eq. (5) for this system are

$$\mathcal{A} = k - m\omega^2 + i\omega\lambda + Ce^{-i\omega\tau}, \quad (28)$$

$$\mathcal{B} = 3B' + i\omega B. \quad (29)$$

The strength of the feedback C acts as the control parameter. The critical point C_c and characteristic frequency ω_c are given by the solutions of the two equations $k - m\omega_c^2 = -C_c \cos(\omega_c\tau)$ and $\omega_c\lambda = C_c \sin(\omega_c\tau)$. If the feedback is rapid compared to the period of oscillation, these expressions reduce to $C_c \approx \lambda/\tau$ and $\omega_c^2 \approx k/m + \lambda/\tau m$.

Two first-order systems. On the cellular scale, inertial effects are negligible in most cases and the dynamics of an active mechanical system is described by a first-order differential equation

$$\lambda\dot{x} = -k(x)x + f_a + f, \quad (30)$$

where $k(x)$ is the nonlinear stiffness of the system. In this case, oscillations can be generated if the active force f_a also evolves in time according to a first-order differential equation, which is coupled to Eq. (30). The simplest conceivable situation is akin to ‘stretch-activation’ in muscle, i.e. we consider an active process that generates a restoring force when the system is displaced, but which relaxes with a time constant τ when the system is stationary (Vilfan and Duke 2003). To obtain oscillations, it is also important for the mechanical system to display a regime of negative elasticity, $k(x) = k - C + Bx^2$; here, k is the bare stiffness and C is a control parameter characterizing a reduction of the stiffness. When $C > k$, the stiffness becomes negative at small displacements.

The combination of negative stiffness and an internal, dynamically-regulated active force is represented by the pair of equations

$$\lambda \dot{x} = -(k - C + Bx^2)x + f_a + f, \quad (31)$$

$$\tau \dot{f}_a = -f_a - \bar{k}x. \quad (32)$$

The coefficients of Eq. (5) for this system are

$$\mathcal{A} = \frac{k + \bar{k} - C - \tau\lambda\omega^2 + i\omega(\lambda + \tau(k - C))}{1 + i\omega\tau}, \quad (33)$$

$$\mathcal{B} = 3B \frac{1 + 3i\omega\tau}{1 + i\omega\tau}. \quad (34)$$

Inspection of Eq. (33) reveals that the Hopf bifurcation occurs at $C = C_c = k + \lambda/\tau$ and that the characteristic frequency is given by $\omega_c^2 = \bar{k}/\lambda\tau - 1/\tau^2$. Thus in this case, the frequency of oscillation is determined by the properties of the active force-generating system, rather than by the mechanical properties of the system.

3.2 Self-adjustment to the critical point

While the properties of critical oscillators can account for many general features of sound detection in hearing, it remains to be explained how a dynamical system could operate sufficiently close to a Hopf bifurcation for the generic behavior of critical oscillators to be apparent. The necessary fine-tuning of parameters raises doubts as to whether a living system can profit from the special properties at a critical point in a reliable way. These concerns have been allayed, however, by the proposition of a mechanism which enables an oscillator to adjust automatically to its critical point.

Feedback regulation of the control parameter (Camalet et al. 2000, Coulet et al 1989, Moreau et al. 2003) is a simple and general mechanism to maintain a dynamical system at a point of operation close to the bifurcation point. This kind of automatic self-adjustment ensures that when the system is quiescent, the control parameter gradually changes so that the system approaches the instability; but as soon as oscillations are detected, the control parameter is stabilized. Self-adjustment works best in the absence of external stimuli, when the highest sensitivity is needed, by adapting the control parameter according to the detected amplitude of vibrations.

Consider a system for which the control parameter can vary in the range from zero to C_{max} , and which oscillates for $C > C_c$. Self-adjustment can be described by the dynamic equation for the control parameter

$$\frac{dC}{dt} = (1 - \frac{x^2}{\delta^2})(C_{max} - C)/\tau_a. \quad (35)$$

Here, δ characterizes the threshold amplitude at which the feedback becomes effective. If the system is quiescent ($x = 0$), the control parameter rises towards its maximum value with a characteristic adaptation time τ_a . When C exceeds C_c , the system starts to oscillate and the amplitude near the critical point varies as

$$|x_1|^2 \simeq \Delta^2(C - C_c)/C_c, \quad (36)$$

where Δ denotes a characteristic amplitude of spontaneous oscillations. The feedback control, Eq. (35), thus brings the system to an operating point $C = C_0$, close to the critical point, for which $x_1^2 \simeq \delta^2$ and (Camalet et al. 2000)

$$\frac{C_0 - C_c}{C_c} \simeq \frac{\delta^2}{\Delta^2}. \quad (37)$$

This quantity describes the relative distance to the critical point achieved by self-regulation. Because the threshold of detection δ can be much less than the typical amplitude of spontaneous oscillations Δ , the self-regulation can ensure that the system operates sufficiently close to the critical point for the generic nonlinear behavior to dominate.

