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The Active Model: The Effect of Stiffness on the Maximum Amplitude Displacement of the Basilar Membrane

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Authors' contributions

This work was carried out in collaboration between all authors. All authors read and approved the final manuscript.

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Original Research Article

Abstract

The human cochlea is the part of the inner ear where acoustic signals are transformed into neural pulses and then signaled to the brain. The cochlear amplifier is essentially a positive feedback loop within the cochlea that amplifies the traveling wave, this mechanism based on the cochlea's microanatomy, as well as, outer hair cell force, to account for the cochlea's characteristic behavior. A proposed theory of the active cochlea that the feed-forward/feed-backward are two mechanisms for the outer hair cell force amplification where an expanding hair cell gives a forward push through the Deiters Cells and a backward pull on the Basilar membrane through the Phalangeal process.

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Many important questions of cochlea mechanics are mathematically complicated, however, they can be studied using numerical simulations. Genetic mutations of type IV collagen lead to a malfunction of Basilar Membrane, resulting in the hearing loss associated with Alport Syndrome, which is a disease that affects the cochlea due to the abnormal structure of the Basilar Membrane (it becomes stiffer). Therefore, a mathematical model of the BM was developed to investigate and show numerically the effect of the stiffness on its structure with the objective to study the ear dysfunction in the active cochlea.

Keywords: Basilar membrane; resonance; outer hair cell; cochlea; active model.

1 Introduction

The cochlea actively amplifies acoustic signals as it performs spectral analysis. The movement of the stapes sets the cochlear fluid into motion, which passes the stimulus energy onto a certain region of the Basilar membrane (BM), the main vibrating organ of Corti in the cochlea. From the base to the apex, BM fibers increase in width and decrease in thickness, resulting in an exponential decrease in stiffness which, in turn, gives rise to the passive frequency tuning of the cochlea [1]. The motion of the BM is sensed by the hair cells [2] of the cochlea, which there are two types, the inner hair cells (IHC) and the outer hair cells (OHC), named for their positions with respect to the curvature of the cochlear spiral. In the case of an IHC, the voltage modulates synaptic transmission to adjacent fibers of the auditory nerve, and in the case of an (OHC) [3][4][5][6], the voltage in influences the intrinsic length of the hair cell itself .

This makes the OHC into an electrically controlled motor that can push on the BM and provide mechano-electro-mechanical feedback. This mechanism is used to pump energy into the cochlear wave as it propagates, thus amplifying the signal and also (as it turns out) improving the frequency resolution of the cochlea [7].

The micro-architecture of the cochlear partition gives rise to feed-forward and feed-backward OHC forces that introduce active bidirectional longitudinal (ABC) coupling between BM segments [8]. The feed-forward is the force resulting from OHC contraction or elongation exerted onto an adjacent downstream (BM) segment due to the OHC's basal tilt, and the feed-backward is the force of OHC delivered onto an adjacent upstream BM segment due to the apical tilt of the Phalangeal Processes (PhP) extending from the Deiters Cells's (DC) main trunk [8].

Cochlear hearing loss involves damage to the structure inside the cochlea, one of such cases can be observed in the response of the BM which gives rise to defects in its pathological structure. Abnormalities in the BM's function can result in many disease. An example of such a diseases is the Alport Syndrome (AS) which is related to the stiffness parameter.

The AS is an inherited disorder of Basement Membrane that affects a type IV collagen network composed of $\alpha 3$, $\alpha 4$, and $\alpha 5$ (IV) chains. The defects in type IV collagen characteristic of AS arise from mutations in the COL4A3, COL4A4, and COL4A5 genes, which encode the $\alpha 3$, $\alpha 4$, and $\alpha 5$ chains of type IV collagen, respectively [9]. The $\alpha 3$, $\alpha 4$, and $\alpha 5$ chains of type IV collagen form a distinct network in several Basement Membrane of the kidney, cochlea, and eye. Functional and structural abnormalities of Basement Membane result in hematuria and progressive renal disease, sensorineural deafness, and ocular abnormalities.

