A Brownian Energy Depot Model of the Basilar Membrane Oscillation with a Braking Mechanism

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High auditory sensitivity, sharp frequency selectivity, and otoacoustic emissions are signatures of active amplification of the cochlea. The human ear can also detect very large amplitude sound without being damaged as long as the exposed time is not too long. The outer hair cells are believed as the best candidate for the active force generator of the mammalian cochlea. In this paper, we propose a new model for the basilar membrane oscillation which successfully describes both the active and the protective mechanisms by employing an energy depot concept and a critical velocity of the basilar membrane. One of the main results is that thermal noise in the absence of external stimulation can be amplified leading to the spontaneous basilar membrane oscillation. The compressive response of the basilar membrane at the characteristic frequency and the dynamic response to the stimulation are consistent with the experimental results as expected. Our model also shows the nonlinear distortion of the response of the basilar membrane.

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I. INTRODUCTION

Remarkable detection capabilities appearing in animal hearing are essentially governed by both a passive mechanical and an active biophysical procedures in the cochlea [1, 2, 3, 4]. The active amplification of the living cochlea was conjectured by Gold in 1948 [5] and is now qualitatively studied widely through the Hopf equation in mathematical models [6, 7, 8, 9, 10]. In order to give a better understanding to the experimental observations, a more accurate model is required. Furthermore the physical origin of the active oscillation remains still unclear. In mammals, the outer hair cells (OHCs) are known to be force generators for auditory sensitivity and frequency selectivity. Proposed mechanisms of the force generation are contraction of the OHC itself [11, 12, 13] and an active motion of the hair bundle [14, 15].

Energy depot model can describe the active phenomena [16, 17], because the energy supplied by the depot can induce a negative dissipation. A similar mechanism for a negative stiffness in the bullfrog’s hair bundle has been reported [18]. It is reasonable to consider the OHC as an energy depot since the OHCs play an important role in the active amplification of the cochlea even though we do not know the exact mechanism of the energy supply. In nature all living things have some mechanisms of protection for survival. We expect that there might be a similar mechanism to protect cochlea from damage by any external factors such as loud stimulation. Hence, we propose a braking mechanism in the cochlea to prevent the basilar membrane (BM) from an excessive oscillation which could damage the cochlea. For this purpose, a critical velocity of the OHC oscillation will be introduced in our model.

In the following sections, we describe our model and reproduce the essential phenomena of the active cochlea observed in recent experiments such as the compressive nonlinearity, the dynamics of the BM response, nonlinear distortion and the spontaneous BM oscillation (SBMO). It will also be pointed out that our model naturally includes the Hopf bifurcation model [6, 7] in the case of weak stimulation. However, in the regime of strong stimulation, the
present model is essentially different from the Hopf bifurcation model.

FIG. 1: The compressive response of the BM. The CF is 10kHz. It shows that the response of the BM is non-linear and compressive at the CF. (Note that the slope of the solid line is less than one.) Otherwise, the response of the BM is a linear function of the stimulation yielding that the slopes are 1. These results agree with the experimental observations [24].

II. ENERGY DEPOT MODEL WITH BRAKING MECHANISM

It is well known that a change of transmembrane potential in the OHC induces a somatic vibration. This implies that a part of the electric energy is converted into the mechanical energy. In this sense, we believe that the OHC functions as an energy depot for the BM. The OHC as the energy depot stores energy supplied and converts it into kinetic energy overcoming dissipation. This energetics can be described by the following energy balance equation [16].

\[
\frac{dE(t)}{dt} = q - cE(t) - d(v)E(t),
\]

where \( E(t) \) is the energy density of the energy depot, \( q \) the rate of the energy pumping into the energy depot per unit area, \( c \) the rate of the internal energy dissipation, \( d(v) \) the rate of the energy converting into the kinetic energy.
of the BM, and \( v \) the velocity of the BM. Considering that constant contribution of \( d(v) \) can be incorporated into \( c \) and that conversion rate of the energy into the kinetic energy of the BM will not be sensitive to the sign of \( v \), we assume that \( d(v) \) is an even function of \( v \) without a constant term. The energy depot model in which \( d(v) = d_2v^2 \) has been extensively discussed \[16\]. In this paper, we include the next higher contribution to \( d(v) \) and introduce a critical velocity of the BM to describe a braking mechanism \[17\]. Hence the conversion rate \( d(v) \) can be written as

\[
d(v) = d_2v^2 \left( 1 - \frac{v^2}{v_c^2} \right),
\]

(2)

where \( v_c \) is the critical velocity. For a finite \( v_c \), the oscillation of the BM can be braked by the negative conversion rate into the kinetic motion of the BM. Note that \( v_c \rightarrow \infty \) corresponds to a system without the braking mechanism. The critical velocity will be roughly estimated from the contraction of the OHC later for our numerical calculation.