Thus in the absence of a stimulus, a self-adjusted active oscillator will be poised very close to the point where it is most sensitive. When stimulated by a weak signal, such that the amplitude of the response only slightly exceeds δ , Eq. (35) indicates that the control parameter is not significantly perturbed by the stimulus; thus the oscillator remains in the immediate vicinity of the critical point and active amplification can be maintained. If the stimulus is stronger, however, and elicits a large response, Eq. (35) indicates that the control parameter gradually decreases so that the system drifts away from the critical point, into the quiescent regime. As a consequence, the amount of active amplification diminishes with time – a feature which does not pose a problem because a strong stimulus can be detected without the aid of amplification. After the termination of a sustained, high-level stimulus, it takes a typical time τ_a for the system to readjust and return to the vicinity of the critical point, where it is most sensitive. Thus this mechanism of detection naturally accounts for a period of adaptation, following a strong stimulus, before the weakest signals can be detected. Note that the adaptation time τ_a must be long compared to the characteristic period of the oscillator, so that the variations in the control parameter caused by the feedback mechanism do not interfere with the limit cycle.

4 Critical oscillators in the auditory system

4.1 Variations on a theme

The main signature of active amplification in the auditory system is oto-acoustic emissions. Such emissions have been detected in all classes of vertebrates (Manley and van Dijk Chapter 6, Probst 1990, Manley and Köppl 1998, Manley 2000), and more recently an active process has been discovered in the hearing of some insects (Göpfert Chapter 5, Göpfert and Robert 2003, Göpfert et al. 2005) The wide range of animal species that benefit from active audition suggests that a variety of realizations of active oscillators may have evolved. The way that oscillators of different frequency are coupled to one another in the auditory system might also be expected to vary according to the inner ear physiology.

While the existence of oto-acoustic emissions is well established, the identification of the cellular processes that are at the origin of these emissions has proved difficult. There thus remains controversy about the nature of the active elements in hearing and their relation to nonlinear oscillators. Evidence from many sources links active amplification to the biophysics of mechanosensory cells and strongly suggests that it is these cells themselves that host the active process. In vertebrates, hair cells are thus the prime candidates for the generation of mechanical oscillations (Dallos 1992, Hudspeth 1997). Active oscillations of the hair bundle have been directly observed in amphibians and reptiles (Martin and Hudspeth 1999, Crawford and Fettiplace 1985, Howard and Hudspeth 1987, Denk and Webb 1992, Benser et al. 1996, Martin et al. 2000). In the mammalian cochlea, inner and outer hair cells can be distinguished (Dallos et al. 1996). Because of their electromotility, outer hair cells have been the focus of the search for active elements (Brownell et al. 1985, Kachar et al. 1986, Ashmore 1987). However, the hair bundles of both inner and outer hair cells could act as active amplifiers, as they do in other vertebrates.

From an evolutionary standpoint, it seems probable that the first active mechanosensors would have been based on a motile system that naturally produces vibrations. An oscillating axoneme, coupled to a mechanosensitive channel, is a possible candidate. Natural selection could have refined a simple feedback system to provide a self-adjustment mechanism that keeps the oscillator close to its critical point. The ions that enter through the channel might bind to the motor proteins that drive the axoneme, for example, thereby affecting the quality of the oscillations. The auditory system of some insects, which is based on mechanosensory neurons, has been shown to employ dynamic oscillators (Göpfert Chapter 5). The anatomy of their sen-

sory apparatus (Eberl 1999) suggests that a structure related to an axoneme might be the mechanical basis of the active oscillator.

4.2 Vertebrate hair bundles

The hair bundles of vertebrate hair cells consist of about 50 stereocilia – stiff, rod-like extensions of the cell with a length of several microns and a diameter of about 300 nm. The stereocilia are arranged in rows of increasing height and each stereocilium is connected, at its tip, to a stereocilium in the adjacent row. The fine filament that forms this bridge is known as a ‘tip link’ (Pickles et al. 1984, Kachar et al. 2000). Shear deformation of the hair bundle stretches the tip links and triggers the opening of mechanosensitive transduction channels to which they are joined (Hudspeth 1989). This leads to a transduction current – an influx of K^+ and Ca^{2+} ions into the cell. Active internal forces, generated internally within the stereocilia by myosin motor proteins, can also modulate the tension in the tip links and thereby affect the transduction current (Hudspeth and Gillespie 1994).