The structural changes observed in AS cochlea may be associated with defective attuning of BM motion and hair cell stimulation, resulting in reduced acuity of hearing [9]. The alteration of the structure of type IV collagen causes a progressive hardening (or multiple) of the BM composed with the Basement Membrane [10][11], therefore the basilar becomes stiffer. As a result, the cochlea cannot fulfill its essential role in the hearing process.

The mathematical model of the cochlea that is studied in the present work was introduced in the Ph.D. thesis of Bo Wen [8], who used the cochlear amplifier mechanism, ABC and The semi-analytical results of a linear version of the active cochlear model.

In the present work, we applied the resonance analysis method in the active cochlear model [12] to analyze the effect of the stiffness on the maximum amplitude displacement of the BM.

2 The Two-dimensional Linear Model

Cochlear modeling has a long history [13][14] and is constantly driven by experiments [15][16]. Solutions to linear models are well studied both analytically and numerically, see [17][18][19][20]. The cochlea is modeled as a rectangular divided into two symmetric compartments by an elastic partition, which will be referred to as the BM (see Fig. 1). Stapes motion sets the cochlear fluid into motion and causes a vibratory deformation of the BM [21].

The variable x represents the distance from the stapes along the cochlear partition, with $x = 0$ at the stapes and the round window and $x = L$ (uncoiled cochlear duct length) at the apex and the helicotrema. The second variable y represents the vertical distance from the wall, with y = 0 at the top/bottom wall of cochlear duct and $y = h$ (cochlear duct radius or height) at the BM [8]. First, we describe the formulation of a two-dimensional (2D) linear model based on the cochlear amplifier mechanism ABC. Next, we show the numerical simulation of the comparison between the values of maximum displacement amplitude of the BM in the normal and abnormal cases (AS).

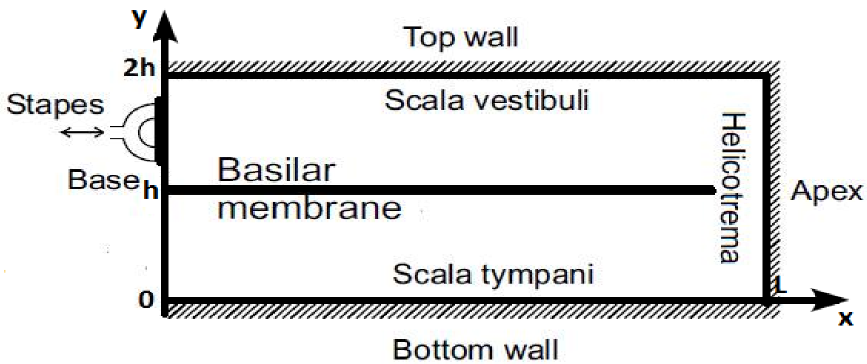


Fig. 1. Two-dimensional cochlear model

The BM is driven by the fluid pressure difference across it. Hence, the BM's vertical motion can be described as follows [8]:

$$m(x)\frac{\partial^2\eta}{\partial t^2}(x) + C(x)\frac{\partial\eta}{\partial t}(x) + k(x)\eta(x) = P_d(x,y) + F_{ohc}(x) \qquad at\ y = h$$

$$\mathrm{F}_{ohc}(x) = \alpha k(x)(\gamma\eta(x-d) - \eta(x+d)) \qquad (2.1)$$

where $m(x)$ is the mass, $k(x)$ is the stiffness, and $C(x)$ is the damping, per unit area, of the BM, η is the displacement of the BM while the first time-derivative of η is its velocity and the second is its acceleration. $P_d(x, y)$ at $y = h$ is the pressure difference between the scala tympani and scala vestibuli at the BM. $F_{ohc}(x)$ combines the feed-forward and feed-backward OHC forces, expressed as a fraction α of the BM stiffness (i.e., OHC motility factor). γ is the ratio of the feed-forward to the feed-backward coupling, representing relative strengths of the OHC forces exerted on the BM segment through the DC, directly, and through the tilt PhP. d denotes the tilt distance, which is the horizontal displacement between the source and the recipient of the OHC force, assumed to be equal for feed-forward and feed-backward cases.