![Graph showing dynamic response of the BM](image)

FIG. 2: The dynamic response of the BM when the CF is 10kHz and the stimulation is 100dB. The onset time is much shorter than the offset time which is not shown in full scale. This result is qualitatively consistent with the experimental observations \[24\]. \( \mu = 600\text{kgm}^{-2}\text{s}^{-1} \), \( d_2/c = 6 \times 10^5\text{m}^{-2}\text{s}^2 \), and \( qd_2/c = \mu \). The stimulation is unloaded at \( t = 9\text{ms} \). The lower panel shows the response represents the case without the braking mechanism, showing a continuous increase as long as the stimulation is on.

Now it is worthwhile to compare our newly proposed model with the one previously introduced in Ref. \[10\]. Whereas we treat the energy density \( E(t) \) of the energy depot(OHC), in Ref. \[10\] the energy density \( e(t) \) of the
propagating hydrodynamic wave is considered. The model in Ref. [10] describes the coupling of the active elements to the propagating wave, while the present model describes the coupling between the energy depot (OHC) and the BM oscillation. The emphasis in this paper is on showing that the active and compressive response arises naturally from the generalized energy depot concept.

III. RESULTS AND DISCUSSION

An adiabatic approximation in which the adaptation of the energy depot is very fast [10] yields that

$$E(t) = \frac{q}{c + d_2 \left(1 - \frac{v^2}{v_c^2}\right)v^2}.$$  

(3)
It should bear in mind that $E(t)$ is not constant. The oscillation of the BM is then governed by

$$
\rho \ddot{v} + \mu v + \kappa R = F_{\text{passive}} + F_{\text{active}},
$$

(4)

where $\rho$ is the density, $\mu$ the physical damping coefficient, $\kappa$ the stiffness, and $R$ the displacement of the BM. $F_{\text{passive}}$ includes the contributions of a sound wave (external stimulation) and a noise. The noise is assumed to be a Gaussian white noise. $F_{\text{active}}$ is the active force density acting on the BM by the OHC,

$$
F_{\text{active}} = \frac{d(v)E(t)}{v} = \frac{q \frac{d_2}{c} \left(1 - \frac{v^2}{v_c^2}\right)v}{1 + \frac{d_2}{c} \left(1 - \frac{v^2}{v_c^2}\right)v^2},
$$

(5)

Note that the Langevin equation, Eq. (1), describes the passive and the active response in a unified and natural way. It should be noted that the active force, Eq. (5), can be either positive or negative depending on the value of $v$. When $v^2$ is smaller than $v_c^2$ (weak stimulation), a positive active force is provided on the BM (active mechanism). On the other hand, when $v^2$ is larger than $v_c^2$ (strong stimulation), a negative active force, hence an extra drag force, is exerted on the BM (braking mechanism).

The mass density of the BM is known to be about 0.77 kg/m$^2$ and the reported damping coefficient, $\mu$, of the BM has a large variation from 600 to 6,000 kg m$^{-2}$s$^{-1}$ depending on the models. For a numerical calculation, we set the damping in the range of 600 $\sim$ 6,000 kg m$^{-2}$s$^{-1}$. It has been reported that the Guinea pig OHCs are able to change its length up to 5% when the transmembrane potential is varied. This corresponds to a displacement of 1$\mu$m for the OHCs of 20$\mu$m at the high-frequency end [21]. Hence, in the regime of high frequency of 10kHz, the adjustable parameter $v_c$ is roughly estimated about 0.01m/s. By considering the OHC as a capacitor and using the observed membrane potential, membrane capacitance [22], and the scale of the OHC [23], we estimate the value of $q$ to be about 0.01kg s$^{-3}$. The response of the BM to the sound wave can be then obtained straightforwardly using Eqs. (4) and (5). In the following calculations, we set $qd_2/c = \mu$ and the characteristic frequency (CF), $\omega_c = \sqrt{\kappa/\rho}$. It will be shown later that these relations arise from the conditions of the Hopf bifurcation. In the present calculations, the noise width of the distribution is chosen to be zero dB.