The micromechanical properties of hair bundles in living hair cells range from adaptive movements in response to abrupt force steps (which have both fast and slow components (Howard and Hudspeth 1988, Benser et al. 1996, Ricci et al. 2000)), to spontaneous oscillations (Crawford and Fettiplace 1985, Howard and Hudspeth 1987, Denk and Webb 1992, Benser et al. 1996, Martin and Hudspeth 1999, Martin et al. 2000, Martin et al. 2003). These are discussed in detail in (Martin Chapter 4). Micromanipulation experiments performed on spontaneously oscillating hair bundles have revealed a frequency selectivity and a compressive nonlinear response that are compatible with the general properties of critical oscillators (Martin and Hudspeth 1999, Martin and Hudspeth 2001, Martin et al. 2001). In the case of hair bundles in the bullfrog sacculus, the violation of the fluctuation-dissipation theorem, Eq. 14, has been shown experimentally (Martin et al. 2001). Thus Brownian motion has been ruled out as the source of fluctuations, and the hair bundle has been proved to be a noisy, active oscillator. Direct evidence of active amplification by hair bundles in the intact reptilian cochlea has also been presented (Manley et al. 2001).

Spontaneous oscillations of the hair bundle could be generated by several different mechanisms which can be characterized by two or more coupled first-order equations, as described in Section 3. In the absence of active processes, the hair bundle mechanics is well characterized by Eq. (30) with $f_a = 0$, where x denotes the hair bundle displacement and f the applied external force. The hair bundle stiffness $k(x)$ is nonlinear and depends on displacement because the transduction channels contribute a gating compliance to the

bundle stiffness (Howard and Hudspeth 1988). Measurements of the stiffness of hair bundles from the bullfrog sacculus show that $k(x)$ can become negative (Martin and Hudspeth 1999, Kennedy et al. 2005) .

The generation of spontaneous oscillations requires an active force f_a , generated inside the hair bundle. The observed properties of hair bundle oscillations in the bullfrog sacculus are best described by assuming that the active force f_a is generated by myosin-Ic adaptation motors in the stereocilia which are themselves regulated by the intracellular Ca concentration (Hudspeth and Gillespie 1994, Holt et al. 2002, Kros et al. 2002). Using the hair bundle deflection x , the motor force f_a and the Ca concentration c , this dynamical system is described by three coupled first-order systems (Martin et al. 2003, Nadrowski et al. 2004). For low frequency oscillations such as those observed in the bullfrog, the Ca concentration changes almost instantaneously compared to the other variables, and the dynamical system then reduces to two coupled first-order systems. It can be represented by equations of the form (30) and (32). Here, Eq. (32) captures the combined effects of the force-velocity relationship of the motors and the regulation of motors by a changing Ca concentration, in a simplified linear description. The existence of spontaneous oscillations requires both negative hair bundle stiffness ($C > k$) and sufficiently strong Ca-feedback of the motor force $\bar{k} > \lambda/\tau$. The full state diagram of the system is discussed in (Nadrowski et al. 2004).

The interplay of nonlinear hair-bundle stiffness, myosin motors and calcium dynamics in the hair bundle can also lead to spontaneous oscillations by other mechanisms (Choe et al. 1998, Vilfan and Duke 2003a). If the reclosure of transduction channels can be triggered by an increase of the intracellular Ca concentration (Howard and Hudspeth 1988, Benser et al. 1996, Wu et al. 1999, Ricci et al. 2000), this also generates an active force which depends on the Ca concentration and can also be described by Eqns. (30) and (32). In such a scenario, the dynamics of adaptation motors is slow and could be used for self-regulation to the critical regime (Vilfan and Duke 2003a).

Finally, a sufficiently large number of motor proteins which operate collectively could become self-oscillatory, even without being coupled to the calcium dynamics. This possibility is based on a general physical mechanism that could operate over a large frequency range (Jülicher et al. 1997). Such motor-induced mechanical oscillations might be relevant to axonemal vibrations and beating (Camalet et al. 2000).

4.3 Mammalian cochlea

The physical basis of the active amplifier in the mammalian cochlea remains controversial. There is much evidence that the specialized outer hair cells can pump energy into the basilar membrane (Fakler Chapter 7, Dallos et al. 1996). The somatic electromotility of outer hair cells can certainly produce large, rapidly changing forces, but there is currently no indication that it can generate spontaneous oscillations. It is possible that it acts as a linear amplifier which boosts nonlinear oscillations generated by another source. Indeed, the hair bundles of outer hair cells have recently been found to generate active forces which could contribute to the amplifier (Kennedy et al. 2005), and an *in vitro* preparation has provided direct evidence for a characteristic resonance in the mammalian cochlea, linked to a compressively nonlinear amplifier that depends on the flow of Ca^{2+} ions through hair-bundle transduction channels (Chan and Hudspeth 2005).