The cochlear partition (CP) is divided into a number of radial segments from the base to the apex with OHCs and PhPs arranged within the Organ of Corti (OC)(Fig. 2). For simplicity, each BM segment contains one DC sitting on the BM, the apical end of one PhP, and the stereocilia end of one OHC. The OHC in segment $i-1$ exerts a force on the BM that sits in the downstream segment i, thereby the BM is pulled to or pushed away from the reticular lamina (RL) (feed-forward), in segment $i+1$ of CP, the motion of the apical tilt of the PhP results in segment i an opposite motion (feed-backward) [12].

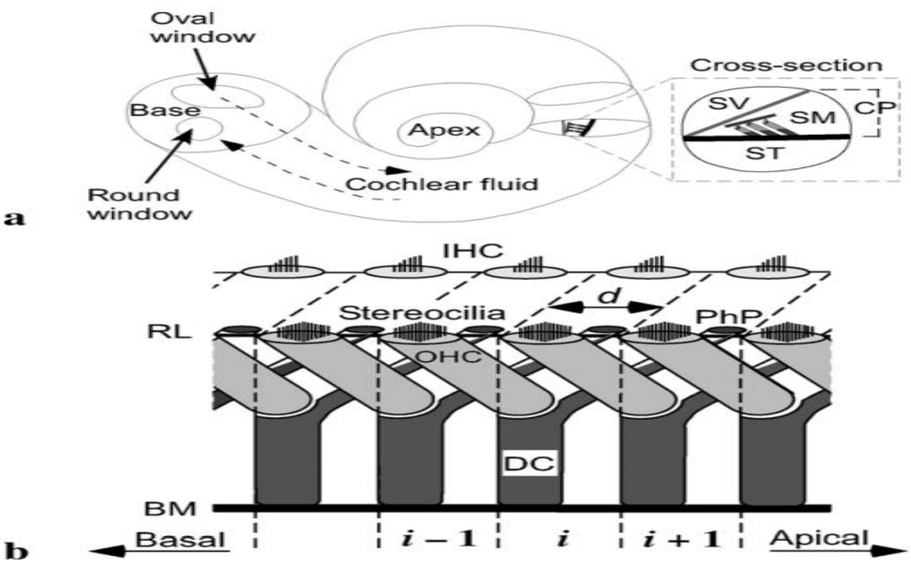


Fig. 2. (a) Cross section of the cochlea, (b) longitudinal view of the CP

The alteration of the structure of type IV collagen causes a progressive hardening of the BM, which means the BM becomes stiffer. Our purpose in this work is to perturb the stiffness $k(x)$ and look how this perturbation affects the amplitude $A(x)$ of the displacement η. If we put $k(x) \leftarrow k(x) + \epsilon$, the differential equation describing the resulting motion of the system is as follows:

$$m(x)\frac{\partial^2\eta}{\partial t^2}(x) + C(x)\frac{\partial\eta}{\partial t}(x) + (k(x)+\epsilon)\eta(x) = P_d(x,y) + F_{ohc}(x) \qquad at\ y = h$$

$$\mathrm{F}_{ohc}(x) = \alpha(k(x)+\epsilon)(\gamma\eta(x-d) - \eta(x+d)) \qquad (2.2)$$

3 Model Simulation Results Using Resonance Analysis Method

Having obtained the mathematical formulation of an active cochlear model, we shall explore its responses or behavior in responding to any sound stimulus. We employed a resonance analysis approach to obtain model responses and then we investigate the effect of stiffness on the BM motion, we simulated the active model using different values of ϵ. To illustrate the effect of the mechanisms feed-forward and feed-backward, is useful to define the amplitude of the BM displacement in response to a pure tone as a function of x. To do so, we make the assumption that the system is linear and in a periodic steady state at the given frequency w of the incident sound. In that case, we shall have:

$$\eta(x,t) = A(x)e^{jwt}, P_d = \tilde{P}_d e^{jwt} \tag{3.1}$$

in which $A(x)$ is the amplitude.