The compressive and dynamical responses of the BM are obtained as shown in Fig. 1 and Fig. 2 respectively. Fig. 1 demonstrates that the response of the BM is non-linear and compressive at the CF, while the response is linear at other frequencies. This compressive response of the BM agrees well with the observations as expected. Fig. 2 shows the time course of the BM response, reproducing the experimental observation that the onset time of the response is shorter than the offset time, although the onset time is somewhat larger than the experimental values [24]. It is important to notice that the velocity of the BM increases continuously as long as the stimulation is being turned on if the braking mechanism is not included ($v_c = \infty$). Hence, the braking mechanism introduced in our model is essential to explain the experimental observation at a sufficiently strong stimulation. A dependence of the BM velocity on $v_c$ is plotted in Fig. 3. The results clearly show that lower critical velocity produces smaller response at the same stimulation, thus producing a supercompressive behavior as observed in experiment [24]. This is the effect of the braking mechanism, which is significantly different from the Hopf bifurcation model. Note that the saturation of the BM response disappears if the braking mechanism is not considered.

The gain of the oscillator is defined as the ratio of the displacement of the BM to the stimulation,

$$
G = \frac{R}{F_{\text{passive}}},
$$

(6)

Using Eq. (4), we obtain the gain, which is a scaling function of the stimulation when the stimulation is not too large, $G \sim F_{\text{passive}}^{-0.65}$. This result agrees well with the experiment [2] and the result of the Hopf bifurcation model [6], $G \sim F_{\text{passive}}^{-2/3}$. Indeed our model includes the Hopf model naturally. To show this, we expand the active force, Eq. (5), up to the lowest nonlinear term when $d_2(1 - v^2/v_c^2)v^2/c$ is small. Eq. (4) is then approximately written as

$$
F_{\text{passive}} = \rho \ddot{v} + \left(\mu - q \frac{d_2}{c}\right)v + \kappa R + q \frac{d_2}{c} \left(\frac{1}{v_c^2} + \frac{d_2}{c}\right)v^3,
$$

(7)
In the Fourier spectra space, this directly corresponds to the Hopf equation \[ \omega_c = \sqrt{\frac{\kappa}{\rho}}, \] \[ \mu = \frac{qd_2}{c}. \] Hence our energy depot model with a braking mechanism reduces to the Hopf bifurcation model in the limit of weak stimulation.

One of the most important results of our model is an amplification of the thermal noise itself in the absence of an external stimulation. At the bifurcation point or when \( qd_2/c < \mu \), the thermal noise is well suppressed. However, when \( qd_2/c > \mu \), so that too much of the internal energy is converted into the kinetic energy, the thermal noise can be largely amplified as shown in Fig. 4. Here, we set the mean average of the noise at 0Pa and the width at 0dB. Since it can be generally assumed that the oscillators are distributed in the vicinity of the bifurcation point, the noise may be amplified incoherently in the absence of the input signal. However, when a weak input signal with the same CF is introduced, it may phase-lock to the already existing amplified noise, thus enhancing the selectivity as
 FIG. 5: Nonlinear distortion of the response of the BM. $f_1 = 7.89$kHz, $f_2 = 8.28$kHz, both strengths of the stimulation are 100dB, the response is measured at the place where the $CF = 7.89$kHz, $v_2^c = 10^{-5}$m$^2$/s$^2$ and $\mu = 600$kgm$^{-2}$s$^{-1}$.

discussed in Ref. [25]. Because it is believed that the SBMO is crucial for understanding the spontaneous otoacoustic emission [26], our model may provide a clue to explore this interesting and important phenomenon. Fig. 5 shows the nonlinear distortion of the response of the BM at the position where the CF is 7.89kHz. The stimulation contains two tunes, $f_1 = 7.89$kHz and $f_2 = 8.28$kHz. The strengths both are 100dB. Our model shows clearly the distortions at $2f_1 - f_2$, $2f_2 - f_1$ in the response of the BM.

IV. SUMMARY

In this paper, we propose a theoretical scheme for the active and passive response of the BM based on a concept of the energy depot model with a braking mechanism. According to the experimental observations, the OHC is assumed to play a role of the energy depot by supplying an active force to the BM and also by reabsorbing an excessive kinetic energy like the regenerative-brake system in automobiles and electric vehicles [27]. It is shown that a single equation of motion, Eq (4), can produce all the essential passive and active behaviors. Moreover, our model shows that the Brownian noise can be sufficiently amplified under a certain condition, thus leading to the SBMO. Although we applied our model only to the mammalian cochlea, it is equally possible to be applied to the nonmammalian vertebrates [28] because the only required physical characteristics are a supply of the active force and a self-adaptation. In this sense, we believe that the concept of the energy depot model with a braking mechanism is quite universal and can be applied to any underdamped biological systems.
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