Despite the uncertainty about the physical basis of the mechanism, there have been numerous propositions that active oscillators play a crucial role in the mammalian cochlea. Undamping of an inertial oscillator is the active mechanism that Gold proposed to exist in the mammalian cochlea (Gold 1948). He reasoned that the motion of individual elements of the basilar membrane is damped by the cochlear fluid, and that a resonant response could occur only if an internally-generated active force, in phase with the velocity, counteracted the damping. Following this lead, nonlinear active models of the cochlear response have been constructed (Neely and Kim Chapter 10, Duifhuis et al. 1985 Kolston et al. 1990, deBoer 1996). Based on an analysis of the basilar membrane response, Zweig has argued that the active amplifier consists of a set of time-delayed feedback oscillators (Zweig 1991). In the following Section, we will discuss a more general model of the cochlear response based on the generic response of critical oscillators (Duke and Jülicher 2003, Magnasco 2003). We argue that this model should be valid whatever the underlying physical basis of the mammalian cochlear amplifier, and that it provides a framework for discussing energy flow and nonlinear effects in cochlear traveling waves.

5 Traveling waves powered by critical oscillators

5.1 Traveling waves in the cochlea

The basic physics of cochlear traveling waves may succinctly be described using a simplified, one-dimensional model (Zwislocki 1948, Zweig 1976, deBoer 1980, Lighthill 1981, Zweig 1991). In this approach, the propagation of a pressure wave in the cochlear fluid and the propagation of an associated disturbance of the basilar membrane, is analogous to the propagation of voltage and current in an electromagnetic transmission line.

The cochlear duct is separated into two channels by the basilar membrane, but these are connected at the apex of the cochlea by a small aperture, the helicotrema (see Fig. 6). 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 with inertial and viscous forces in the fluid, together with the incompressibility of the fluid, leads to the equation

$$2\rho b\partial_t^2 h + \eta\partial_t h = \partial_x [bl\partial_x p] , \quad (38)$$

which relates the height profile $h(x, t)$ of the basilar membrane to the pressure difference across it. Here, b and l denote the width and height of the cochlear channels, respectively. The damping coefficient η is proportional to the fluid viscosity, and ρ is the fluid density.

The pressure difference p acts to deform the basilar membrane, and the resultant wave propagation depends crucially on the way the cochlear partition responds. If the partition is simply a passive element (e.g. in the dead cochlea), the response relation close to the basal end, where the stiffness $K(x)$ of the basilar membrane is high, takes the simple form $p = K(x)h$. Then Eq. (38) becomes a damped, linear wave equation, the speed of propagation of the membrane disturbance is $c = (K(x)l/2\rho)^{1/2}$, and the distance that the wave travels before it gradually gets dissipated depends on a balance between damping and elastic forces. If the cochlear partition is an active system, however, the wave can be regenerated as it progresses. We will see that this provides a way of transporting the incident energy to a localized region of the cochlea.

5.2 Active traveling waves

We describe the amplifier in the active cochlea as a set of critical oscillators which are located on the cochlear partition, and which are positioned in such a way that they can drive the motion of the basilar membrane. Motivated by the observed variation of the characteristic frequency with place in the cochlea (von Békésy 1960, Greenwood 1990), we describe the position dependence of characteristic frequencies as

$$\omega_r(x) = \omega_0 e^{-x/d}, \quad (39)$$

so that the oscillators near the base have the highest frequencies, and those near the apex the lowest.

When a sound stimulus with a single frequency component enters the ear, the local pressure changes periodically in time, $p(t) = \tilde{p}e^{-i\omega t} + c.c.$, where *c.c.* denote the complex conjugate. If the response of the cochlear partition is governed by the critical oscillators, the local displacement at frequency ω can be written

$$\tilde{p} \simeq \mathcal{A}(\omega)\tilde{h} + \mathcal{B}|\tilde{h}|^2\tilde{h}. \quad (40)$$

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 \mathcal{A} and \mathcal{B} denote the complex coefficients introduced in Eq. (5).

Combining Eq. (38) describing the wave mechanics with Eq. (40) for the local amplifier, we obtain a nonlinear wave equation for the deformation of the basilar membrane. In frequency representation, it reads (Duke and Jülicher 2003)

$$-2\rho b\omega^2\tilde{h} - i\omega\eta\tilde{h} = \partial_x \left[bl\partial_x \left(\mathcal{A}(x, \omega)\tilde{h} + \mathcal{B}|\tilde{h}|^2\tilde{h} \right) \right]. \quad (41)$$

Here, the complex linear response coefficient $\mathcal{A}(x, \omega)$ depends on both position and frequency. There are, however, a number of constraints on its functional form. Most importantly, because each of the oscillators is assumed to be critical, the linear response vanishes at the local characteristic frequency $\omega_r(x)$: $\mathcal{A}(x, \omega) \simeq \alpha(\omega - \omega_r(x))$ for small $\omega - \omega_r$. In addition, decomposing $\mathcal{A} = A' + iA''$ into a real and an imaginary part, we note that $A'(\omega)$ is an even function, while $A''(\omega)$ is odd. Both vanish at the characteristic frequency ω_r . Finally, the response of the cochlear partition at zero frequency should reflect a simple, passive elastic response, so that $\mathcal{A}(x, 0) \simeq K(x)$. The typical functional form of $\mathcal{A}(\omega)$ is shown in Fig. 6.