If we use the Taylor formula of the function $\eta(x-d)$ and $\eta(x+d)$, then we replace by their expression in the system (2.2) (section 2), the equation that model the force of OHC can be written as following:

$$F_{ohc}(x) = \alpha(k(x)+\epsilon)\left[(\gamma-1)\eta(x) - d(\gamma+1)\frac{\partial \eta}{\partial x}(x) + \ominus(d)\right] \tag{3.2}$$

While the value of $d = 71.10^{-3}mm$ is very small ($d \to 0$) so the $\ominus(d) \to 0$ and $\frac{\partial \eta}{\partial x}$ also small, Therefore the expression $d(\gamma+1)\frac{\partial \eta}{\partial x}(x)$ can be neglected.

Substituting the displacement, its first derivative and second derivative and considered η as common factor, we obtain an equation that model the displacement as a function of the other

$$\eta = \frac{1}{jw}\frac{\tilde{P}_d e^{jwt}}{C(x) + j(wm(x) + \frac{(k(x)+\epsilon)(\alpha(\gamma-1)-1)}{w})} \tag{3.3}$$

The above equation can be expressed in a simpler form defining complex mechanical impedance as follows:

$$\mathbf{Z}_m(x) = C(x) + jX_m(x) \tag{3.4}$$

$$X_m(x) = wm(x) + \frac{(k(x)+\epsilon)(\alpha(\gamma-1)-1)}{w} \tag{3.5}$$

The mechanical impedance may also be expressed in polar form by $\mathbf{Z}_m(x) = r_m e^{j\Theta(x)}$, where r_m is the absolute value of the impedance and $\Theta(x)$ is the phase angle :

$$r_m = \sqrt{C(x)^2 + X_m(x)^2} \tag{3.6}$$

$$\Theta(x) = tan^{-1}\frac{X_m(x)}{C(x)} \tag{3.7}$$

From equations (3.6) and (3.7), the displacement complex is written as

$$\eta = \frac{1}{jw}\frac{\tilde{P}_d e^{jwt}}{r_m(x)e^{j\Theta(x)}} \tag{3.8}$$

The equation (3.8) is simplified to a single exponential term reducing algebraically as follows.

$$\eta = \frac{1}{jw}\frac{\tilde{P}_d e^{j(wt-\Theta(x))}}{r_m(x)} \tag{3.9}$$

Then we proceed to obtain the real part and complex part using Euler's identity

$$\eta = \frac{1}{jw}\frac{\tilde{P}_d}{r_m(x)}[cos(wt-\Theta(x)) + jsin(wt-\Theta(x))] \tag{3.10}$$

and therefore the displacement of each membrane section is defined by the real part of the equation (3.10):

$$\eta = \frac{\tilde{P}_d}{wr_m(x)} sin(wt-\Theta(x)) \tag{3.11}$$

The amplitude is defined by $A(x) = \frac{\tilde{P}_d}{wr_m(x)}$ and can be algebraically expressed with the terms of mass, damping and stiffness, by the following expression:

$$A(x) = \frac{\tilde{P}_d}{\sqrt{(w^2C(x)^2 + [(k(x)+\epsilon)(\alpha(\gamma-1)-1) + w^2m(x)]^2}} \tag{3.12}$$

The equation (3.12) shows that the amplitude for each section of the membrane depends of the frequency w and the physical characteristics of mass, damping coefficient and stiffness .