Whatever the precise choice of $\mathcal{A}(\omega)$, Eq. (41) can be solved for the amplitude $\tilde{h}(x)$ of the basilar membrane displacement. The appropriate boundary conditions are $|\tilde{p}(0)| = p_{\text{in}}$, where p_{in} is the amplitude of the incom-

ing pressure, and $\tilde{p}(L) = 0$ because the channels are connected at the helicotrema. The traveling wave patterns which correspond to these solutions are $h(x, t) = \text{Re}(\tilde{h}(x)e^{i\omega t})$. Examples of these waveforms are shown in Fig. 6.

There is a characteristic place $x = x_r$ in the cochlea where the frequency of the wave is matched by the frequency of the critical oscillators, $\omega = \omega_r(x_r)$. Far from this resonance point, the wave equation Eq. (41) describes traveling waves which are linear for small vibration amplitudes. A wave that enters at $x = 0$, first encounters active oscillators which have a high characteristic frequency, compared to the wave frequency, $\omega < \omega_r$. At this point, the response is dominated by the real part of the linear response A' , which differs little from the passive stiffness of the membrane. But the imaginary part is negative, $A''(\omega) < 0$, indicating that energy is pumped into the wave by the critical oscillators. This pumping can negate, or even overcome the effects of viscous friction and thus maintain or enhance the amount of energy carried by the wave. As the wave continues, it passes regions with smaller values of A' , and its speed of propagation $c \approx (A'l/\rho)^{1/2}$ declines. Because the energy flux is undiminished (or has even increased, due to the active pumping), the fall in wave velocity implies an increase in the amplitude of the wave. The displacement of the basilar membrane therefore grows as the wave 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. (41) rapidly becomes more important than the linear term. This leads to a strongly nonlinear response of the basilar membrane in this region. The wave slows to a halt as it approaches the characteristic place and, as it does so, the energy that it carries is absorbed by the active oscillators (the imaginary part of the cubic term in the response is positive). At positions beyond the characteristic place, $x > x_r$, A' becomes negative and consequently the wave number $q \sim \omega/(A')^{1/2}$ becomes imaginary, indicating the breakdown of wave propagation. Any small amount of energy that remains in the wave is thus reflected from the characteristic place and the displacement of the basilar membrane decays very sharply for $x > x_r$.

A cochlear partition activated by critical oscillators thus provides a natural mechanism for the phenomenon known as ‘critical layer absorption’, whereby a wave comes to a stop at a particular place, but takes sufficiently long to do so that practically all of the energy that it carries can be absorbed there (Lighthill 1981). The traveling wave attains a peak amplitude before it reaches the resonant point, at a location $x = x_p < x_r$ which is very close to the characteristic place at low amplitudes, but which moves towards the base as the level of the stimulus increases. The peak 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. Direct observations of the motion of the basilar membrane (Rhode 1971, Sellick et al. 1982, Ruggero et al. 1997, Nilsen and Russell 2000, Robles and Ruggero 2001) reveal many features of the cochlear response that are consistent with the general properties of an active traveling wave that is driven by critical oscillators (Duke and Jülicher 2003).

5.3 Two-tone interference in active traveling waves

In Section 2, we discussed the nonlinear interference effects that appear in the response of an individual critical oscillator when it is stimulated by multiple frequencies. These have their counterparts in an active traveling wave that is powered by a set of critical oscillators. When a sound stimulus containing two frequency components ω_1 and ω_2 (with $\omega_1 < \omega_2$) enters the cochlea, the critical oscillators on the cochlear partition respond at both those frequencies, but also at the distortion product frequencies. As a result, the traveling wave contains a whole spectrum of components (as has been observed experimentally (Robles et al. 1991, Rhode and Cooper 1993, Robles et al. 1997)), and each of these components reaches a peak amplitude at a different place. In particular, the distortion products that have a lower frequency than the stimulus tones travel further than them, and peak at their characteristic place, where the principal components ω_1 and ω_2 have already decayed. This localized oscillation of the membrane at distortion product frequencies explains why these lower frequencies, such as $2\omega_1 - \omega_2$ and $3\omega_1 - 2\omega_2$, can be heard (Helmholtz 1954, Zwicker 1999). At the same time, the peak response to ω_1 is diminished by the presence of ω_2 , and vice versa. Such two-tone suppression has been directly observed in the response of the basilar membrane (Ruggero et al. 1992, Rhode and Cooper 1993). For stimuli with components of equal level, the suppressive effect of the lower frequency component ω_1 is greater, because this component travels through the characteristic place of the other component ω_2 , and interferes with the response of the critical oscillators there. The response of a cochlea in which the active elements are critical oscillators thus accounts for the main features of the psychoacoustic phenomenon of two-tone suppression (Zwicker 1999).

6 Discussion

Traditionally, the cochlear amplifier has been modelled using an approach that starts with a linear harmonic description and adds a positive feedback. As the feedback strength increases, the gain of the system grows and the

system eventually becomes unstable. A description of the cochlear amplifier based on critical oscillators is not inconsistent with such an approach, but it has several advantages. First, because critical oscillators are inherently nonlinear systems, the description underlines that nonlinearities are closely linked to the active mechanism and are, in fact, an unavoidable byproduct of active amplification. Second, the concept of the active amplifier as a self-regulated system that automatically adjusts itself to the vicinity of a critical point solves a difficulty of traditional approaches – namely that unstable behavior must be avoided, but at the same time positive feedback is required to produce an active amplifier. Third, our analysis indicates that the characteristic frequency of oscillation depends on the properties of the underlying nonlinear dynamical system; instead of depending on the stiffness and mass of passive harmonic oscillator elements alone, the characteristic frequency is determined, to a large degree, by the typical time scales of the active cellular processes which drive the cochlear amplifier.

Previous models of the cochlear traveling wave that have been based on coupled nonlinear oscillators have encountered the problem that such a system can become chaotic. The description presented in Section 5 neatly sidesteps this issue, by basing the analysis on the fundamental Fourier modes, together with the higher harmonics resulting from nonlinearities. Deterministic chaotic dynamics is irrelevant in the cochlea because stochastic fluctuations are important at the cellular scale on which the active amplifier operates. These fluctuations conceal any chaotic behavior that could result from the coupling of several nonlinear oscillators, but emphasize the generic behavior in the critical regime. Even though the Hopf bifurcation is hidden by fluctuations, the general signatures of critical oscillators are typically apparent over a wider range of parameters for noisy systems than for deterministic ones.

The noise that occurs in complex dynamical systems due to the rapid, irregular dynamics of many degrees of freedom might also provide an explanation of oto-acoustic emissions – the prime indicator of active processes in the cochlea. The spontaneous noisy motion of a critical oscillator, in the absence of any external stimulus, can exhibit spectral peaks at the oscillation frequency, because the noise is amplified by the active dynamical system. In the cochlea, the noisy motion of many critical oscillators, vibrating at different frequencies, would lead to the generation of many wave-like excitations which travel along the basilar membrane and interact via nonlinearities. In such a situation certain spectral components could be selected as eigenmodes of the cochlear cavity, and these frequencies would appear in the spectrum of spontaneous emissions (Shera and Guinan Chapter 8, Shera 2003).

In conclusion, the concept of self-regulated critical oscillators provides a

unifying description of the principal features of sound detection in auditory systems. The essential singularity in the response of an individual critical oscillator provides the frequency selectivity, high sensitivity and a wide dynamic range required by hearing organs. Clear experimental evidence that hair bundles in the bullfrog sacculus operate as critical oscillators has been presented. As yet, there is no such evidence at the cellular level for critical oscillators in the mammalian cochlea. But we have shown that critical oscillators that cover a range of frequencies, that are located within the cochlea partition, and whose dynamics is coupled through the fluid, can account for the transport of energy to a particular frequency-dependent location in the cochlea, the nonlinearity of the response at that place, the generation of distortion products, and the existence of spontaneous oto-acoustic emissions. The close correspondence with the measured features of the cochlear response provides a compelling argument that critical oscillators are the key element of the active cochlear amplifier.

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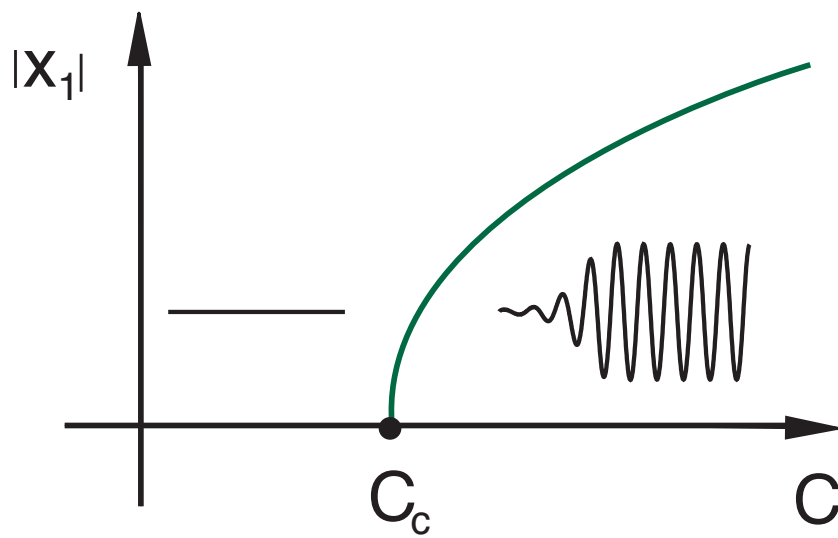