The amplitude A(x) can be expressed as function of frequency and distance, if we consider that $w = 2\pi f$, so we can expressed the equation (3.12) by

$$A(x) = \frac{\tilde{P}_d}{\sqrt{(2\pi fC(x))^2 + [(k(x)+\epsilon)(\alpha(\gamma-1)-1) + (2\pi f)^2m(x)]^2}} \tag{3.13}$$

3.1 Simulation results

From equation (3.13), we can develop a computational model to obtain the distance where the maximum displacement of the BM to a specific excitation frequency of the system occurs, which depends on the physical characteristics of the Basilar Membrane (see Fig. 3).

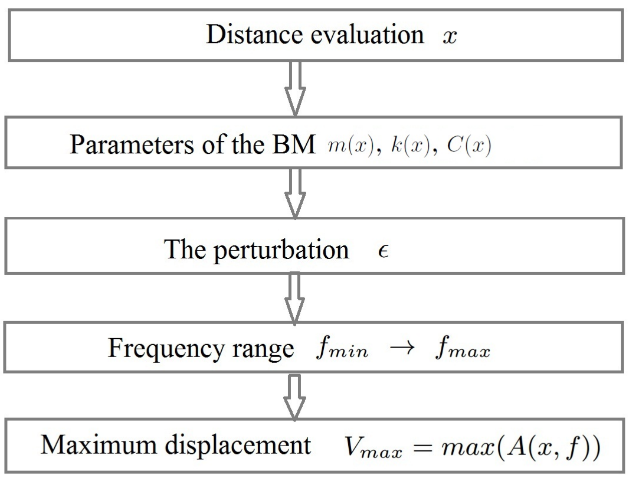


Fig. 3. The diagram of the computational model of the BM using resonance analysis

In our work, we modeled the abnormal case (AS) of the BM for which the harmonic oscillator depends on stiffness, mass, damping and frequency. For the values of $m(x)$, $C(x)$ and $k(x)$, we used the parameters of Neely.

Table 1. represents the values of $m(x)$, $C(x)$ and $k(x)$ proposed by Neely [21]

Parameter	Symbol	Value	Unit
Mass	$m(x)$	0.15	g/cm^2
Damping	$C(x)$	200	$dyn.s/cm^3$
Stiffness	$k(x)$	$10^9\ e^{-2x}$	$dyn\ cm^3$
OHC motility factor	α	0.2	
Forward-to-backward ratio	γ	0.3	

We use the method of resonance analysis , and we increase the value of ϵ in the modeling equation of the BM displacement, thus, we can observe how an increase of ϵ might lead to the decrease of amplitude, which can be observed in AS.

The Tables 2, 3, 4, 5 and 6 shows the comparison between the results obtained in normal and abnormal (AS) cases using the linear active cochlear model includes the feed-forward and the feed-backward forces, for that, we take the values of $\alpha = 0.2$

Table 2. The maximum amplitude displacement using the parameters of Neely for $\epsilon = 10(dyn/cm^3)$

Distance (cm)	Amplitude$_N$ (cm)	Amplitude$_{AS}$ (cm)	Frequency (Hz)
0.1209	$6.47269619\ 10^{-8}$	$6.47269615\ 10^{-8}$	12 294
0.6095	$1.05513526\ 10^{-7}$	$1.05513524\ 10^{-7}$	7 560
1.7470	$3.29375915\ 10^{-7}$	$3.29375914\ 10^{-7}$	2 433

Table 3. The maximum amplitude displacement using the parameters of Neely for $\epsilon = 10^2(dyn/cm^3)$

Distance (cm)	Amplitude$_N$ (cm)	Amplitude$_{AS}$ (cm)	Frequency (Hz)
0.1209	$6.47269619\ 10^{-8}$	$6.47269584\ 10^{-8}$	12 294
0.6095	$1.05513526\ 10^{-7}$	$1.05513506\ 10^{-7}$	7 560
1.7470	$3.29375915\ 10^{-7}$	$3.29375461\ 10^{-7}$	2 433