Figure 1: Schematic representation of the amplitude of spontaneous limit cycle oscillation $|x_1|$ as a function of a control parameter C near a supercritical Hopf bifurcation. At a critical value $C = C_c$ a quiescent, non-oscillating state becomes unstable. For $C > C_c$ spontaneous oscillations appear with an amplitude and frequency that depends on C . The oscillation amplitude grows continuously as $|x_1| \sim (C - C_c)^{1/2}$.

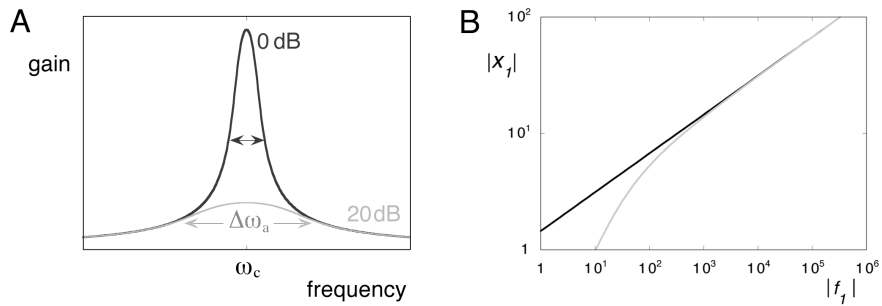


Figure 2: Typical response of an active oscillator, poised at a Hopf bifurcation, to mechanical stimulation at fixed frequency. A: As the stimulus level decreases, the gain increases and the bandwidth $\Delta\omega_a$ of active amplification decreases. B: A truly critical oscillator, stimulated at its characteristic frequency, displays an essential singularity, Eq. 8 (black curve). If a critical oscillator is stimulated at a frequency that differs from its characteristic frequency, or if a dynamic oscillator is not precisely critical, its response is linear at low levels (gray curve).

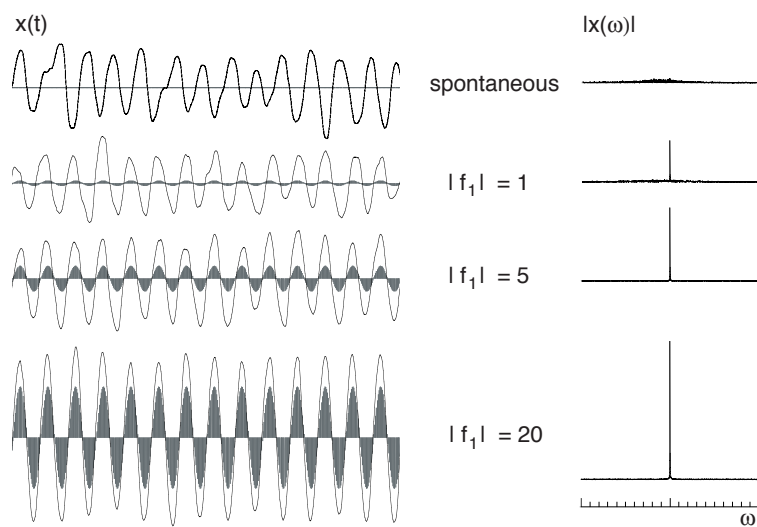


Figure 3: Role of fluctuations in the response of a critical oscillator. Spontaneous oscillations (top line) are noisy and lack phase coherence. A periodic stimulus at the characteristic frequency of the oscillator (with level indicated by the shaded curve) causes phase locking, although the overall amplitude of the response does not necessarily increase. Corresponding to this enhancement of the phase coherence, a peak emerges in the Fourier transform of the response (right column).

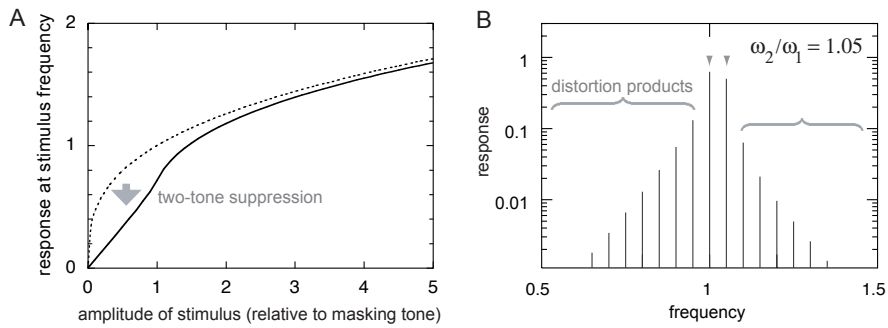


Figure 4: Two tone-suppression and distortion product generation in the response of a critical oscillator. A: The response of a critical oscillator to a stimulus at its characteristic frequency (dashed line) is suppressed (full line) in the presence of a second, ‘masking’ frequency. B: The response of a critical oscillator to a stimulus containing two frequencies ω_1 and ω_2 (arrowed) displays a characteristic spectrum of distortion products. New components appear at frequencies $n\omega_1 + m\omega_2$, where n and m are integers, because of nonlinear couplings. Most notable are the distortion product frequencies $2\omega_1 - \omega_2$ and $2\omega_2 - \omega_1$, but many other components with frequencies $\omega_1 + n\Delta\omega$, where $\Delta\omega = \omega_1 - \omega_2$ are important.

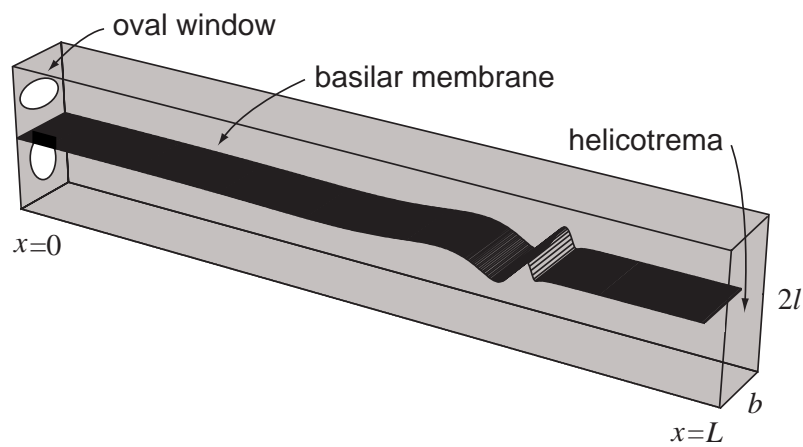


Figure 5: Schematic representation of the cochlea. The fluid-filled duct is divided into two channels by the basilar membrane. Sound enters at the base and travels towards the apex, where the two channels are connected by the helicotrema. The system behaves as a transmission line and couples basilar membrane vibrations hydrodynamically. We assume that critical oscillators operate along the cochlear partition as local active elements, and that their characteristic frequency decreases continuously from base to apex.

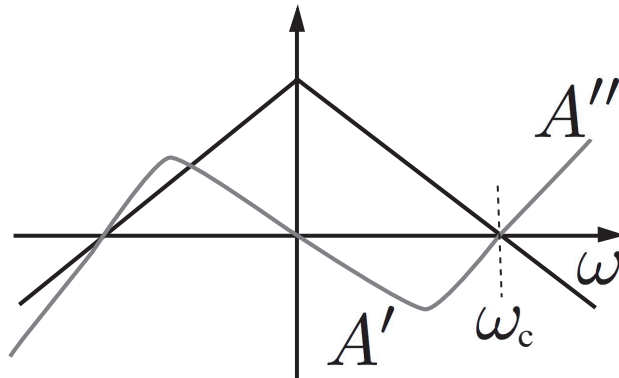


Figure 6: Schematic representation of the the linear response function $\mathcal{A} = A' + iA''$ of a critical oscillator. The real (reversible) part A' is an even function of ω while the imaginary (irreversible) part is odd. Both functions vanish for $\omega = \pm\omega_c$, where ω_c is the oscillation frequency at the critical point.

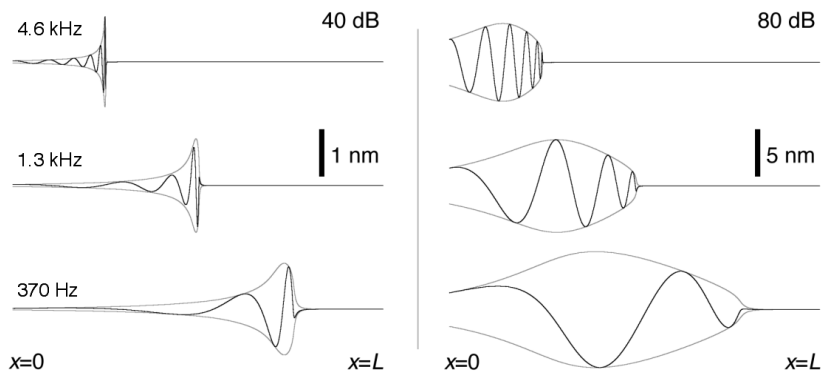


Figure 7: Active traveling waves resulting from the hydrodynamic coupling of critical oscillators located on the cochlear partition, with characteristic frequencies decreasing from base to apex. These waves are solutions to the nonlinear wave equation, Eq. (41).