Table 4. The maximum amplitude displacement using the parameters of Neely for $\epsilon = 10^3(dyn/cm^3)$

Distance (cm)	Amplitude$_N$ (cm)	Amplitude$_{AS}$ (cm)	Frequency (Hz)
0.1209	$6.47269619\ 10^{-8}$	$6.47269267\ 10^{-8}$	12 294
0.6095	$1.05513526\ 10^{-7}$	$1.05513327\ 10^{-7}$	7 560
1.7470	$3.29375915\ 10^{-7}$	$3.29370902\ 10^{-7}$	2 433

The results confirm the difference between the values of the amplitude in normal (Amplitude$_N$) and abnormal (Amplitude$_{AS}$) cases of the BM displacement. We taken different location along the BM to conclude the behavior of the maximum amplitude displacement in the both cases. In our study, we find that there is a decrease on the amplitude of the BM when we increase the value of the perturbation ϵ (i.e that becomes stiffer), this occurs a malfunction in the structure of the BM which contribute to hearing loss.

Table 5. The maximum amplitude displacement using the parameters of Neely for $\epsilon = 10^4 (dyn/cm^3)$

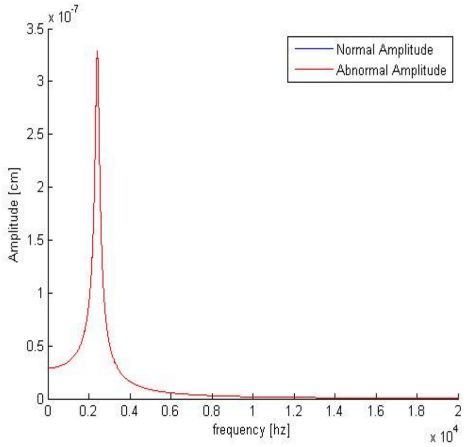
Distance (cm)	Amplitude_N (cm)	Amplitude_{AS} (cm)	Frequency (Hz)
0.1209	$6.47269619\ 10^{-8}$	$6.47265936\ 10^{-8}$	12 294
0.6095	$1.05513526\ 10^{-7}$	$1.05511466\ 10^{-7}$	7 560
1.7470	$3.29375915\ 10^{-7}$	$3.29323252\ 10^{-7}$	2 433

Table 6. The maximum amplitude displacement using the parameters of Neely for $\epsilon = 10^5 (dyn/cm^3)$

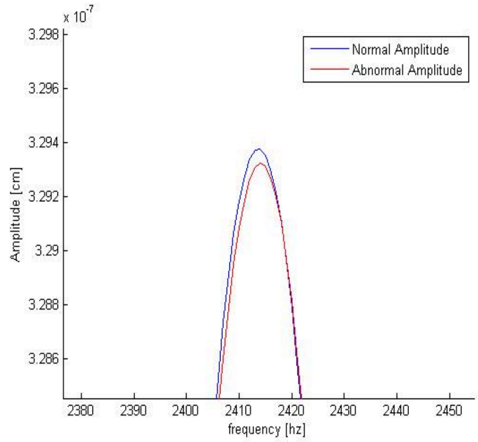
Distance (cm)	Amplitude_N (cm)	Amplitude_{AS} (cm)	Frequency (Hz)	Frequency_{AS} (Hz)
0.1209	$6.47269619\ 10^{-8}$	$6.47225343\ 10^{-8}$	12 294	12 295
0.6095	$1.05513526\ 10^{-7}$	$1.05494889\ 10^{-7}$	7 560	7 561
1.7470	$3.29375915\ 10^{-7}$	$3.28829661\ 10^{-7}$	2433	2 436

The same results for the Table 6 but we can observe that there is a changes in the values of the frequencies (Frequency_{AS}), they increase when we increase the stiffness (ϵ upper than 10^5).

The Figs. 4 and 5 show the maximum amplitude displacement $A(x)$ in normal and abnormal cases, for the position $x = 1.7470\ cm$ at different values of the ϵ ($\epsilon = 10^4,\ 10^5$).

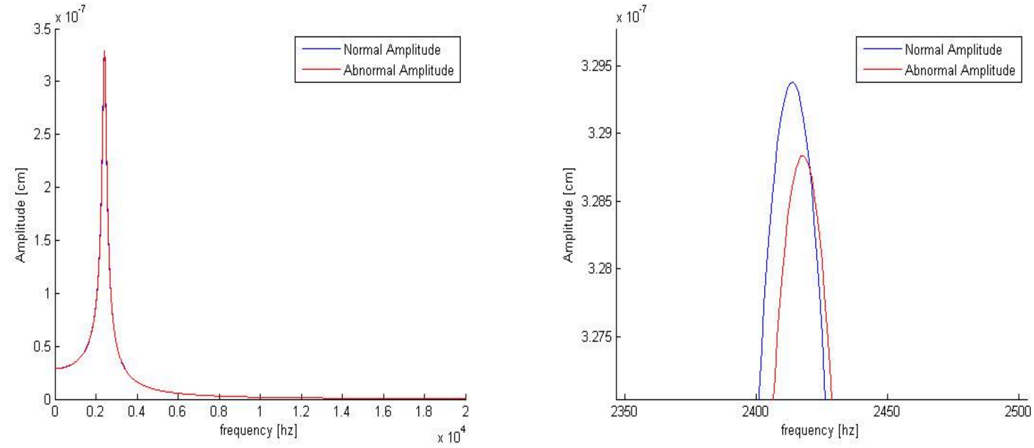


(a)



(b)

Fig. 4. (a): Basilar membrane displacement for both the normal case and the abnormal case (AS) for $\epsilon = 10^4 dyn/cm^3$ (b): Zooming of (a)



(a) (b)

Fig. 5. (a): Basilar membrane displacement for the normal and the abnormal (AS) cases for $\epsilon = 10^5 dyn/cm^3$, (b): Zooming of (a)

The principal change observed in the graphics are in the values of the amplitude and the frequency, we remark that when we increase the perturbation ϵ the value of the maximum amplitude displacement decrease, also the frequency increase when $\epsilon \succeq 10^5$, so this changes lead to loss of hearing.

4 Conclusions

The human cochlea is a remarkable device, able to discern extremely small amplitude sound pressure waves, and discriminate between very close frequencies, mathematical models of the cochlea have been developed in order to understand the truth function of the cochlea.

The Basement Membrane is important in the structure and function of the basilar membrane. The AS causes the malfunction in the structure of the Basement Membrane, resulting a stiffer BM, for this, we investigated the influence of the stiffness's increase on human hearing.

Following the example of an existing model, a linear model of active cochlea has been developed which uses the feed-forward and the feed-backward forces to describe the dysfunction of the stiffer BM (AS).

Our purpose in this work is to perturb the stiffness $k(x)$, which means the BM becomes stiffer $k(x) \leftarrow k(x) + \epsilon$, in order to observe the maximum amplitude displacement of the BM in AS case using the resonance analysis to obtain numerical approximations in the abnormal case. Our study observed mathematically the AS and showed that the amplitude decreases when we increase the stiffness of the BM.

The comparison between normal and abnormal cases showed that there is a decrease in the maximum amplitude displacement of the BM, also an increase in the value of the frequency when the epsilon above than 10^5. Although the model of this paper could be improved in many ways, the most important direction for future research, in our opinion, is to model the active mechanism in a more physiological way, taking into account the details of the tilt distance d of the OHC.

Competing Interests

Authors have declared that no competing interests exist.

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